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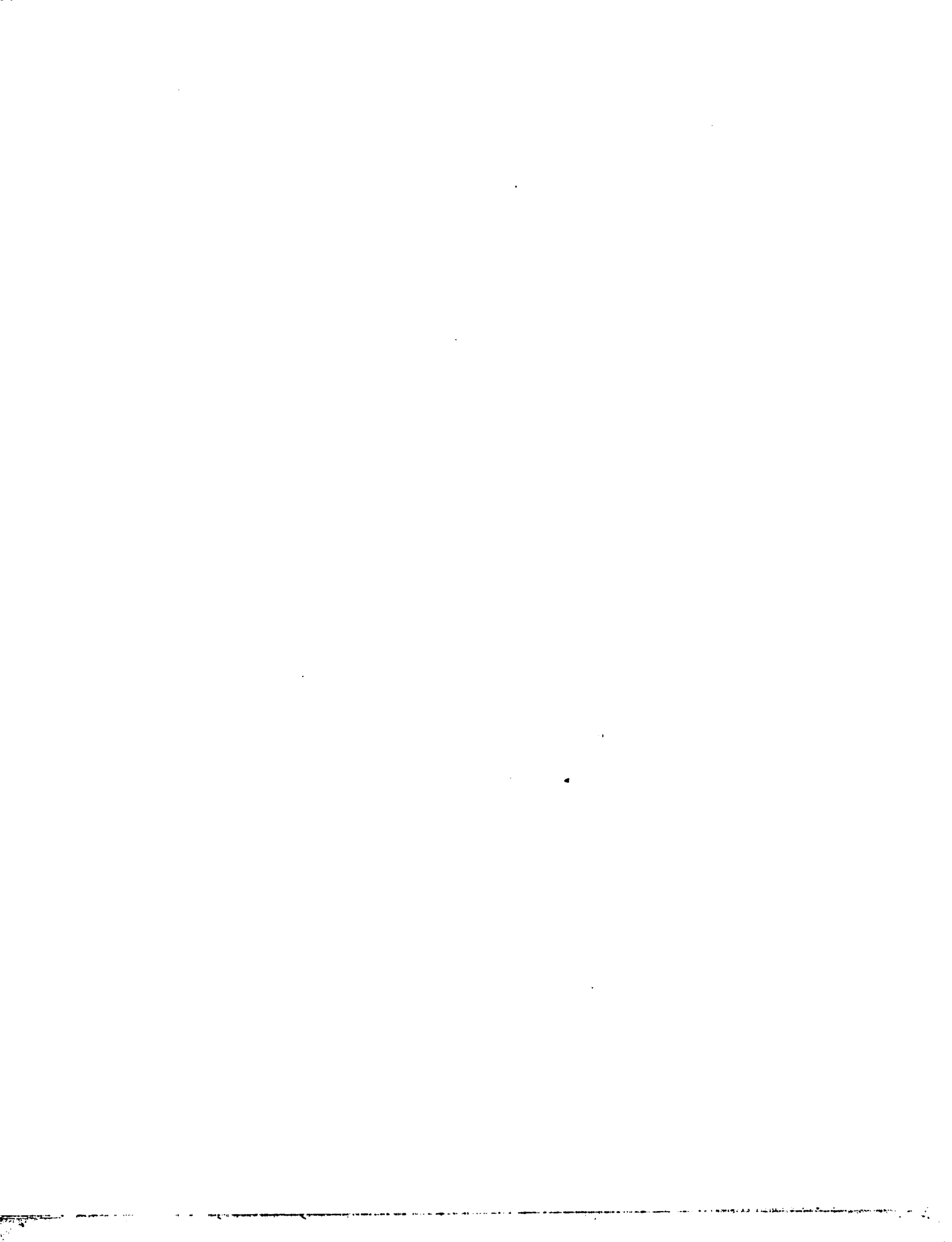
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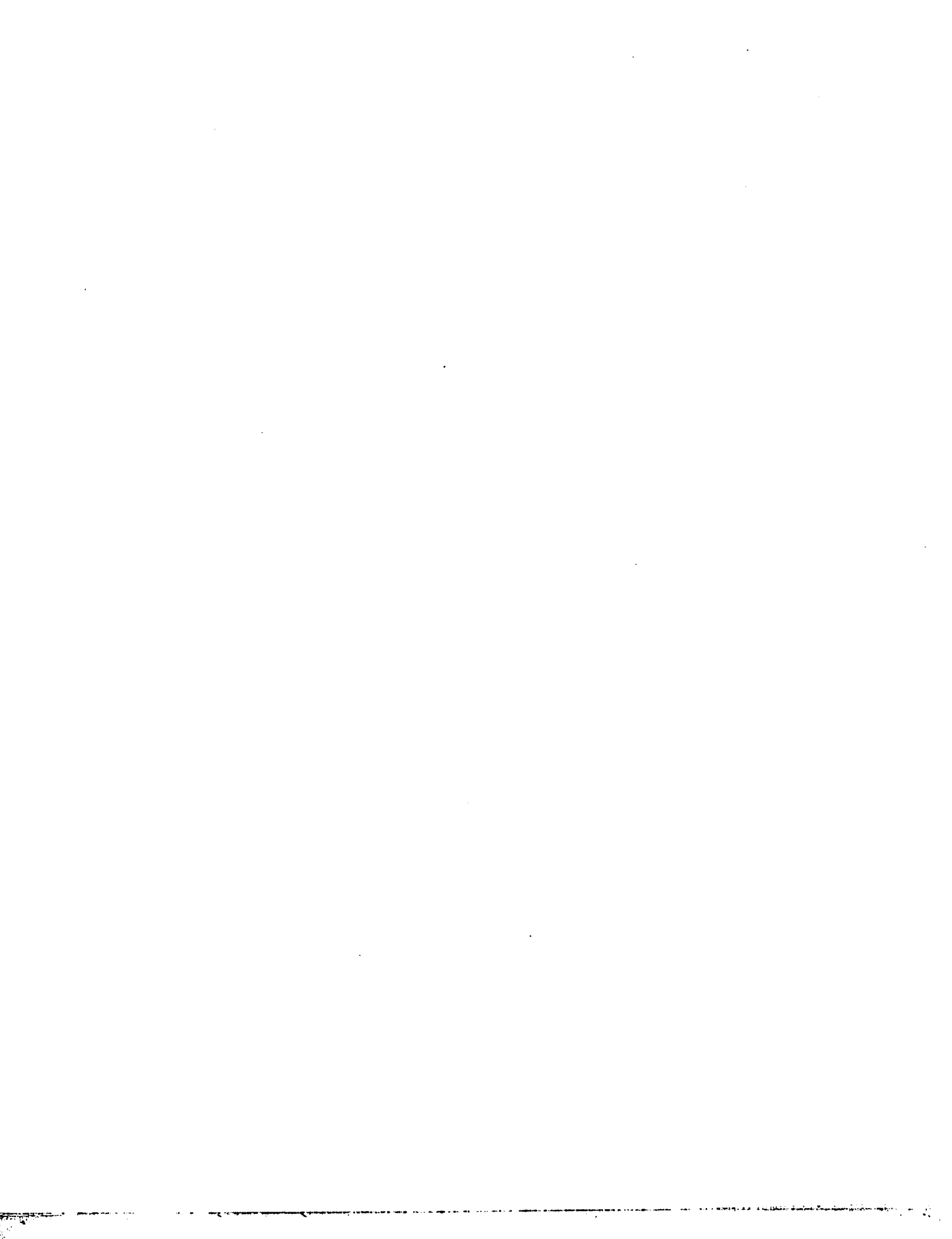
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**A SYSTEMATIC REVISION OF THE GENUS DIOSCOREA (DIOSCOREACEAE)
IN THE INDIAN SUBCONTINENT**

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A SYSTEMATIC REVISION OF THE
GENUS DIOSCOREA (DIOSCOREACEAE) IN THE INDIAN SUBCONTINENT

by

ANTHONY HAROLD MAGDON JAYASURIYA

A dissertation submitted to the Graduate
Faculty in Biology in partial fulfillment
of the requirements for the degree of
Doctor of Philosophy, The City University
of New York.

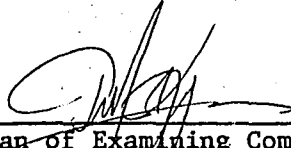
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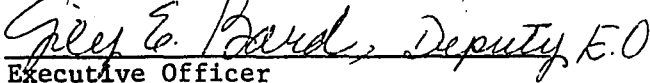
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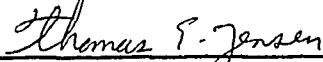

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ABSTRACT

A SYSTEMATIC REVISION OF THE GENUS DIOSCOREA (DIOSCOREACEAE)
IN THE INDIAN SUBCONTINENT by ANTHONY HAROLD MAGDON JAYASURIYA.
A dissertation submitted to the Graduate Faculty in Biology in
partial fulfillment of the requirements for the degree of Doctor
of Philosophy, The City University of New York. 1983. Advisor:
Dr. Tetsuo M. Koyama, The City University of New York and The New
York Botanical Garden.

The genus Dioscorea (sensu stricto) includes all true yams
and is very widespread and diversified. Organography of the
genus is discussed with emphasis on the taxonomic use of
morphological variation within the genus. Information available
on chemistry is reviewed with special reference to the secondary
chemical compounds and their use in taxonomy. Distribution of
edible yams is discussed with a historical perspective.
Systematics of 21 species in 6 sections of the genus are studied.
One new species from Sri Lanka is described. Morphological,
anatomical, and chemical features are used in taxonomy and the
inter- and intra-populational variations are carefully considered
in delimiting the species. The morphological variation in the
tubers, and to some extent also in the bulbils, is heavily
influenced by selection under cultivation. The taxonomic
significance of these features is therefore minimized. Subgenera
are not recognized, but the traditional sections are accepted

with certain modifications. The separation of the sections Triumphostemon and Lasiophyton is strongly recommended as evidenced by their differences in morphology, anatomy, and chemistry. Unjustifiable taxonomic inflation of the genus by some workers is obvious and, therefore, some previously described species and many varieties must be reduced to synonymy. Keys are provided for sections and species within them. Ample correlation between vegetative and reproductive morphology is observed among these species, and these characters are liberally used in the keys. Furthermore, characters of both staminate and pistillate plants are generally used in these keys. For each taxon, the nomenclature has been critically examined, and all names are typified. Anatomy of the fruit in representative species of 5 sections is investigated. The results showed interesting differences, which are used to consolidate these sections. A Synopsis of the major classifications of the species in the Indian Subcontinent is presented.

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INTRODUCTION

Delving into the taxonomy of genus Dioscorea, in the Indian Subcontinent, was undertaken after some considerations. Primarily the taxonomic confusion prevailing in the genus invites the attention of systematists. Various taxonomists, including Kunth (1850), Uline (1897), Prain & Burkill (1914, 1936, 1939), Knuth (1924), and Burkill (1960), attempted to classify the genus and made great contributions to the understanding of its diversity. However the taxonomic concepts which guided these workers have apparently led to the inflation of the genus and thereby introduced considerable difficulty in using keys to its subgeneric taxa. The dioecism evidently compounded this problem. Numerous species and varieties were proposed to accommodate inter- and infra-populational variations. Similarly the morphological diversity of tubers, caused by selection, in many food yams led to the naming of many infraspecific taxa. It is, therefore, obvious that the classification of the genus should be reconsidered in the light of modern concepts in taxonomy. The present project was undertaken to make a contribution toward this goal.

The edible yams were known to man from prehistoric times, and many such species are presently cultivated in various parts of the world. During the last few decades, certain species of Dioscorea were utilized as a source of precursors for the synthesis of

hormones. Therefore the economic importance of the genus justifies intensive research on the taxonomy of this group.

The subgenera proposed by Kunth (1850) and adopted by others (see Taxonomic Review) are not accepted in this treatment. However the sections, pertaining to the species in the Indian Subcontinent, are followed with modifications and consolidations wherever necessary. Species are delimited using reproductive and vegetative characters taking into consideration the inter- and infra-population variations. Some species and several varieties proposed by previous authors are apparently unjustifiable and eliminated in this work (see Synopsis). Effort was made to use characters of both staminate and pistillate plants in defining species and synthesizing keys. Therefore, with respect to the Indian Subcontinent species, this treatment differs considerably from those of Prain & Burkill (1914, 1936, 1939) and Knuth (1924).

It is clearly evident that the diversification of the genus is concomitant with seed-dispersal strategies and thereby correlated with morphology and anatomy of the fruit. These characters are of importance to taxonomy and also to imply the phylogeny within the genus. However, investigation of fruit anatomy in Dioscorea and its application in taxonomy are very scanty (see Organography). Therefore the fruit anatomy was investigated to test the validity of certain sections of the genus, and interesting results were obtained.

TAXONOMIC REVIEW

The genus Dioscorea was proposed by Plumier (1703) in the honor of the Greek physician Pedenios Dioscorides. Before and after this, other names, such as Ricophora and Rhizophora were used to designate the genus by others. However, Linneaus established the genus Dioscorea in his *Genera Plantarum* (1737), and in *Species Plantarum* (1753) he described eight species under this genus. Since that time, with the discovery of more and more species, several generic names appeared designating various species or groups within the genus.

By the middle of the nineteenth century, the genus had grown to nearly 200 species, and Kunth (1850) provided a relatively profound monograph for the family. He, however, retained Oncus and Testudinaria as separate genera. Further, he proposed the genus Helmia for those species with wings from the base of the seed, and placed those species with round seed-wings in Dioscorea. Bentham and Hooker (1883) combined Borderea, Epipetrum, and Helmia and treated them as sections under Dioscorea, while rejecting several other genera proposed by Salisbury (1866). However, the generic status of Oncus and Testudinaria was unchanged. Pax (1888), while maintaining Borderea, Oncus, and Testudinaria as distinct genera, reduced Kunth's genera, namely Helmia and Dioscorea (*sensu stricto*) to sections Helmia and Eudioscorea respectively. In his treatment of Dioscorea for the Flora of British India, Hooker (1892)

realized the necessity of a more elaborate infrageneric classification and placed the species in seven unnamed sections. Characters such as the number of fertile stamens and seed-wing were used to delimit sections.

Uline (1897) divided the genus into 50 sections and placed them in two subgenera, namely Helmia and Eudioscorea. Meanwhile, he retained the generic distinction of Bordera and Epipetrum but did not refer to Oncus. In the revised classification Uline (1898) introduced a third subgenus, Testudinaria, in which he included sections Eutestudinaria and Stenophora. This revision contains 51 sections, and a reference to Oncus as a genus.

Prain & Burkill (1914) presented a synopsis for the Dioscorea of the Old World, excluding Africa. They recognized eight well-defined sections, of which three (Shannicorea, Combilium, and Stenocorea) were proposed for the first time. Bordera was reduced to a section and, for the first time, Oncus was placed in Dioscorea.

The first modern monograph of the Dioscoreaceae was by Knuth (1924), which he later summarized (1930). Knuth basically followed the concept of Uline, retaining Bordera, Epipetrum, and Higinbothamia as genera and accepting Uline's subgeneric concept, with the addition of Stenophora as the fourth subgenus. He classified over 600 species of Dioscorea in 60 sections. This work, though remarkably comprehensive, was inevitably limited to study of often incomplete herbarium specimens, which led to

errors such as describing the same species twice, once from staminate and once from pistillate material. However, for general identification of Dioscorea species, Knuth's keys, which solve some problems and introduce others, remain the most complete.

Prain & Burkill (1936, 1939) presented an extremely informative monograph for the Dioscorea in Asia, in which 147 species were grouped in nine sections. They did not accept the subgeneric concepts initiated by Kunth and developed by Uline and Knuth, and followed by even contemporary botanists such as Ayensu (1972). Further, they pointed out that subgenera obscure the relationships among the sections and explained how their system differs from that of Knuth (1924) in delimiting sections within the genus, with reference to Asian species.

Burkill (1951a, 1952, 1960) provided much insight into the genus, as well as the family, and a key for the Old World sections was finally presented. He emphasized the importance of *underground organs, i.e. rhizomes and tubers*, above all other characters, which of course made the key very difficult to use.

Perhaps the most valuable taxonomic treatment of the New World species is that of Matuda (1954), including more than 60 species of Dioscorea in Mexico. Useful discussions on the taxonomy of the genus have been made by Burkill (1960) and Ayensu (1972).

ORGANOGRAPHY

Rhizome and Tuber

Underground organs are economically the most important parts of the plant and are also of great taxonomic importance. The rhizome, in contrast to the tuber, is restricted within the genus. As generally accepted, the rhizome is a thick, cauline, and horizontal organ (Fig. 1). During germination, a part of the epicotyl swells into a rhizome-precursor which maintains its horizontality and becomes the rhizome (Burkill 1936, 1960). Holm (1925), however, demonstrated in D. villosa that the rhizome originates from the hypocotyl. With subsequent growth, the rhizome exhibits distinct polarity as the apex continues to grow while it dies behind. The rhizome of Dioscorea ranges from a relatively long and slender form, as in D. nipponica, to compact, but still more than one-noded form as in D. prazeri. In D. villosa, the storage area is increased by the plagiotropic lobing of a single internode of the rhizome.

The rhizome is the most important feature which characterizes the section Stenophora, a relatively large group distributed in the temperate eastern Asia and N. America. It is believed that the rhizome is more primitive than the tuber and consequently Stenophora is presumably an ancestral group within the genus. Furthermore, the great development of the rhizomatous

species in the eastern Asia suggests a possible eastern origin of the genus. Within the section Stenophora, those species with long and slender rhizomes, e.g. D. deltoidea, D. nipponica etc., are considered ancestral to those with short and stout rhizomes, e.g. D. prazeri. The subtropical and tropical distribution of latter species suggests that the tropical conditions favor the thickening of the rhizome, and perhaps the evolution of the tuber. However, these two processes are believed to be nonhomologous.

Anatomical investigations of the rhizome of D. caucasica (Ayensu 1972) showed that the epidermis is composed of compact, thick-walled, cuboidal cells with cytoplasmic contents. The cortex is compact, 3-4 layered, and contains cytoplasm. In mature specimens the outer cortex is suberized and the cell walls are much thickened. The inner cortical cells are uniform and constitute 6-12 layers. An endodermoid layer, represented by 2-3 layers of sclerenchyma, separates the cortex from the vascular cylinder. Numerous starch grains of variable size and shape fill the parenchyma cells surrounding the vascular bundles. Tannin cells are principally restricted to the cortex.

The tuber, within the genus Dioscorea, is generally the most efficient and diversified underground organ (Fig.1). The morphology of these storage organs is complex and their mode of development is peculiar. They do not show nodes and internodes, nor well-marked sheathing leaves, and their mode of growth is not

obviously a development of the basic sympodial monocotyledon pattern, although Holttum (1955) suggests that they are in fact a development of that pattern.

The tuber constitutes the edible portion of the food yams. Two main types of tubers may be distinguished: those which are perennial and survive for the whole lifetime of the plant, and those which are renewed annually. The extreme case of the perennial tubers is represented by the section Testudinaria, where enormous, extensively lignified structures are formed. All food yams, however, are renewed annually.

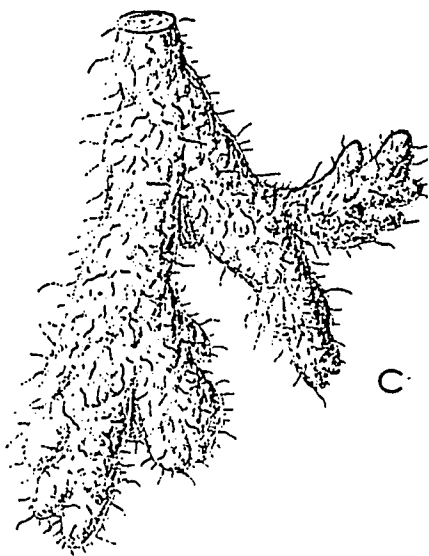
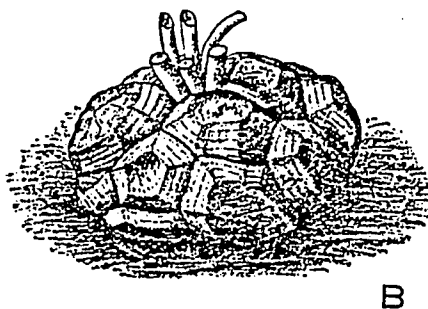
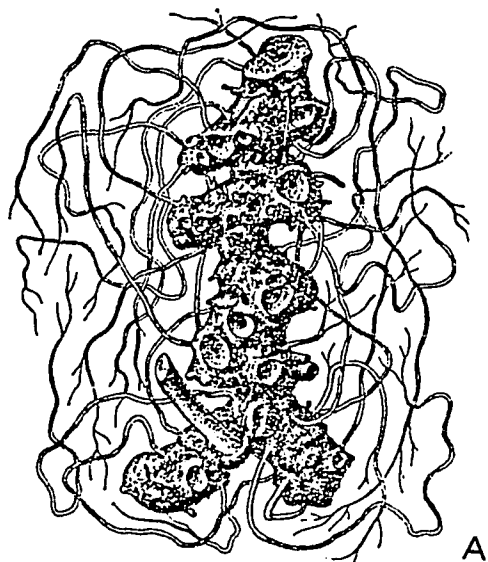
The morphogenetic origin of the tuber has been a subject of much controversy. Dutrochet (1835), referring to the genus Tamus in Dioscoreaceae, regarded the tuber as a subterranean stem which he called a "rhizome". Duchartre (1854) challenged this and declared the tuber a root; this view was supported by de Bary (1887) and Sachs (1893). Morot (1882) held the view that these tubers are stem in character and that each develops from a single reduced internode after germination. This idea explains the absence of scales on the tuber. However, Burkill (1960) hypothesized that the tuber evolved from the rhizome by thickening and plagiotropic lobing followed by shortening of the rhizome and the enlargement of one or few plagiotropic lobes. In the case of tuberous Old World species, the multiple-noded rhizome appears to be suppressed, or it may be represented by the perennial bud. Intermediate species with combinations of

Fig. 1. Underground stems in Dioscorea (after Knuth 1924)

A. Rhizome of D. villosa (x 1/3)

B. Tuber of D. elephantipes (x 1/2)

C. & D. Tubers of D. dumetorum (x 1/6)



elongated rhizome and tuber have not been found. Displacement of the rhizome by the tuber accompanied many other major changes such as deep burial of the tuber and the activation of only one stem which was encouraged to climb as high as possible.

Observations in several species of Dioscorea have confirmed that the tuber is hypocotylar in origin. In D. pyrenaica apparently the whole hypocotyl takes part in the process. In D. elephantipes, and also in Tamus, the growth is a lobe arising out of the hypocotyl. Martin & Ortiz (1963) observed, in the new world species D. floribunda and D. spiculiflora, that the hypocotyl opposite the first shoot rapidly enlarges into a bulge initiating the tuber (Fig. 2C). It soon acquires a vertical axis about which it becomes radial, and pushes the primary root to one side. The growth is the result of rapid cell division of the ground tissue of the hypocotyl and hence the organ may not properly be called either stem or root. Almost immediately adventitious roots grow from the young tuber. All further tuber growth results from diageotropic or plagiotropic lobing of the original structure.

Martin & Ortiz (1963) investigated the further development of the tuber in the aforementioned species and Ayensu (1972) described their anatomical features in several species of Dioscorea. The meristematic activity of the cells just below the epidermis gives rise to a clearly visible multilayered cork, thus of primary origin (Fig. 2A). The tip of the growing tuber,

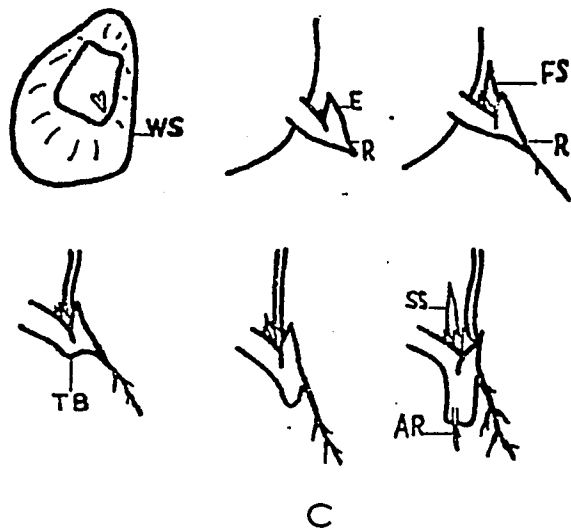
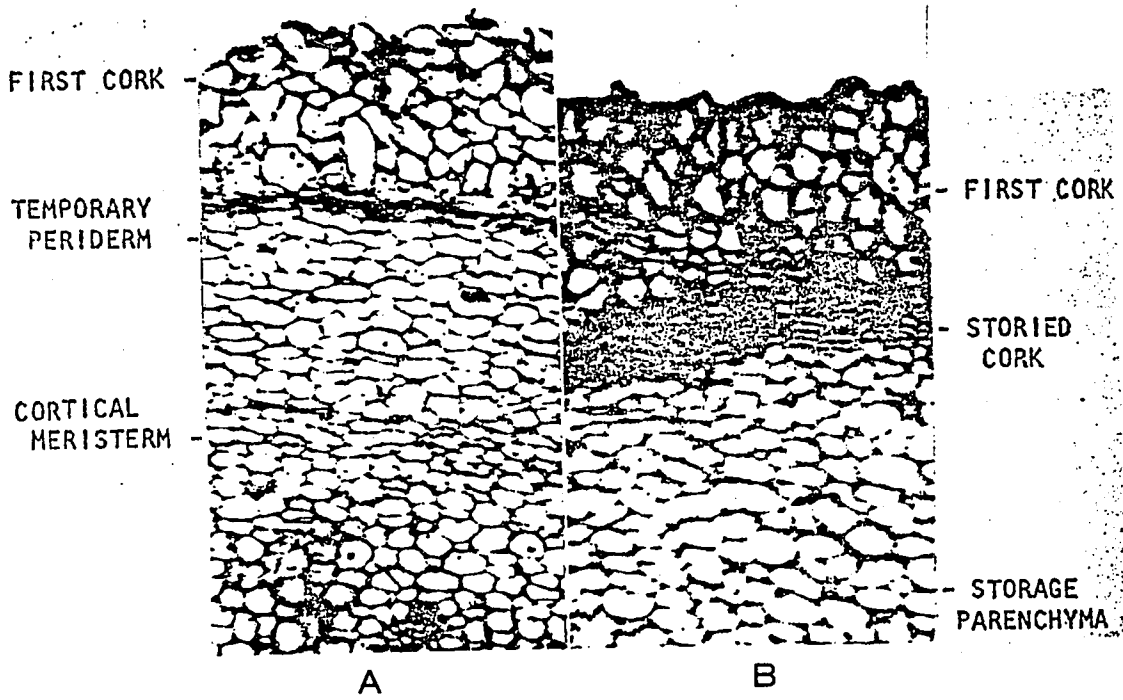
therefore, is covered by cork rather than by a root cap. The cambium is well defined; it produces storied cork towards the periphery, often in many layers, which is composed of tightly compressed suberized cells in radial rows (Fig. 2B). With the development of storied cork, the periderm is isolated from the living tissue and ceases activity. The occurrence of cork in the tubers of some species of the Dioscoreaceae had earlier been reported by von Mohl (1845), de Bary (1884), Kny (1886), Cordemoy (1893), and Goebel (1905). These investigators also determined the presence of cambium and secondary thickening in tubers of Dioscorea and Tamus.

The growth of the tuber in diameter is a type of secondary growth caused by the activity of the cambium, which is a direct continuation of the primary thickening meristem near the apex of the tuber. The cortex consists of large, often rounded or somewhat oval parenchyma cells separated by intercellular spaces. It generally becomes compressed with age. No endodermis is clearly distinguishable, but the innermost cortical cells are often devoid of starch. The inner ground tissue is composed of either thin- or thick-walled parenchyma cells which are filled with starch grains. Collateral vascular bundles are sporadically distributed throughout the inner ground tissue.

The shapes of the tuber have been attributed to physical condition of the soil as well as variability of cambial growth. Archibald (1967) observed in D. sylvatica, a variety of shapes of

Fig. 2. Anatomy and development of the tuber (after Martin & Oritz 1963)

- A. T. S. of young tuber of D. spiculiflora (x 120)
- B. T.S. of mature tuber of the same (x 120)
- C. Early development of seedling and tuber of D. floribunda (x 2); WS, winged seed dissected to show endosperm and embryo; R, emerging radicle; E, epicotyl; FS, first shoot; TB, tuber bulge; SS, second shoot; AR, adventitious root.



the tuber influenced by texture, depth, composition, and the rocky nature of the soil.

Martin & Oritz (1967) also demonstrated the dorsiventral orientation of the tuber. This is revealed very early by the tendency for adventitious roots to form on the side towards the radicle. This side is ventral when diageotropic growth occurs. The starch supply of the tuber is concentrated in the old tissue. It therefore tends to occur in great quantities in the ventral side. The dorsal surface gives rise to new aerial shoots. The growth of the tuber is more pronounced on the dorsal than on the ventral side.

Although Burkill (1960) and Martin & Oritz (1963) reported morphological similarities between the the rhizome and the tuber, the former is generally epicotylar in origin. Therefore these two types of underground systems are probably not homologous and are independently derived. Hence the evolution of the tuber from the rhizome, as proposed by Burkill (1960), probably did not occur. Nevertheless, more data on rhizome development in a wide range of species are needed to make definite conclusions.

The relative evolutionary success of tuberous species within the genus indicates that the tuber is more advanced than the rhizome. The morphological diversity of the tuber and secondary chemical compounds among the storage products are of taxonomic importance, especially at sectional level (see Systematic Treatment).

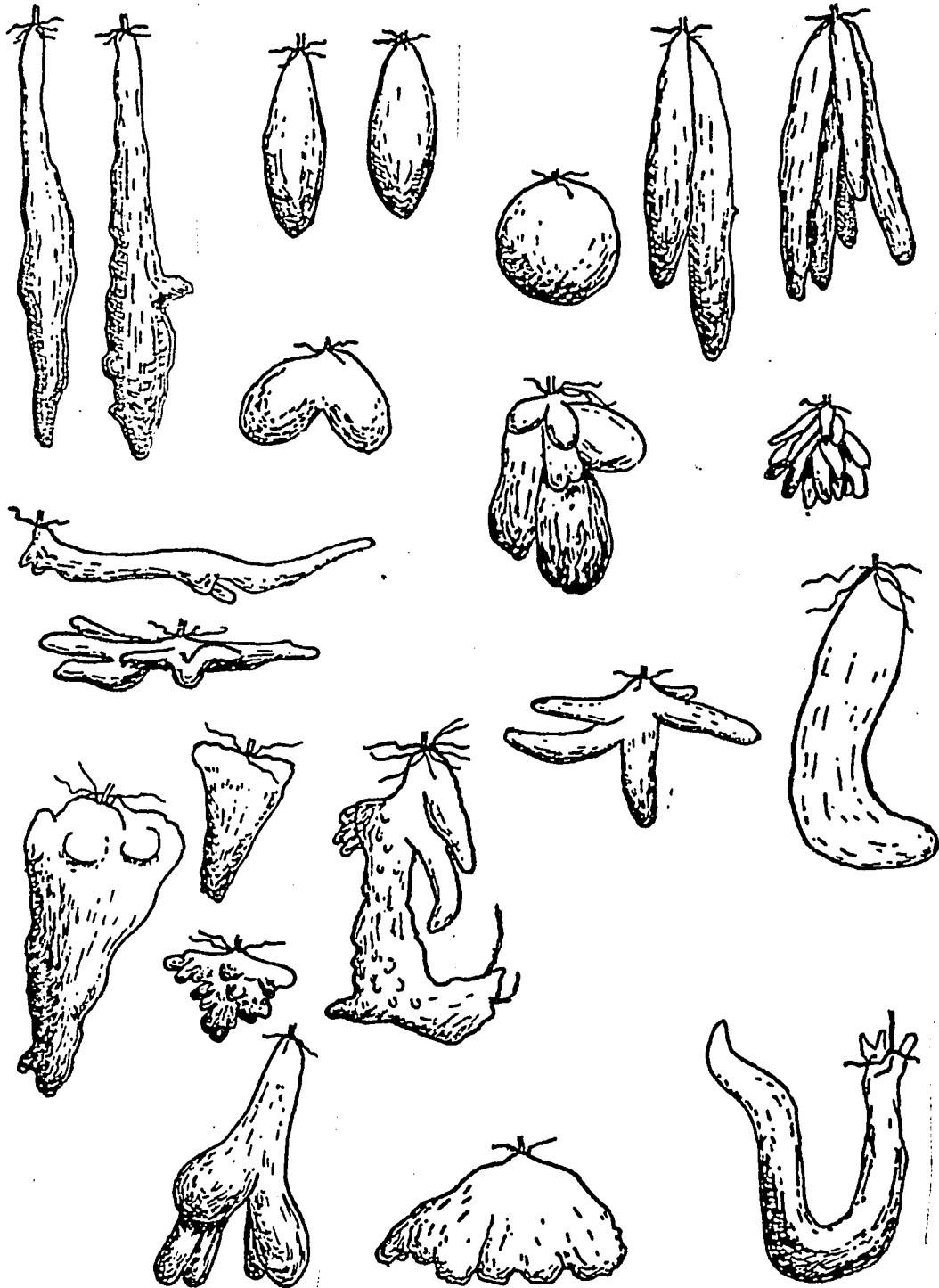
Among the cultivated species, the tuber exhibits a great variety of forms due to selection by man. For instance, in D. alata tubers vary from solitary to several, lying beneath the soil-surface to deeply penetrating, globose or ovoid to long and cylindrical, unbranched to branched etc. (Fig. 3). This species is not known in the wild and its section, namely Enantiophyllum, is characterized by long, cylindrical, and deeply penetrating tubers. Therefore, those forms of D. alata producing such tubers are considered closer to the wild ancestors of this species than those producing globose or ovoid tubers beneath the soil-surface.

Roots

Studies of the Old World species of Dioscorea show the general monocotyledonous pattern in which the primary root is short-lived. Adventitious roots emerge from the hypocotyl at the base of the primary root.

Roots differ in size and are of two kinds; long roots which are diageotropic and spreading in the top soil, and rootlets that are mainly short-lived. In the section Paramecocarpa short roots may be lignified internally and, after the cortex is sloughed off, become thorns. Such thorns are scattered over the tuber and certainly protective. In wild forms of D. sativa (sect. Dioscorea) and D. praehensilis (Enantiophyllum), the lateral roots of some long roots are modified into thorns in the same way.

Fig. 3. Polymorphism in tubers of Dioscorea alata due to cultivation (x 1/15, after Burkill 1939).



In D. sativa thorny roots persist dead in the soil for years and accumulate, forming a formidable armor protecting tubers from herbivores, such as wild boars.

Aerial Stem

The aerial stem is typically annual, although exceptions have been recorded. Hauman (1916) described D. multiflora as having persistent stems. Archibald (1967) observed in D. cotinifolia, D. sylvatica, and D. mundtii that only the uppermost parts of the stem are deciduous and the lower laterals and main stem remain dormant during the winter. When the growing season starts, new shoots are produced from buds either on the main stem or lower laterals.

Despite the the fact that the stem is annual, some species in mesic habitats attain considerable heights. D. mangelotiana reaches 40 m in length and 4 cm in diameter (Miege 1958), while D. sansibarensis and D. cochleari-apiculata attain 12 mm in diameter (Ayensu 1972). However, even the largest species of Dioscorea do not spread over the top of the forest in the way that other perennial climbers do. Slenderness of the stem is adapted to economize energy and maximize the speed of twining. In some species, the stem is short and erect and such dwarfism is associated with shortened periods of adequate humidity and warmth. Dwarfism is of taxonomic importance although it is very rare in the Old World. Such a rarity, D. pyrenaica from Spanish

Pyrenees, is adapted to survive in rocky habitats (Fig. 4). Another, D. hexagona, from savannas of Malagasi, has a erect stem which reaches only up to about 40 cm. In contrast, extreme dwarfism is relatively common in the New World. For example, section Pygmaephyton, consisting of seven dwarf species (Knuth 1924), is chiefly restricted to xeric habitats in Chile. D. minima and D. multinervis, from Mexico, are some of the other New World dwarf species (Fig. 4).

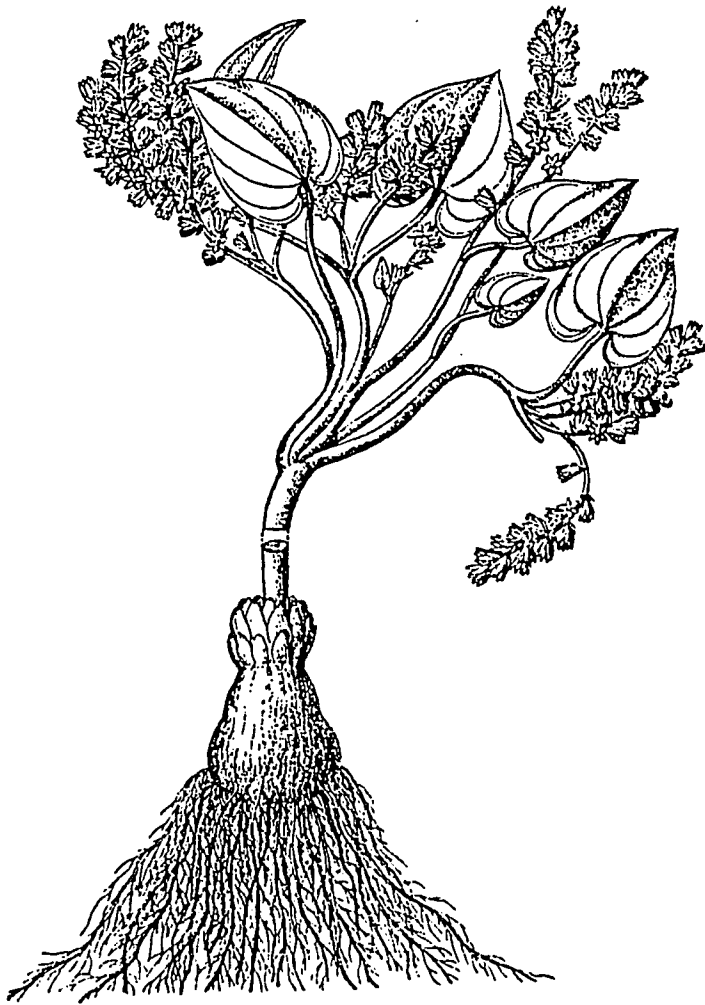
Allard (1945) demonstrated the response D. villosa to the stimulus of day length. It was apparent that the first year seedlings were greatly dwarfed by short days of 10-12 1/2 hrs. In this series of experiments, it was also revealed that the short days triggered the production of bulbils.

The genus is characterized by its weak-stemmed habit. Except for the rare dwarfism, they climb by twining. The direction of twining or twisting is generally consistent within a section. The Old World section Enantiophyllum, the largest in the genus, is dextrorse (right-handed or anti-clock-wise) in its twining (Fig. 5). As a few exceptions have been reported (Prain & Burkill 1936, Allard 1947, Ayensu 1972), doubts have been expressed concerning the taxonomic reliability of the direction of twining. Prain & Burkill (1936) considers some of these variants to be the products of hybridization, which is a strong possibility. As the exceptions to the consistency of the direction of twining occur relatively more frequently among the

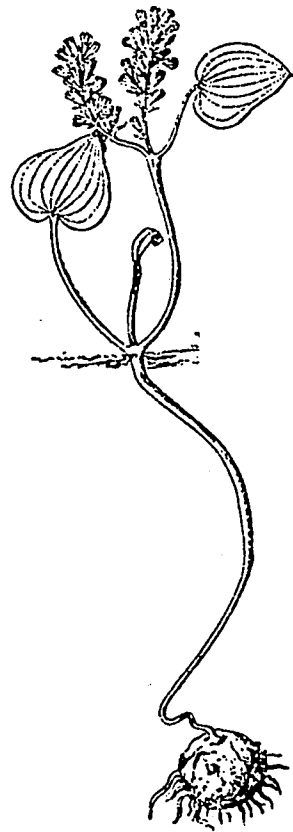
Fig. 4. Dwarfism in Dioscorea (after Knuth 1924)

A. Habit of D. pyrenaica (x 1)

B. Habit of D. minima (x 1)



A

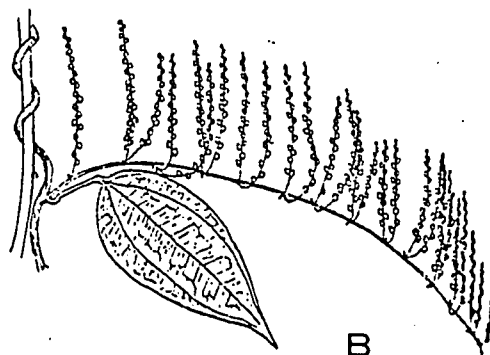
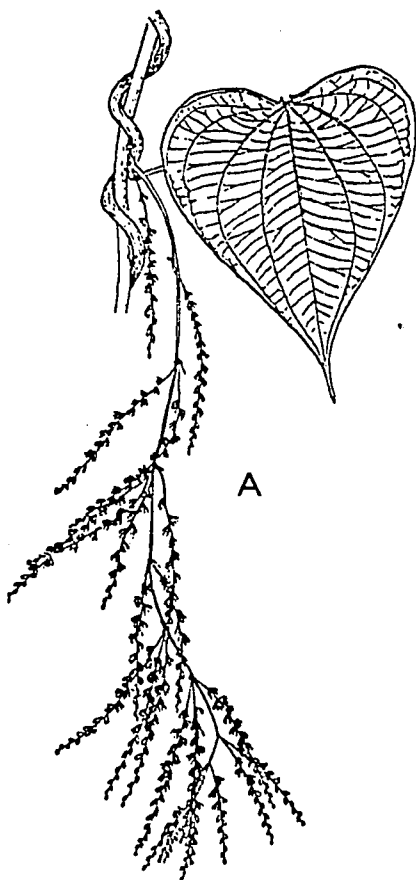


B

Fig. 5. Direction of twining in Dioscorea

A. Sinistrorse twining in D. bulbifera (x 1/2)

B. Dextrorse twining in D. laurifolia (x 1/2)



New World sections of the genus, Burkill (1960) advocates caution in using this character in the classification of the New World species. However, the direction of twining can be used to define six well-marked sections accomodating the Indian Subcontinent species.

The twining behavior of plants has long interested critical scientific observers. Darwin (1867) noted the constancy of this in different species. Twining is governed by both genetic and environmental factors, although the extent to which these factors influence the direction of twining is not clearly known. Twining stems circumnutate at their tips in dextrorse or sinistrorse direction and this enables them to wind upwards around a suitable support. Copeland (1916) concluded that the rate of growth of young shoots is independent of light, but stem elongation is reduced in darkness while nutation tends to cease, and for this reason, twining also ceases in darkness.

Bulbils

Many species of Dioscorea produce bulbils in axils of the leaves (Fig 22A; 26A, B). Sometimes they are seen on staminate inflorescences, in the axils of bracts subtending spikes or branches of panicles. Rarely they are found at the articulation between petiole and the leaf.

The occurence of bulbils, and sometimes their shape and size, are of considerable taxonomic interest. They have not been

observed in sections Stenophora, Dioscorea, and Lasiophyton. They occur abundantly in the section Opsophyton and in some species of Trieuphorostemon. Apparently, only a few species of the section Enantiophyllum produce bulbils. Prain & Burkill (1914, 1936, 1939) used the shape and the nature of bulbils to recognize varieties within some species, for e.g. D. bulbifera (see Systematic Treatment). Because this species has been domesticated for its edible bulbils, selection has induced a wide variety of shapes and sizes. Such variations do not justify infraspecific recognition. However, in wild plants of some species interspecific differences are observed. For instance, the glossy black bulbils in D. melanophyma and the pubescence in young bulbils in D. kamoensis are notable.

The morphogenesis of the bulbil, like that of the tuber, has been subjected to different views. Dale (1901) demonstrated that a leaf axil in D. bulbifera could have as many as 6-8 buds; a bulbil develops external to the posterior-most bud which is the youngest and closest to the subtending leaf. Bulbils possess polarity similar to a stem. Goebel (1905) and Burkill (1912) noted it in D. japonica and D. bulbifera respectively. Despite the differences in size, and sometimes in shape, the anatomy of the bulbil resembles that of the tuber (Dale 1901, Ayensu 1972). Dale (1901) concluded that the bulbil and the tuber are morphologically identical. Goebel (1905) supported this view by suggesting that the bulbil is an arrested tuber. However,

these organs are morphogenetically not identical, due to the hypocotylar origin of the tuber. The anatomical resemblance between the tuber and the bulbil is apparently due to parallelism while performing a storage function as perennating organs.

Burkill (1937) observed the mode of germination of the bulbils of D. macroura (= D. sansibarensis) and concluded that the bulbil is a resting organ, containing the primordium of a branch system in which the branch-tip primordia are located in the older, adaxial parts of the bulbil. In other words it is a whole branch that fails to become elongated; on this abbreviated branch, the leaves are not laid down in an orderly sequence, and the vascular bundles, like those in a tuber, pursue an irregular course. Burkill's conclusion seems most appropriate.

Bulbils are specially adapted for vegetative propagation under natural conditions. They are usually much smaller than the underground tubers, but in certain forms of D. bulbifera, they are the main storage organs. Bulbils tend to form late in the annual growth cycle of the plant, when development of stems and leaves is complete or even when they are beginning to die away. When stem cuttings are cultured, as has been performed in some economically important species such as D. alata, the formation of a bulbil-like organ is the first stage in the rooting.

It has been noted that mature bulbils are less dense than water whereas immature ones, like the underground tubers, are denser. Hence their dispersal by flood waters is possible.

Prickles

The stems of many species are armed to a greater or lesser degree with prickles. They are absent or less frequent, for example, in the sections Stenophora and Lasiophyton, which are protected by herbivore-deterrent compounds, namely saponins and alkaloids respectively. On the other hand, most species in sections Enantiophyllum, Triumphorostemon, and Dioscorea have edible tubers, and their stems are amply provided with prickles.

The prickles arise above vascular bundles and are strengthened by collenchyma. When present, they are larger and crowded upon the lowest part of the stem above the ground. This would discourage any herbivore having to dig for the tubers. The armature diminishes rapidly upward along the stem. In addition to the protective function, prickles also assist in supporting the stem on the host plant. In a few species, e.g. D. pentaphylla and D. tomentosa, prickles appear on abaxial surfaces of the petiole and rarely on those of the midrib.

Narrow wings develop on the stem of species such as D. alata, D. belophylla, colocasiaefolia, and D. hamiltonii and they are inconsistent in D. bulbifera. Many others, although they bear neither prickles nor wings, have longitudinal ridges on the stem, helping to prevent them slipping from their support.

Phyllotaxy and Leaves

Burkill (1960) described three types of phyllotaxy observed in the genus. In the commonest type, as occurring in D. opposita (section Enantiophyllum), the preliminary parastichal set passes into tristichy and returns to distichy. The passage from one to another is gradual and it depends on the diameter of the stem immediately below the apex at the horizon where elongation sets in and overwhelms increase in diameter. The pattern of the leaf traces at the nodes indicates that two leaves are brought to the same horizon by suppression of the internode between them. It is further revealed that the two traces of the paired leaves did not approach each other at all and that there was nothing like a nodal plate. This pattern therefore is one of alternate leaves spirally arranged. The second type, which occurs in the section Stenophora, and as observed in D. villosa, begins from an off-spiral condition and passes into a disorderly phyllotaxy resulting in leaves more or less in same plane along the axis. The third type is the decussate pattern exhibited by D. alata (Enantiophyllum) and Burkill (1960) postulates that the decussate arrangement entered the genus relatively late in its evolution. Burkill's view seems probable, as the section Enantiophyllum exhibits many other special features.

In the Indian Subcontinent species of Dioscorea, the taxonomic application of phyllotaxy is limited. Alternate leaves

predominate in all sections except Enantiophyllum. Although opposite leaves are common in the latter, examination of a large number of specimens revealed that no single species is consistent in this character. Therefore, the use of opposite versus alternate leaves to delimit species within the Enantiophyllum, as liberally adopted by Knuth (1924) and Prain & Burkill (1939), is avoided in this treatment.

The typical dioscoreaceous leaf is simple with a long petiole including a pulvinus at each end, and a broad lamina with three or more campylodromous primary veins, of which three or five reach the apex of the leaf. The apex of the leaf is usually drawn into a "forerunner tip" and contains one or more glands which open to the exterior through pores. All these features are intimately associated with the climbing habit. Climbers with broad leaves are found in several other genera in Liliales such as Smilax, Eustrephus, Geitonoplesium, Lapageria, Bomarea, and Stemona. In the forest, a large leaf is advantageous for a rapidly climbing annual stem in its effort to reach light. Such a climber is met with intense competition as the supporting trees spread their leaves and therefore, the expenditure on lower leaves possibly soon becomes unremunerative. The majority of the forest species of Dioscorea produce leaves with 50-100 cm². However, very large leaves over 1200 cm² have been recorded in D. sansibarensis, and leaves of D. bulbifera may reach over 800 cm² in cultivation (Burkill 1960).

The simple cordiform leaf may become deeply cordate and the auricles become greatly extended toward the petiole as seen in D. alata. This is accompanied by increase in arcuation of the primary veins toward outside. Lobed leaves are seen in section Stenophora of Asia and N. America and in sections Rhacodaphyllum and Macrourea in Africa (Fig. 6).

Compound leaves are a special feature in the genus (Fig.6). They characterize sections, although such sections are few in number. The largest among them is Triephorostemon which is widely distributed in Asia extending to Pacific region. This is the only section in Asia which produces more than three leaflets. Section Lasiophyton is chiefly African with one species occurring in Asia. Although Prain & Burkill (1914, 1935) combined these two sections into Lasiophyton, several morphological, anatomical, and chemical features indicate that they show no intimate relationship with each other (see Systematic Treatment). Therefore it is believed that the compound leaves in these sections have arisen independently.

Compound leaves enable a larger assimilating surface to be exposed per axil, and this feature is still more closely associated with the twining habit. If the total area of leaflets is calculated, the trifoliate leaf of D. dumetorum attains over 1500 cm² and that of D. hispida nearly 1000 cm². The largest recorded area of over 1900 cm² belongs to D. cochleari-apiculata.

Fig. 6. Variation in leaf forms and arrangement of primary veins in Dioscorea (A-L, x 1/7; M-V, x 1/3; after Burkill 1960).

A. D. smilacifolia

B. D. sylvatica

C. D. sansibarensis

D, E. D. rupicola

F-H. D. undatiloba

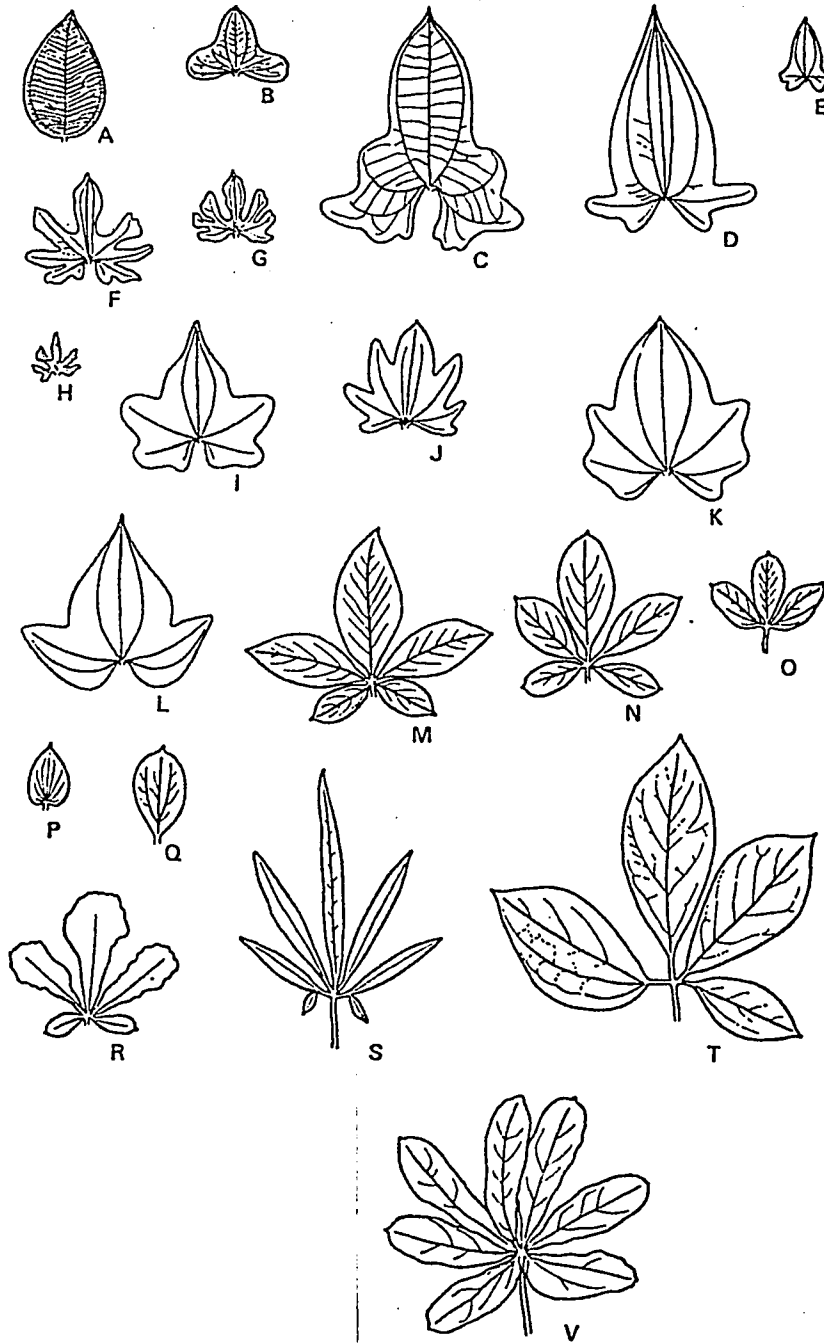
I. D. bryoniaefolia

J. D. diversifolia

K. D. nipponica

L. D. membranacea

M-T, V. D. quartiniana



The efficacy of the compound leaf is further enhanced by the ability of its leaflets to independently adjust their light-fixed posture and to yield independently to the pressure of the wind. Among species with compound leaves, occasionally simple or lobed leaves or too-few leaflets occur, especially among rapidly growing stems or inflorescences. This is due to heteroblasty in which the leaf fails to attain the normal form due to its nutrient supply being channelled to other rapidly growing systems such as the stem-apices or the inflorescences.

The venation in the typical dioscoreaceous leaf is campylodromous with five or more (up to 13) primary veins arising from the base. It is considered that the primaries are longitudinal veins of a typical monocot leaf forced into arcuation by the broadening of the dioscoreaceous leaf. The first pair of primary veins outlines an elliptic or somewhat obovate area and reaches the apex. The subsequent pairs become increasingly arcuate following the shape of the leaf. Towards the apex they become rapidly submarginal, and indistinct. When leaves are elliptic, as in some species in the section Enantiophyllum, the venation becomes acrodromous basal accompanied by the reduction of the number of primaries, usually to three.

The interspaces between primaries are reticulately veined. The secondaries are usually straight, as they are fixed at both ends, and are pulled taut as the primaries become arcuate.

Tertiary and higher order veins are randomly reticulate with distinct resolution. Areoles are well developed, quadrangular to polygonal, and enclose branched veinlets. The nature of the reticulation, whether it is distinctly raised or obscure on one or both surfaces of the leaf, is a useful character in recognizing many species.

Anatomical investigations (Ayensu 1972) indicate that the uniformity in leaf anatomy does not provide taxonomically useful data at sectional level. The epidermis is generally 1-layered and the stomata are anomocytic (ranunculaceous). However, he also reported that variations such as a multiple epidermis and adaxial stomata occur in a few species.

The petiole is long in a typical cordiform dioscoreaceous leaf. Its length is apparently associated with the development of auricles of the leaf. Conversely, it tends to become shorter in relatively narrower leaves, as observed in some species of the section Enantiophyllum. Short petioles and narrow leaves occur in the Malagasian species D. hexagona and D. heteropoda and in the Brazilian species D. anomala and D. stenophylla. These species grow in savannas and evidently the aforementioned characters have entered by parallel evolution.

Stipules in Dioscorea comply with the definition of stipules (Radford et al. 1974), although it is questionable whether they are homologous with those in the majority of stipulate genera. Sinnot & Bailey (1914) observed in the

majority of the angiosperm genera with stipulate leaves, the stipules are produced over the laterals of the three bundles entering a leaf. Dioscorea appears to follow the same pattern.

The presence of stipules is not consistent within a species, and hence this character has to be used cautiously in taxonomy. For example, although D. bulbifera is characterized by the auriculate stipules, it is common to find that they are absent in some specimens of the species.

Stipules in Dioscorea, as they appear in D. alata, D. bulbifera, D. belophylla, and D. melanophyma etc., are extensions of the two adaxial wings of the petiole. Stipules of D. sativa, D. birmanica and D. pentaphylla are modified into prickles, thus adding to the armor of the plant. Soft prickles appear in place of stipules in several species of the section Stenophora, e.g. D. tokoro and D. tenuipes.

Trichomes and Secretory Organs

Staudermann (1924) and Metcalfe (1963) demonstrated the usefulness of trichomes in the taxonomy of monocots, although they are less common in monocots than in dicots. Earlier several workers made observations and investigations which led to further knowledge about the secretory organs in Dioscorea (Kunth 1850, Bokorny 1882, Correns 1889, Raciborski 1900, and Queva 1894).

Ayensu (1972) used the term "glandular trichomes" with reference to epidermal or subepidermal appendages that exhibit

either a unicellular stalk with a bicellular to multicellular head, or internal glands. Multicellular glands, each consisting of a unicellular stalk and a bulb-like head divided by anticlinal and periclinal walls, are reported in some species of Dioscorea, e.g. D. alata, (Ayensu 1972). Non-glandular trichomes (Hairs) are tabular or branched epidermal appendages, which may be either unicellular or multicellular.

Internal glands or "honey glands", often referred to as extra-floral nectaries, are embedded in the parenchyma of aerial vegetative organs such as leaves, petioles, and stems. In leaves, they usually develop on the lower surface, although in some species they are produced on both sides (Oar 1926). They have been studied in reasonable detail by many workers. Correns (1889) and Oar (1926) showed that each of these glands develops from a single epidermal cell which divides and pushes its proliferation into the tissues. The body of the nectary is lens-shaped and the bulk of it is embedded in the mesophyll (or cortex in the stem). Its free outer surface is devoid of a true epidermal layer, but protudes slightly beyond the level of the encircling epidermis and is coated with a thin cuticle (Fig 7A). Correns (1889) and Grout & Williams (1980) demonstrated that each gland is closely associated with leaf veins and in many cases it is located at the terminal points of such veins. However, veins have never been observed to pass through the boundary cell layer of the nectary. Oar (1926) called this type "superficial"

extra-floral nectaries and demonstrated their presence in D. bulbifera (Opsophyton), D. scortechinii (Trieuphorostemon), and D. hispida (Lasiophyton) among Asian species.

It is of further interest to note that in D. hispida, the sheath of parenchyma that normally surrounds and delimits the nectary and whose cell walls become partially suberized, is replaced by an almost unbroken sheath of lignified elements. This sheath, in some places, consists of more than one layer, and its cells are without protoplasmic contents and large pits occur on the walls. This feature provides further support to keep the sections Lasiophyton and Trieuphorostemon apart.

Oar (1926) recognized another type of gland, which he termed "internal" extra-floral nectaries, in D. esculenta (Dioscorea), D. piscatorum (Paramecocarpa) and several species in the section Enantiophyllum including D. alata and D. glabra. Although "internal" nectaries are also epidermal in origin, they are markedly irregular in outline, deeply sunken and open to the exterior through a pore formed by an invagination of the epidermis. They are also notably larger than the superficial glands (Fig. 7B).

Both types of extra-floral nectaries are also reported in some New World species, indicating the occurrence of parallel evolution. Although their taxonomic value seems promising, examination of a more representative collection of species would be required before the utility of this character can be affirmed.

Further evidence of their taxonomic potential is that, in none of the species examined by Oar (1926), are the two types of glands found to occur together, nor do species with superficial nectaries and those with internal nectaries belong to the same section of the genus. Moreover, the consistency of their absence has been demonstrated in some sections, for e.g., Stenophora is apparently devoid of glandular trichomes or extra-floral nectaries.

Oar (1926) mentions that the extra-floral nectaries of a few species, notably D. piscatorum (Paramecocarpa), were deep-seated, i.e. "internal" type, but did not show the characteristic lobing. Nectaries of such intermediate nature have also been observed in D. rotundata (Enantiophyllum), as evident from their ovoid shape and wide but shallow pores (Grout & Williams 1980).

Grout & Williams (1980) demonstrated that the anatomy and ultrastructure of extra-floral nectaries in Dioscorea and the chemical composition of their secretions are typical of those in a variety of other non-dioscoreous genera. The densely cytoplasmic inner cells and dark-staining organelles appearing plastidial in nature further reveal this similiarity. However, the aforementioned investigation did not indicate the prominence of golgi bodies and extensive endoplasmic reticulum, which are reportedly conspicuous in active gland cells.

Qualitative chromatographic and quantitative analysis showed that fructose, glucose, and sucrose together with traces of

galactose were the principal sugar components of the glandular secretion. A positive reaction was given in the ninhydrin test. These results confirm that the secretion is typical nectar and these leaf glands are indeed extra-floral nectaries. These same sugars are found in floral nectar of Tamus communis, also in the Dioscoreaceae (Percival 1961).

Oar (1923, 1926), Schaede (1939) & Ayensu (1972) investigated a peculiar and complex form of glands in the leaf-tip of D. sansibarensis (Fig. 7C). Typically the leaf-tip matures prior to the lamina, hence called the forerunner tip. Its activity, however, soon wanes while the lamina continues to grow. In D. sansibarensis the leaf-tip does not cease to grow early, but elongates up to ca. 8 cm. A series of elongated glands are located in this leaf-tip. In contrast with "superficial" and "internal" extra-floral nectaries, leaf-tip glands owe their inception to a process of invagination of the upper endermis and their secretory elements develop from the epidermal outgrowths, thus differing essentially from the former types of glands. The lumen of the gland is filled with a mucilaginous secretion. A slit-like duct along the whole length of the gland connects the lumen to the exterior. The fluid of the gland cavities harbors a species of bacterium which when isolated in pure culture on artificial media is found to be capable of nitrogen-fixation to a appreciable degree. Further, the nitrogen content of the glandular leaf-tip is greatly in

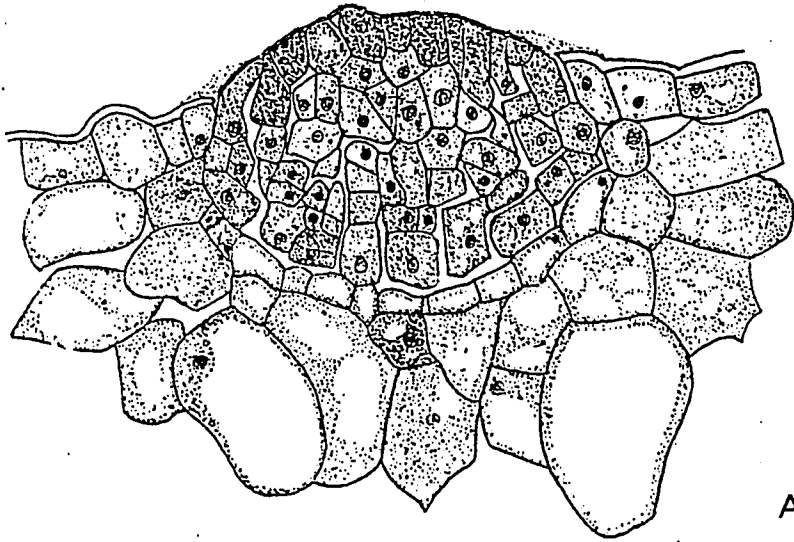
Fig. 7. Extra-floral nectaries in Dioscorea (after Oar 1926)

A. L.S. of a "superficial" nectary of D. pentaphylla (x 350).

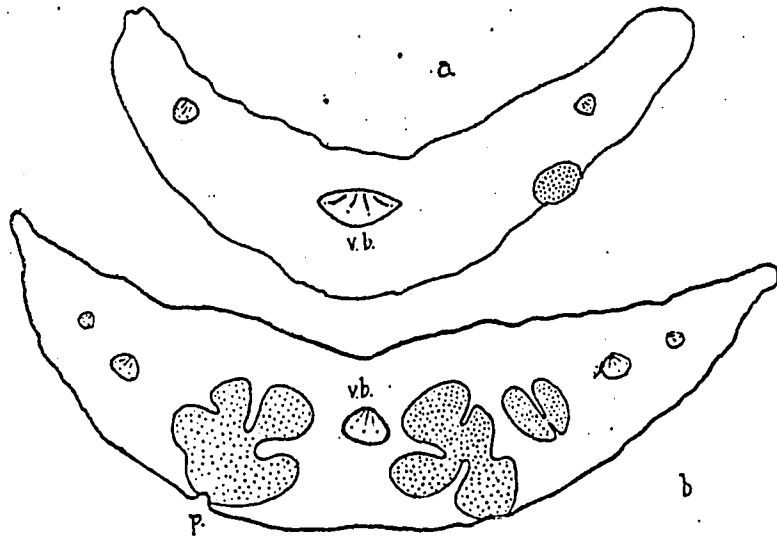
Ba. Diagrammatic T.S. of leaf-tip of D. scortechinii showing the relative size and simple form of a "superficial" nectary (dotted area); vascular bundles (v.b.) are also indicated (x 27).

Bb. Diagrammatic T.S. of leaf-tip of D. cayenensis showing lobed "internal nectaries" (dotted area); the shallow depression (p) indicates the position of the pore (x 27).

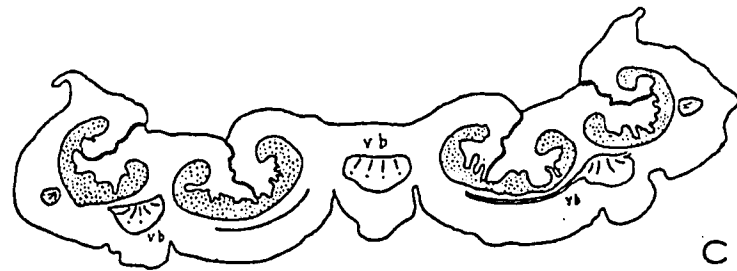
C. Diagrammatic T.S. of leaf-tip of D. macroura; dotted areas represent glands; thick lines leading from glands to the upper surface indicates the course of the ducts.



A



B



C

excess of that lamina. These facts, in conjunction, suggest the possibility of symbiotic nitrogen-fixation in D. sansibarensis. Although bacteria-containing glands in Dioscorea do not fit the definition of a true leaf nodule symbiosis (Lersten & Horner 1976), it is believed that this association is of important physiological significance to both organisms.

Miege (1958) has shown that the scale leaves near the base of the stem of D. manganotiana are up to 4 cm long with a trace of a lamina and a very distinct forerunner tip with its margins incurved so that they make a funnel in which mucilage is accumulated and bacteria live. The duration of these bodies is short and they perish as the assimilating leaves appear.

More than half of the species of Dioscorea are glabrous, and many which have hairs are but scantily clad. The nonglandular hairs are of many different types among the Old World species, while in the New World there is scarcely any variety except in length.

Simple hairs, in the form of finger-like outgrowths of epidermal cells, occur in the section Opsophyton. However, it is interesting to note that D. bulbifera, the most widespread species of the section, is glabrous in Asia and often pubescent in Africa. Simple hairs also occur in certain species of the section Stenophora, for example D. deltoidea (Fig. 8A).

Two-celled hairs are characteristic of the sections Triumphorostemon and Lasiophyton (Fig. 8C, D). Each hair is

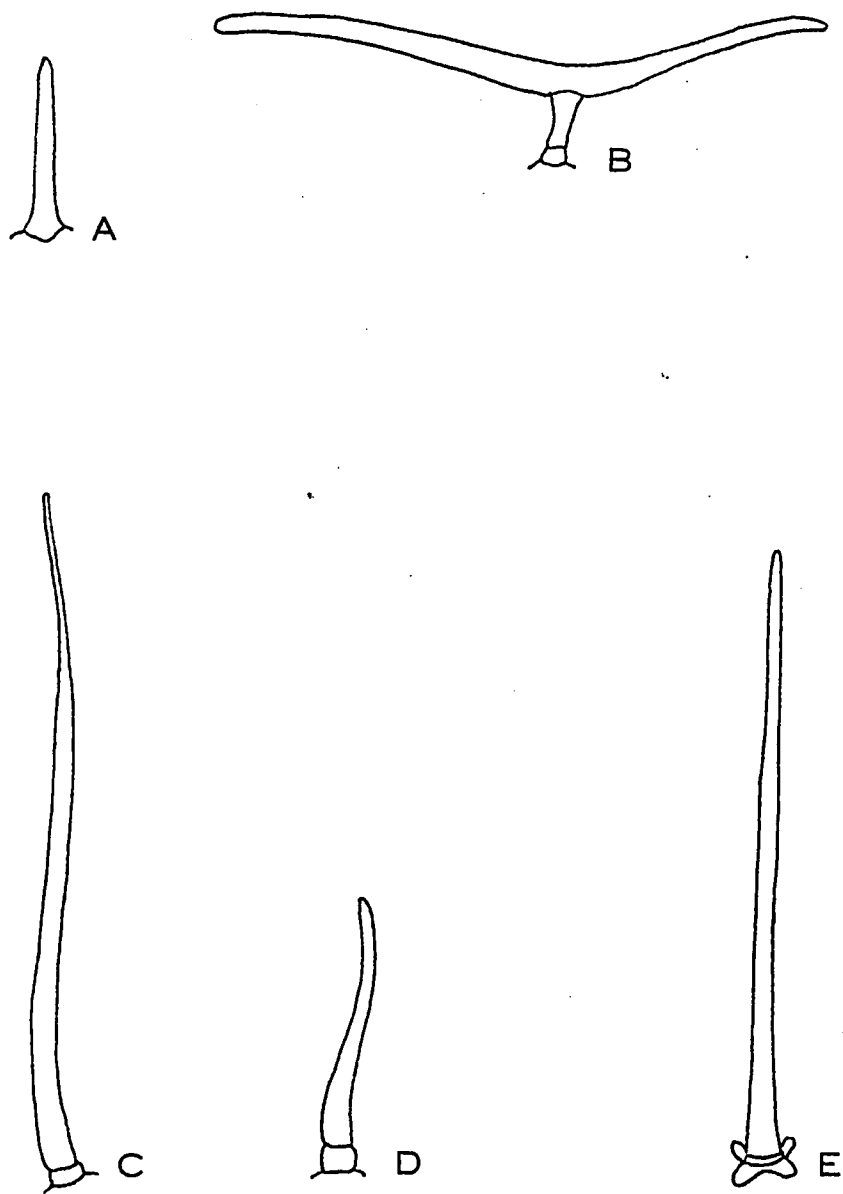
founded on a epidermal cell and consists of a short basal cell and a long, very acute apical cell. Homology of the trichomes indicates a relationship between two sections, and in fact, Prain & Burkill (1914, 1936, 1939) and Burkill (1960) placed them in one section, the Lasiophyton. However, they differ in so many important morphological, anatomical, and chemical features, that their separation is strongly recommended.

T-shaped hairs (the arm of the T being ca. 5-8 times as long as the stalk) are present in D. esculenta (Fig. 8B), only species of the section Dioscorea (= Combilium, sensu Prain & Burkill 1914, 1936). Such hairs are also found in D. preussii in the section Macrocarpaea. However, the other characters of these two sections do not suggest a relationship and the resemblance in their trichomes is evidently a case of parallelism. Further, the cross-wall between the stalk and the arms of the hair differs among the two species, thus indicating the non-homologous nature of these trichomes. Stellate hairs are confined to sections Asterotricha and Syntepaleia, while stiletto hairs characterize the sections Paramecarpa and Enantiophyllum (Fig. 8E). Dendroid hairs occur in a few species of Enantiophyllum.

Within the genus Dioscorea, as complex hairs are confined to species and sections in Asia and Africa, and they are absent in those in America and Malagasy. It is believed that the appearance of hairs in the genus was not very remote and they evolved from a glabrous ancestral condition to the simple type followed by complex hairs.

Fig. 8. Epidermal hairs in Dioscorea (x 300)

- A. D. deltoidea (sect. Stenophora)
- B. D. sativa (sect. Dioscorea)
- C. D. tomentosa (sect. Triephorostemon)
- D. D. hispida (sect. Lasiophyton)
- D. D. pubera (sect. Enantiophyllum)



Inflorescences and Flowers

The genus Dioscorea is almost invariably dioecious. Reported occurrences of monoecious, androdioecious, and gynodioecious individuals have been mentioned by Burkill (1960). Staminate plants outnumber pistillate ones and produce a greater number of inflorescences and flowers. The ratio of flowers in both sexes has not been determined for Dioscorea, although it is known for Tamus.

Flowers are invariably arranged in spikes which are simple (Fig. 19A, 21, 33) or assembled into panicles (Fig. 22A, 31A), the latter rare among pistillate inflorescences. Among Asian taxa, simple staminate spikes generally characterize sections such as Stenophora, Dioscorea and Paramecocarpa and several species within Enantiophyllum. Panicles are frequent in Lasiophyton, Triephorostemon and a majority of Enantiophyllum. In D. alata and some related species in Enantiophyllum, the spikes or the branches of staminate panicles are flexuous. Anthesis is normally acropetal along the spike, but in D. esculenta (sect. Dioscorea) staminate flowers open irregularly along the axis of the spike.

Flowers are generally solitary, although staminate flowers may occur in cymules of 2-4 flowers in Stenophora, Dioscorea and rarely in Enantiophyllum. The staminate flowers are small and inconspicuous. Among Old World species they are mostly 2-4

mm in diameter, the largest being 5-7 mm across in D. buchananii from Africa. The largest flowers yet recorded for the genus are those of D. insignis from Mexico, in which the linear-lanceolate tepals are 2-3 cm long (Fig. 9).

Staminate flowers are sessile or pedicelled. In the section Triumphorstemon, the true pedicel is replaced by a pediment, which supports the staminate flower along with its bract and bracteole. Each flower is subtended by a large bract and a smaller bracteole of which the former encloses the staminate flower partially or completely. The perianth is in two cycles of three parts each, and the tepals are more or less free at the base or united to form a campanulate perianth as in sections Stenophora and Dioscorea. They tend to be relatively thick in the pistillate flower.

The stamens are typically six, in two cycles, and in several species the inner whorl is absent or staminodial. Lasiophyton is the only Asian section in which all members have only three fertile stamens. Among the other Asian sections, staminal sterility is found among some species of Stenophora and very rarely in Enantiophyllum. In the New World species, staminal sterility is relatively common, and such sections outnumber those in the Old World. Uline (1897) and Knuth (1924, 1930) used the staminal sterility to a great extent in the classification of the genus into sections. However, due to a certain degree of inconsistency of this character among the Old World taxa, Burkill

Fig. 9. Dioscorea insignis; staminate plant showing 2-3 cm-long flowers (Hinton et al. 14716).



THE NEW YORK BOTANICAL GARDEN
PLANTS OF MEXICO

HERBARIUM OF G. D. S. HENSON

No. 14716
10-2-1916
Pico de Orizaba

By river in mixed forest; vine 12. high
on bush; flower: white; leaf: green;
Stem: reddish; alt. 65cm; Distr.:
Caltzaco, Gro., Mex., coll. H. S. G. et al.

NEW YORK BOTANICAL GARDEN
TYPE SPECIES: type is Hinton et al.
A. H. S. G. et al.



(1960) did not regard it as a firm sectional character. Nevertheless in the Indian Subcontinent species, staminal sterility is consistent within the sections. Furthermore it is apparent that this character is generally useful in delimiting groups of species within sections in the Old World in a more satisfactory manner than what Burkill has suggested.

The filaments are free or adnate to the base of tepals. Anthers are tetrasporangiate, dithecal, and open by longitudinal latrorse dehiscence. The thecae remain close together or they are well separated on a broadened connective, as in section Trieuphorostemon. The tapetal cells are binucleate and glandular and the endothecium is fibrous (Rao 1953). Pollen grains are binucleate, monosulcate to infrequently disulcate or trichotomosulcate, subspheroidal, and measure 9-18 x 14-31 x 8-17 microns (breadth at polar view, length at polar view, and height at equatorial view respectively). The sulci are as long as the longitudinal axis of the grain. The exine is 0.5-1 microns thick and the tectum is psilate. The sexine is granulate with LO-pattern and the nexine is thinner than the sexine (Huang 1972).

Pistillate flowers are sessile or short pedicelled and their bracts, bracteoles, and perianth generally resemble those in staminate flowers. Staminodes are usually present. The pistil consists of three carpels united to form a compound, inferior, trilocular ovary with axile placentation. The styles are

distinct or connate with separate stigmas. Each stigma is usually channelled above and terminally lobed into 2 or 3 arms. The ovules are two in each loculus and are anatropous, bitegmic, and crassinucellar. The embryo sac is 8-nucleate (Rao 1953).

Fruits and Seeds

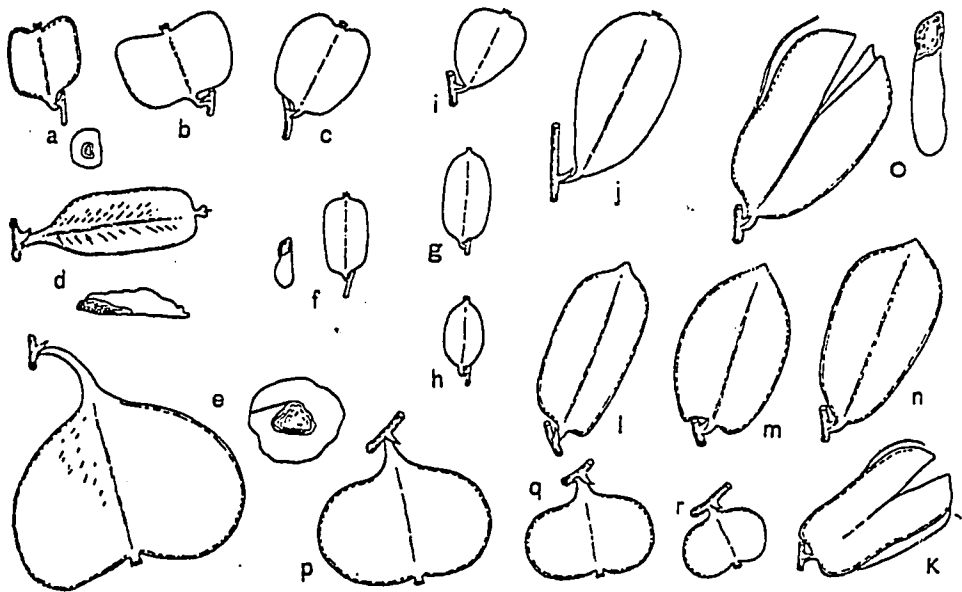
Morphology

Seeds of Dioscorea are adapted to wind dispersal and hence are winged. They develop in pairs in each loculus of the ovary, which extends its 3-ridged wall to accommodate seeds, and becomes a 3-winged capsule of various shapes (Fig.10). The fructifications are usually pendulous due to the weight of the capsules, which open to varying degrees by loculicidal dehiscence.

The nature of the capsule and the seed and the mode of dehiscence are closely correlated with the habitat of the species and they are of great taxonomic importance. Section Enantiophyllum, the largest in the genus, provides an interesting example of such adaptations. Most of its species occur in humid or monsoon forests of the Old World and most of them are large twiners capable of reaching reasonable heights in the forest. The seed-wings are large and surround the seed entirely. Such seeds are adapted to glide in the gentle air. The wings of the capsule are also similarly shaped, i.e. broadly semicircular, and they dehisce circumferentially. Gliding seeds also occur, for example in the African sections Asterotricha and Rhacodophyllum,

Fig. 10. Capsules and seeds in Dioscorea showing the angle at which they stand when mature (modified after Burkill 1951).

- a. D. prazeri (sect. Stenophora)
- b. D. membranacea (" ")
- c. D. sativa (" Dioscorea)
- d. D. flabellifolia (" Stenocorea)
- e. D. sumatrana (" ")
- f. D. bulbifera (" Opsophyton)
- g. D. pentaphylla (" Trieuphorostemon)
- h. D. tamarisciflora(" ")
- i. D. elmeri (" ")
- j. D. cumingii (" ")
- k. D. scortechinii (" ")
- l-o. D. hispida (" Lasiophyton)
- p. D. orbiculata (" Enantiophyllum)
- q. D. divaricata (" ")
- r. D. pubera (" ")



but their wings are located at the opposite ends of the seed.

In contrast the seeds with wings extended from one side are adapted to swirl in gusty wind and are ineffective in still air. Species with such seeds are characteristic of open forest or scrub and typical of sections Lasiophyton, Triumphorstemon, Brachyandra, Opsophyton, Paramecocarpa, Shannicorea, and Testudinaria. In the latter three, the wings are directed toward the apex of the capsule, while in the others they are directed toward the base of the capsule. Correspondingly, the capsule is elongated, and flexed due to post-fertilization curvature of the pedicel. Dehiscence is limited to the apex, which results in the formation of a triradiate aperture at the top of the capsule to liberate the seeds. As observed in Triumphorstemon and Opsophyton, and perhaps in some others, capsules are very light and produced in relatively large numbers. Furthermore they are closely arranged and imbricate, thus acting as a pendent, elongate sail enabling the fructification to swing vigorously in a gusty wind (Fig. 24).

The position of seeds along the placenta varies with the type and the direction of seed-wing relative to the capsule. Seeds are positioned closer to the base of the capsule if their wings are directed towards the apex and vice versa. Round-winged seeds are more or less medial in position. Burkill (1960) hypothesized that the basal and medial seeds antedate the apical

seeds which belong to some of the most wide-spread Old World species such as D. bulbifera, D. pentaphylla, and D. hispida. However the presence of medial seeds in taxonomically distant sections, namely, Stenophora and Enantiophyllum suggests that this feature has evolved more than once within the genus. Although Stenophora is considered to be a archaic section, Enantiophyllum is believed to be of relatively recent origin as suggested by its great diversity. Therefore Burkill's view cannot be fully accepted.

The reduction of the seed-wing and the capsule-wing is correlated with the dwarf habit of the plant. This is a special adaptation to savanna or open rocky habitats, as seen in D. pyrenaica in the Old World and D. perdicum and D. multinervis in the New World.

It is often observed that one or more of the six seeds abort, and as a result, one or two wings of the capsule also do not develop. This tendency seems to have been fixed in the Mexican species D. cyphocarpa and D. tacanensis, where only one capsule-wing develops with one seed in it. It is not apparent whether the capsules are dehiscent or not. Such a fruit may be defined as a samara, which is characteristic of the genus Rajania, which probably evolved from Dioscorea.

Knuth (1850) proposed two subgenera based on seed-wing to classify species of Dioscorea (see Taxonomic Review). Uline (1897) and Knuth (1924) developed this concept and even a

contemporary botanist like Ayensu (1972) followed this classification. However it is evident that taxonomically distant sections have similar seed-wings, e.g. circumferential wings in Stenophora and Enantiophyllum and basal wings in Opsophyton and Trieuphorostemon. This strongly indicates that this character has evolved independently within the genus. Therefore, the aforementioned subgeneric concept does not imply taxonomic or phylogenetic significance, and hence is not followed in this treatment. However, the nature of the seed-wing is useful in defining sections within the genus.

The growth of the developing fruit-wall facilitates the enlargement of the loculi to accomodate flattened seeds and their wings. The expansion of the fruit-wall takes place due to relatively rapid elongation and arcuation of the dorsal bundles accompanied by expansion of the pericarp between them and the placenta, while the ventral bundles elongate at a slower rate. The wall becomes gradually thinner from the center toward the margin and this thinness of the wall facilitates dehiscence at maturity. The decrease in strength toward the apex of the fruit-wing enables dehiscence to start distally. Dehiscence may take place loculicidally on one or both sides of the dorsal bundle along the margin of the fruit-wing, and if it occurs on both sides, the dorsal bundle separates from rest of the tissue like a fine wire, but stays attached to extremities of the wing. The inner surface of the capsule wall becomes perfectly smooth

when dry, allowing efficient liberation of the seeds. In sections such as Opsophyton, Triumphostemon, and Lasiophyton, in which seeds are liberated by sudden agitation, preparation for this begins immediately after fertilization by recurvature of the capsule.

Fruit anatomy

Although a considerable amount of information is available on the anatomy of various vegetative organs of the Dioscoreaceae, investigations of inner structure of the fruits and seeds and their taxonomic applications are very scanty. Pascher (1959) randomly investigated the fruit-wall anatomy of the New World species, such as D. pilosiuscula and D. sessiliflora, and observed that the nature of the thickening of the cell wall in various layers differs among these species. However, usefulness of fruit-wall characters in differentiating sections of the genus was not explored. During the present project, the fruit-anatomy of sections of Dioscorea, representing the Indian Subcontinent, was investigated.

Methods and materials. Each section was sampled using two species, wherever possible. The section Dioscorea was excluded, as no mature capsules were available for D. sativa, the only species representing this section (sensu Prain & Burkill 1936). The middle region (Fig. 11) of mature capsules was sectioned by

means of conventional paraffin technique and the sections were stained with saffranin and fast green. Acid phloroglucinol was used to test for the presence of lignin in the tissues. The following specimens were used in this investigation:

1. D. (Stenophora) deltoidea. Koelz 8826 (NY), India, Himachal Pradesh, Chamba State, Khajar.
2. D. (Stenophora) prazeri. Bis Ram 67 (JEPS), Nepal, Naumala.
3. D. (Opsophyton) bulbifera. Fernandes 2034 (A), India, Maharashtra Pradesh, Siddapur.
4. D. (Trieuphorostemon) tomentosa. Comanor 756 (PDA), Sri Lanka, Trincomalee Dist., Kantalai.
5. D. (Trieuphorostemon) pentaphylla. Müller-Dombois 68022505 (US), Sri Lanka, Hambantota Dist., Ruhuna National Park.
6. D. (Lasiophyton) hispida. Hooker s.n. (GH), India, Sikkim State, Sikkim.
7. D. (Enantiophyllum) oppositifolia var. oppositifolia. Fernandes 1770 (GH), India, Maharashtra Pradesh, Sirsi.
8. D. (Enantiophyllum) belophylla. Stewart 1013 (NY), India, Punjab State, Gurdaspur Dist., Pathankot.

Results and discussion. A transverse or a longitudinal section through one half of the capsule-wing shows the outer and inner epidermal layers and usually distinct hypodermal layers (Fig. 11). Their walls are variously thickened or lignified in different sections of the genus (Fig. 12-16). The cortex, consisting solely of parenchyma, becomes gradually narrowed

distally. The dorsal bundles, each consisting of phloem and xylem enclosed in a sheath of sclerenchyma or thick-walled parenchyma, did not show appreciable variation within the genus. The vascular area of the ventral bundle is distally capped by a zone of fibers and flanked on either side by fibers or lignified parenchyma or thin-walled parenchyma. The nature of the bundle cap and the flanking tissue is variable among the five sections investigated in the genus. A bundle of fibers connects each ventral bundle to the core of the fruit consisting very thick-walled fibers. Vascular traces supplying the seeds lie on either side of the base of this fiber bundle. Three vascular areas, bundle cap, fiber bundle, and flanking tissues are together termed as the ventral bundle complex. Results of the present investigation of fruit-wall anatomy in five sections are shown in the Table 1 and Fig. 12-16. With regards to the species investigated, it is evident that the five sections differ from each other in a number of anatomical features of the fruit. They are readily distinguished using the following key.

Key to five sections of Dioscorea based of fruit anatomy

1. Inner epidermis thin or thick-walled, lignification scanty or not evident; outer and inner hypodermis stratified with brachysclereids and thin-walled parenchyma. Enantiophyllum
1. Inner epidermis thick-walled, lignified; outer and inner hypodermis uniformly parenchymatous.
 2. Bundle cap 10-15 layers wide (tangential); central vascular area of ventral bundle complex flanked by fibers or lignified parenchyma.
 3. Outer epidermis not lignified, walls distorted; outer hypodermis thick-walled, walls distorted; Inner hypodermis thick-walled; inner epidermis lignified; bundle cap ca. 15 layers wide and 1-3 layers thick (radial). Stenophora
 3. Outer epidermis lignified, walls not distorted; outer hypodermis thin-walled, walls not distorted; inner hypodermis thin-walled; inner epidermis semilignified; bundle cap 10-12 layers wide and 6-8 layers thick. Lasiophyton
2. Bundle cap 4-8 layers wide; central vascular area of ventral bundle complex not flanked by fibers or lignified parenchyma.

4. Inner hypodermis thick-walled, \pm lignified, raphides absent; bundle cap 3-4 layers wide and 2-4 layers thick; Opsophyton
4. Inner hypodermis thin-walled or semilignified, raphides present; bundle cap 5-8 layers wide and 2-7 layers thick; Trieuphorostemon

Among sections of the genus investigated, Enantiophyllum shows the unique feature of having both hypodermal layers stratified with brachysclereids. This is evident to the naked eye as narrow, transverse bands on outer and inner surfaces of the capsule-wing. Furthermore, the inner epidermis is not or scantily lignified, and hence differs from all other sections in which the epidermis is heavily lignified. This study also provides further support for the separation of Trieuphorostemon from Lasiophyton. Heavily lignified inner epidermis, thin-walled outer hypodermis with undistorted walls, large bundle cap, and fibers flanking the central vascular area readily differentiate Lasiophyton from Trieuphorostemon.

Fig. 11. General structure of Dioscorea fruit.

- A. Outline of a fruit of D. hispida (sect. Lasiophyton);
broken lines showing region used for anatomical
investigation.
- B. Same of D. oppositifolia (sect. Enantiophyllum).
- C. Diagrammatic T. S. of fruit. a, dorsal bundle; b,
ventral bundle complex; c, seed; d, line of dehiscence.
- D. Diagrammatic T. S. of one wing with ventral bundle
complex. e, outer epidermis; f, outer hypodermis; g,
inner hypodermis; h, inner eppidermis; i, cortex;
j, bundle cap; k, central vascular area; l, fiber bundle;
m, lateral vascular area.

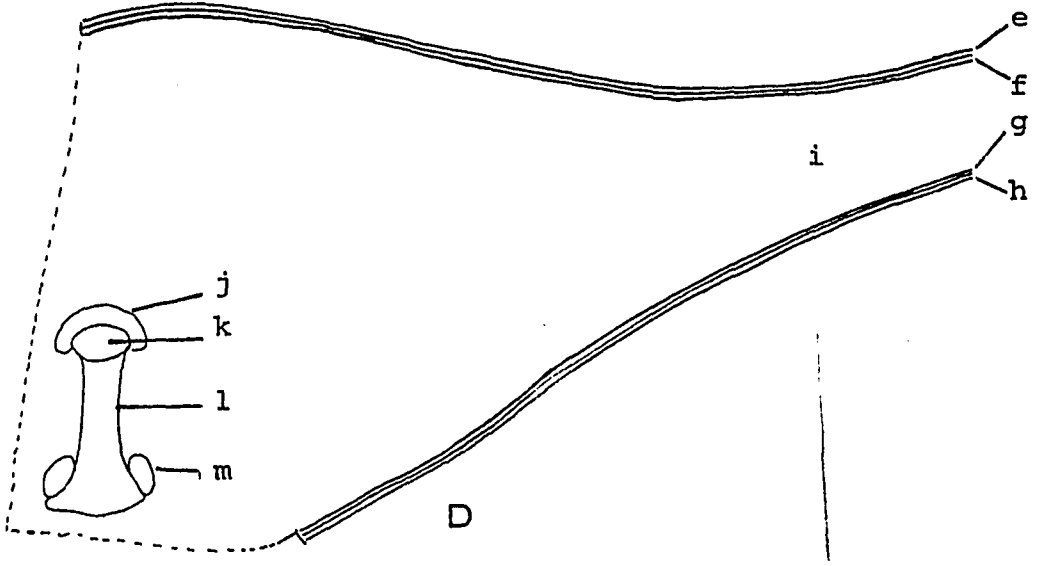
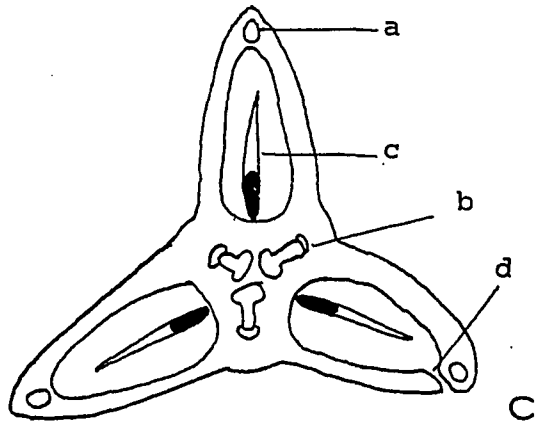
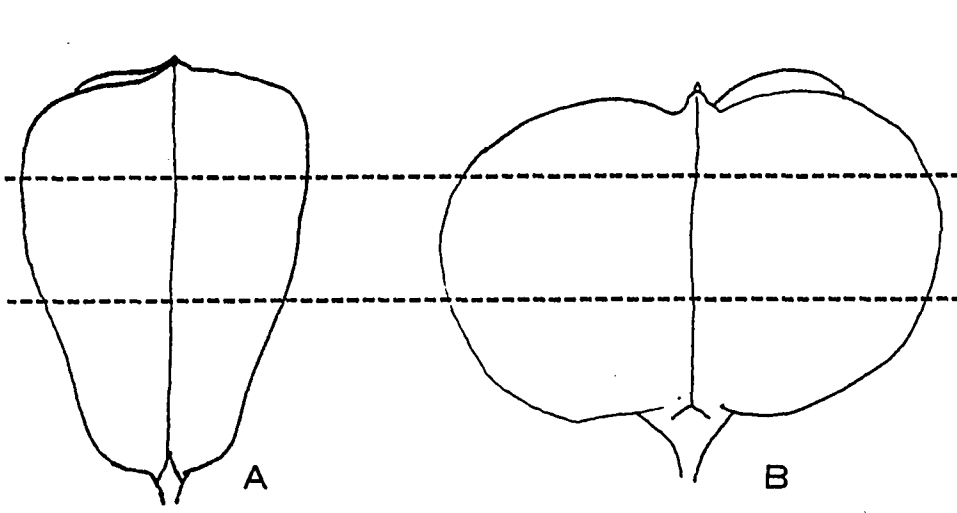
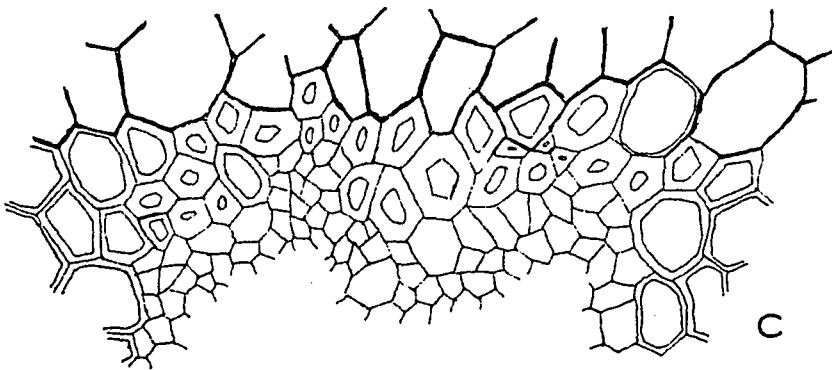
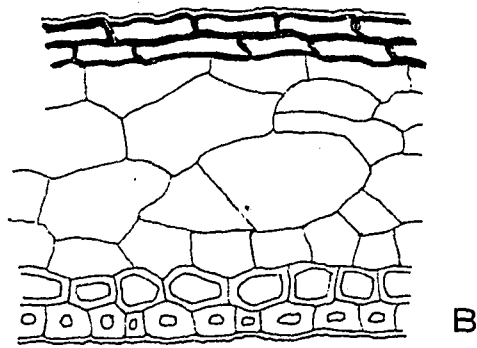
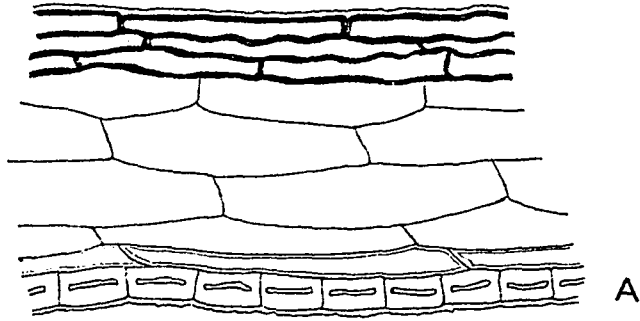


TABLE 1. FRUIT ANATOMY OF FIVE SECTIONS OF DIOSCOREA

	STENOPHORA	OPSOPHYTON	TRIEUPHORSTEMON	LASIOPHYTON	ENANTIOPHYLLUM
OUTER EPIDERMIS	Thick-walled, walls distorted, narrow rect. T.S., rect. L.S.	Thick-walled, slightly lignified, rect. T.S. & L.S.	Thick-walled, walls distorted, rect. T.S. & L.S, hairs present	Lignified, cells larger than inner epidermal cells, 4-5 sided T.S & L.S	Thick-walled, cells very small, rect.T.S & L.S.
OUTER HYPODERMIS	Thick-walled, walls distorted.	Thick-walled, walls not distorted, cells large.	Thick-walled, walls distorted.	Thin-walled, walls not distorted.	In patches: (i) brachysclereids or (ii) parenchyma: Thin-walled, Rect.-5-sided T.S., 4-6 sided L.S.
INNER HYPODERMIS	Semilignified, long & narrow T.S., 5-6 sided L.S.	Semilignified, squarish to short rect. T.S. & L.S.	Thin-walled or semilignified, 4-6-sided T.S & L.S.	Thin-walled, long & narrow T.S., 5-6-sided L.S.	In patches: (i) brachysclereids or (ii) parenchyma Thin-walled, cells large, 5-6-sided T.S. & L.S.
INNER EPIDERMIS	Heavily lignified, squarish to rect. T.S., squarish-5-L.S.	Lignified, squarish T.S. & L.S.	Lignified, squarish T.S & L.S.	Semilignified, cells smaller than outer epid. cells, narrow rect. T.S., squarish L.S.	Thin or thick walled, cells very small, rect. T.S & L.S.
BUNDLE CAP	± 15 layers wide (tangential), 1-3 layers thick (radial), walls very thick.	3-4 layers wide, 2-4 layers thick, walls thick.	5-8 layers wide, 2-7 layers thick, walls relatively thin.	10-12 layers wide, 6-8 layers thick, walls thick.	6-7 layers wide, 3-4 layers thick, walls thick
VENTRAL BUNDLE COMPLEX	Central vascular area flanked by lignified parenchyma.	Central vascular area flanked by thin-walled parenchyma.	Central vascular area flanked by thin-walled parenchyma.	Central vascular area flanked by fibers	Central vascular area flanked by thin-walled parenchyma

Fig. 12. Fruit anatomy of Dioscorea deltoidea (sect. Stenophora)

- A. T. S. of wall showing outer epidermis and outer hypodermis with thick-walled distorted cells, inner hypodermis with semilignified cells, and inner epidermis with heavily lignified cells (x 400).
- B. L. S. of the same (x 400).
- C. T. S. of upper part of ventral bundle complex showing bundle cap consisting of fibers and central vascular area flanked by lignified parenchyma (x 400).



Fif. 13. Fruit anatomy of Dioscorea bulbifera (sect. Opsophyton)

- A. T. S. of wall showing outer epidermis and outer hypodermis with thick-walled cells, inner hypodermis with semilignified cells, and inner epidermis with heavily lignified cells (x 400).
- B. L. S. of the same (x 400).
- C. T. S. of upper part of ventral bundle complex showing bundle cap consisting of fibers (x 400).

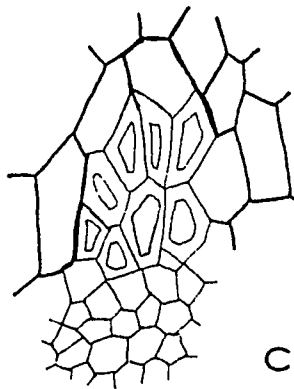
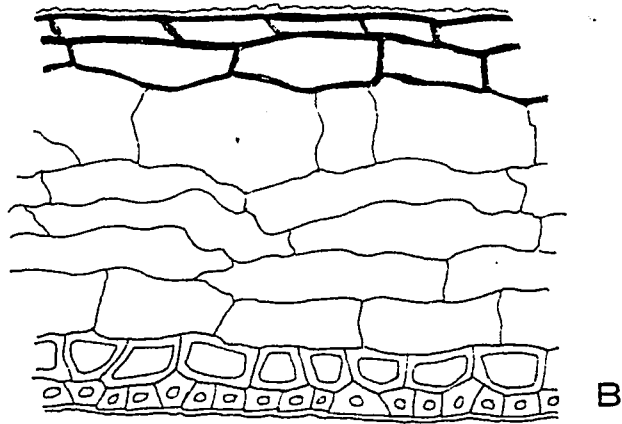
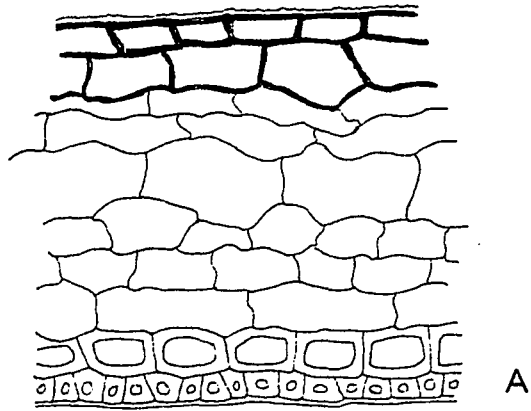


Fig. 14. Fruit anatomy of Dioscorea pentaphylla and Dioscorea tomentosa (sect. Triephorostemon).

- A. T. S. of wall (D. pentaphylla) showing outer epidermis and outer hypodermis with thick-walled distorted cells, inner hypodermis with thin-walled cells, and inner epidermis with lignified cells (x 400).
- B. L. S. of wall (D. tomentosa) showing a raphide bundle and inner hypodermis with semilignified cells (x 400).
- C. T. S. of upper part of ventral bundle complex (D. pentaphylla) showing bundle cap consisting of fibers (x 200).

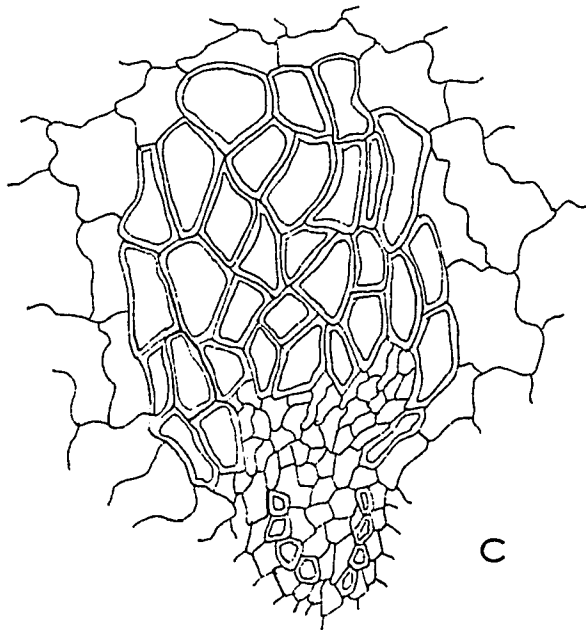
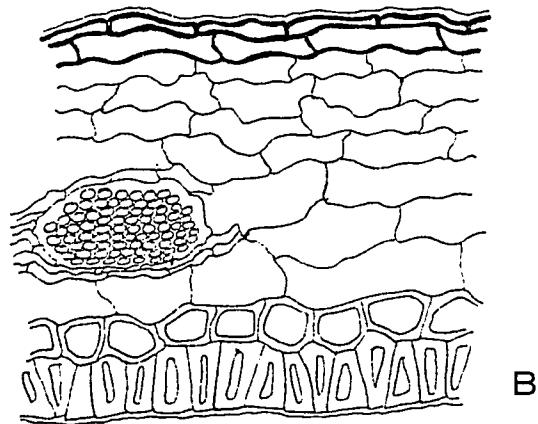
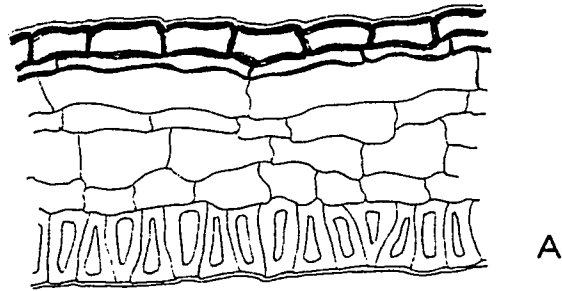


Fig. 15. Fruit anatomy of Dioscorea hispida (sect. Lasiophyton)

- A. T. S. of wall showing outer epidermis with heavily lignified cells and inner epidermis with relatively small semilignified cells (x 200).
- B. L. S. of the same (x 200).
- C. T. S. of upper part of ventral bundle complex showing large bundle cap consisting of fibers and central vascular area flanked by fibers (x 400).

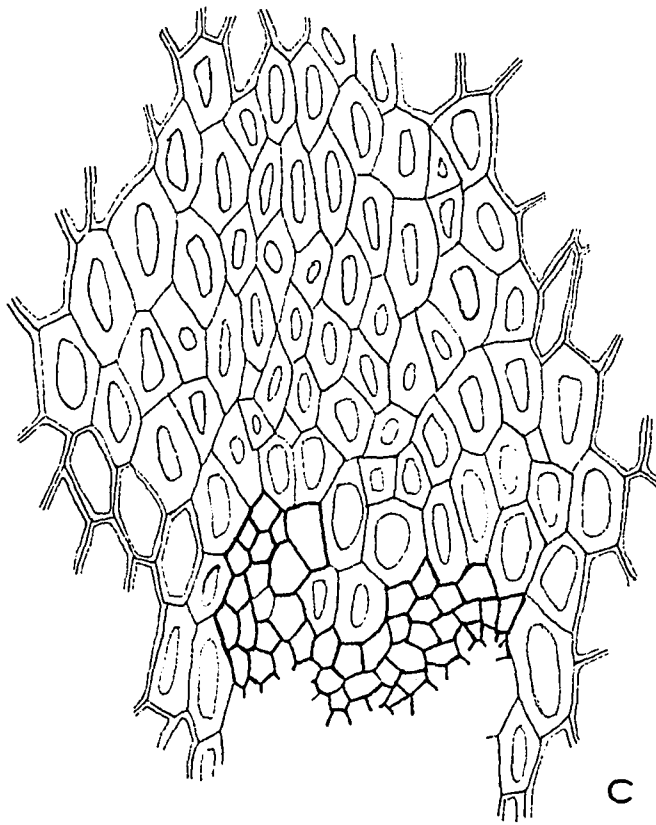
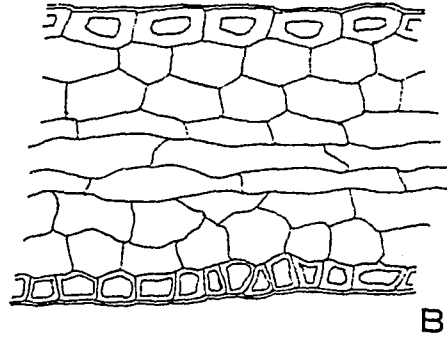
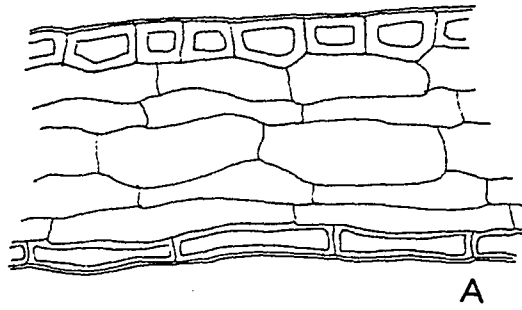
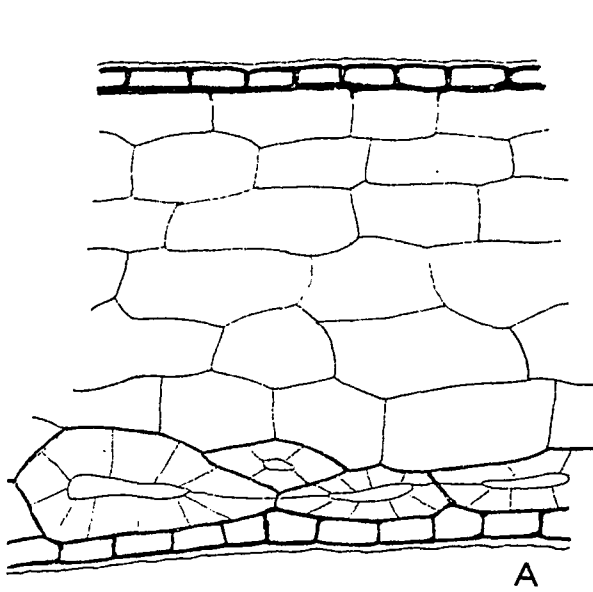
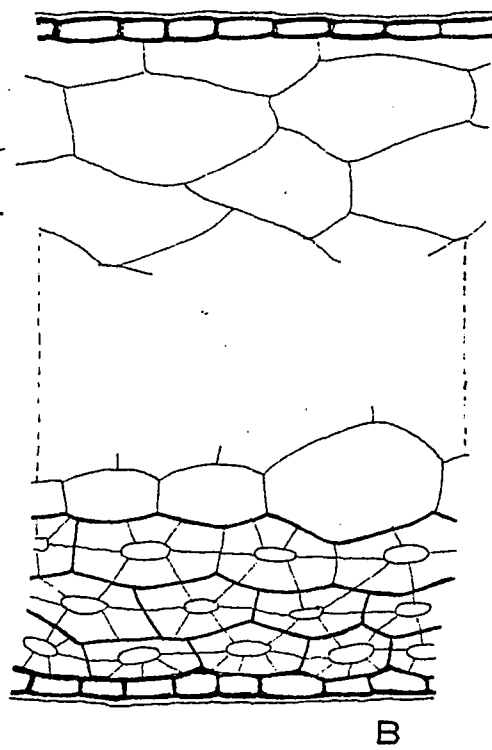


Fig. 16. Fruit anatomy of Dioscorea oppositifolia (sect. Enantiophyllum).

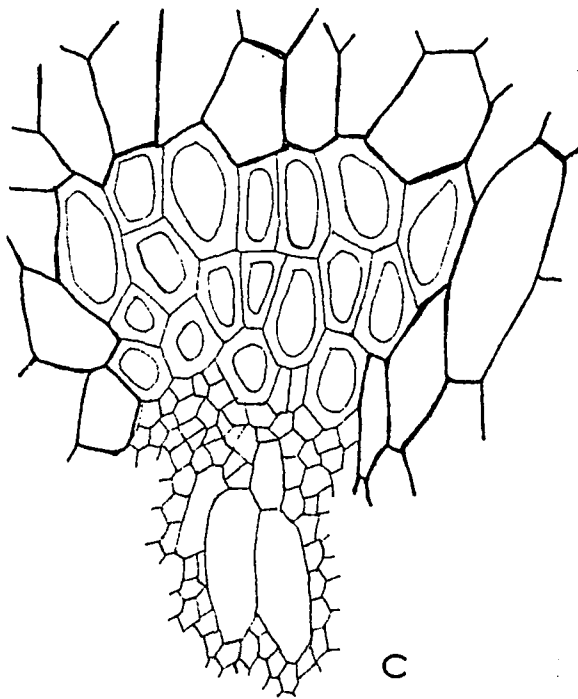
- A. T. S. of wall showing outer and inner epidermal layers with thick-walled cells and inner hypodermis with brachysclereids.
- B. L. S. of the same.
- C. T. S. of upper part of ventral bundle complex showing bundle cap consisting of fibers (x 400).



A



B



C

GEOGRAPHICAL DISTRIBUTION AND ECOLOGY

The genus Discorea is very widespread, extending not only throughout the tropics, but also far into the subtemperate and temperate regions. Nevertheless, the distribution of its various sections is geographically well defined. Disregarding the cultivated species, Stenophora is the only section common to the Old and New Worlds. It is chiefly distributed in eastern Asia but extends to N. America. D. bulbifera, common to Africa and Asia, is the only transoceanic species.

Generally the genus is restricted to altitudes below 2000 m, although some species have been recorded at higher altitudes, e.g. D. deltoidea at c. 3000 m in the Himalayas and c. 3600 m in S.W. China, D. kamoensis up to 4200 m in S.W. China (Prain & Burkill 1936) and D. ancachsensis from the Peruvian Andes at 3800-3950 m (Knuth 1924). Therefore it is evident that the sections Stenophora and Triumphostemon contain some of the most hardy species in Asia in terms of resisting cold temperatures. It is also interesting to note that D. alata grows in cultivation up to about 3000 m in China, an exceptional situation in the otherwise less hardy section Enantiophyllum. Despite its success in high mountainous habitats in northern latitudes, for instance over 30°, the genus shows a marked inability to survive altitudes above 2000 m in more equatorial latitudes, such as 10°.

Prain & Burkill (1936, 1939) made useful observations on the moisture requirements of various species of Dioscorea in Asia. Apparently the temperate or subtemperate species are able to survive with an annual rainfall of 380-500 mm, whereas in tropical situations they need at least 750 mm. Prain & Burkill (1936,1939) also showed that they do not grow in saline soils.

The vast majority of Dioscorea species are twiners, forming an important element of the scrub or forest including tropical rainforest. They are also efficient climbers, rapidly reaching the levels of suitable light conditions in the forest. The features such as annual stems, underground storage organs, twining habit, and broad leaves with long petioles and pulvini are canalized to achieve maximum efficiency in vegetative and reproductive functions of the plant. The adaptations to scrub or forest habitats with reference to seed-dispersal strategies have been briefly discussed earlier. Also the influence of the different habitats on the size and the heights reached by various species has been mentioned.

Evidently a climate that does not reliably provide at least 6 months of adequate humidity and warmth is not suitable for these perennials. Environments approaching such trying conditions have been conquered by certain species of Dioscorea, but not without great modification of their morphological features. They have forfeited the climbing habit and become dwarfed; the dwarfism has already been discussed (see Aerial stem).

There are many dwarf species of Dioscorea in the New World. Apparently their great home is the Pacific slopes of the Andes where they survive open, arid, and rocky conditions. In such barren environments, the wings on the seeds and capsules become less important and hence a tendency is seen towards their reduction, as exemplified by D. humilis.

Extreme dwarfism in the Old World is exhibited by D. pyrenaica (section Borderea), which is adapted to rocky habitats of the Spanish Pyrenees (Fig. 4A). The stem of D. hexagona, a savanna species in Malagasy, does not exceed 40 cm in height. Should it happen to grow on a edge of the savanna, the stems may twine on branches of low shrubs, indicating its twining ancestry.

The tubers of Dioscorea, being rich in starch, attract a variety of herbivores such as rodents and wild boars. Various defense mechanisms such as deep burial of tubers, production of cork on tubers, prickles, thorny roots, and synthesis of poisonous compounds have been discussed elsewhere.

Due to dioecism, species of Dioscorea need external agents to pollinate them, but, information about their pollination is almost non-existent. With glutinous pollen, wind pollination is not likely to occur, flowers are often greenish, nearly white, yellowish, cream, or rarely pink. Floral nectar is not reported, although the fragrance has been recorded in many species, for e.g. D. bulbifera.

CHEMISTRY

Chemical Composition and Nutritive Value

The tuber constitutes the edible portion of the yam. However, in D. bulbifera, the bulbils or "aerial tubers" are mainly used for food. Coursey (1967) compiled the results, obtained by several workers, of the proportions of carbohydrates, fats, proteins, minerals, and moisture content of the tubers of many edible species of Dioscorea. These analyses indicate that the edible yams, like other root or tuber crops, are composed primarily of carbohydrates, and their high water content frequently accounts for about two-thirds the weight of the tuber. The moisture content has been shown to vary to a considerable degree both between species and within a species. It also varies in different parts of the tuber and during its development and the period of dormancy (Clemente 1918, Brown 1931).

The carbohydrates consist mainly of starch, with only small amounts of sugar, usually much less than 1%. Due to the availability of cheaper sources, notably corn and cassava, yams do not afford a promising raw material for the commercial manufacture of starch. The starches of a number of Indian species have been examined by Rao and Beri (1952 a, b; 1953 a, b; 1955), while those of some material grown in Nigeria have been described by Greenwood-Barton (1961) and Osisioqu (1973).

A very comprehensive review of Dioscorea starches was made by Seidemann (1964).

The protein content, as calculated from the total nitrogen, is low, but is not negligible from a dietary point of view. Useful information on the crude protein and constituent amino acids are reported by Takahasi (1928), Hollo (1964), Martin & Thompson (1973), Splittstoesser et al. (1973), and Francis et al. (1975). The fat content, as is usual for tubers, is minute.

Crude fiber and ash contents are distinctly variably, but are generally similar to results obtained with other tubers. The nutritionally important mineral, calcium, has been analysed by several workers and values ranging from 8 to 24 mg/100 g are reported (Winton & Winton 1935, F.A.O. 1954, Greenwood-Barton 1961, Platt 1962). Values of 1.2 and 7.4 mg/100 g for iron (Winton & Winton 1935, Platt 1962) and 41 mg/100 g for phosphorus are also known.

Vitamins, especially vitamin C, occur in yams in quantities large enough to make major contributions to human nutrition in areas where they are extensively consumed (Platt 1962, Coursey & Aidoo 1966).

Like other root and tuber crops, yams are usually regarded as being purely starchy or carbohydrate foods, which supply little but calories to the diet. However, it must be appreciated that when quantities of a single foodstuff as high as 1 kg a day are consumed, the total intake of even of minor constituents may

be high enough to make appreciable contributions to the nutrition of the consumer. In this context, yams, in addition to their caloric value, are also significant sources of iron, thiamine, vitamin C, and, to a lesser extent, protein, calcium, riboflavin and nicotinic acid.

There is comparatively little taxonomic variation in composition among the main edible species, the degree of variation within one species being about as great as between species. So few analytical data are available, however, that it would be premature to draw any definite conclusions.

Secondary Chemical Compounds

Apart from man, animals such as hogs, hedgehogs, rodents, yam beetles, and nematodes consume the tubers, and perhaps the rhizomes, of various species of Dioscorea. The synthesis of toxic substances by some species of the genus is one of the most effective means of protecting themselves from these herbivores. Many phytotoxins, belonging to various classes of compounds, have been found to occur in various species of Dioscorea.

Alkaloids

Although alkaloids have been detected in several species of Dioscorea in Asia and Africa (Willaman et al. 1953), appreciable amounts of these compounds are known to occur only in a few species. D. hispida contains extremely poisonous dioscorine

(C₁₃ H₁₉ O₂ N) which produces general paralysis of the central nervous system, the effects resembling those of picrotoxins (Pinder, 1951, 1952, 1953). A similar compound (C₁₃ H₂₁ O₂ N), supposedly dihydrodioscorine, has been isolated from D. dumetorum and it has been suggested that the compound is a mixture of stereoisomers of dihydrodioscorine (Bevan et al. 1956, Bevan & Hirst 1958). Like dioscorine, dihydrodioscorine is toxic, acting as a convulsant poison, although the toxicity appears to be less intense than in the former.

Flavonoids

Among the Indian species of Dioscorea, flavonoids have been detected in the leaves of D. pentaphylla (Kapoor et al. 1975), and their absence has been demonstrated in D. bulbifera, D. deltoidea, D. glabra, and D. melanophyma (Kapoor 1969). However, the identity of these flavonoids and their relative quantities in different species are not known.

The pale yellow color of the tubers most forms of D. cayenensis is probably due to the presence of traces of carotenoids. Beta-carotene reportedly occurs in D. alata (Ruberte 1975) and the pinkish, reddish or purple color of the tubers of certain forms of this species is imparted by anthocyanins, e.g. cyanidin-glycosides, principally cyanidin-3, 5-diglucoside (Rasper & Coursey 1967). The colored tubers of some forms of D. trifida, and possibly other species, probably derive their color from similar compounds.

The tuber-tissue of many forms of such species as D.alata and D. rotundata rapidly becomes brown when exposed to air. This reaction is due to the enzymatic oxidation of polyphenolic compounds. The main substance responsible for browning is a catecholamine, with two weakly-oxidizable leucoanthocyanidins occasionally present (Martin & Ruberte 1976).

The presence of large quantities of tannins (6.4%) in D. cirrhosa has been mentioned by Burkill (1935), and Endres et al. (1962) report a quantity of tannins as high as 38% (dry weight) in a dark-red fleshed form of D. alata.

Terpenoids

Color reactions, solubilities, and UV-absorption spectra of bitter and related non-bitter compounds from tubers of D. bulbifera showed them to be terpenoids and they appear to be related to furanoid nor-diterpenes. Different forms of D. bulbifera varied in bitterness, but all contained both bitter and non-bitter compounds (Telek et al 1974).

Saponins and steroidal sapogenins

Saponins are easily detected by the formation of soapy lather in water. They can also be tested by hemolytic reaction, in which blood cells become ruptured and release hemoglobin into the surrounding fluid, when saponins are added to a suspension of blood cells.

A saponin molecule is a complex polycyclic system linked

through oxygen with a glucoside unit. On acid, alkali, or enzymatic hydrolysis it yields a free sugar and an aglycone which is called a sapogenin. Three sapogenins that have been isolated from many species of Dioscorea are diosgenin, botogenin, and kryptogenin.

Interest in these steroidal sapogenins has developed rapidly during the last few decades due to their close relationship to various hormones of the human body, especially various sex hormones and corticosteroids such as cortisone. The corticosteroids are used as anti-inflammatory agents, metabolic stimulents, and general stress-reaction protectives, while modifications of sex hormones form the basis of oral contraceptives (Applezweig 1962). The synthesis of these hormones using sapogenins, especially diosgenin, as starting materials has been developed (Applezweig 1962, Fieser & Fieser 1959).

Numerous species of Dioscorea have been found to contain sapogenins (Marker et al. 1943; Barua et al. 1954,1956; Tsukamoto & Kawasaki 1954; Wall et al. 1954a, 1954b, 1955, 1957, 1959,1961; Correll et al. 1955; Kichenko 1961; Akahori 1965; Tien-Hsi Cheng 1965; Kapoor et al. 1969). The greatest developments have taken place in Mexico, while some species in Central America, S.Africa, India and China also have been exploited for the same purpose.

An attempt to elucidate the biosynthesis of diosgenin has been made by Heftmann et al. (1961) and the isolation of

sapogenins from the tubers has been described by Applezweig (1962) and A.J. Feuill in Coursey (1967). The distribution and selection of high yielding species, their propagation, culture and harvesting have been dealt in Correl et al. (1955).

Use of secondary chemical compounds in taxonomy

The presence and absence of certain secondary phytochemical compounds have been used to substantiate the phylogenetic overview of angiosperm families, especially the monocotyledons (Dahlgren 1982). However, it is difficult to support or challenge the phylogenetic relationships, on a comprehensive scale, within the Dioscoreaceae on biochemical data due to the paucity of such information.

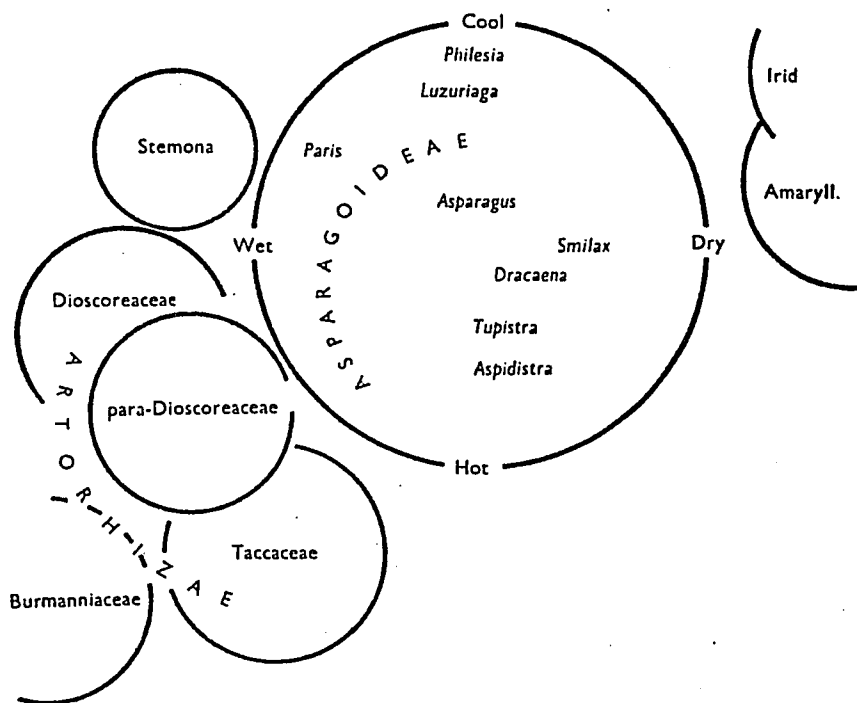
The available data on alkaloids indicate the affinity of such species as D. hispida, D. dregeana, and D. dumetorum, belonging to the section Lasiophyton. This further support the separation of this section from Triephorostemon, which lacks any appreciable quantities of similar alkaloids. The occurrence of traces of alkaloids in D. alata and D. elephantipes is reported (Coursey 1967); however, without further information on the identity and the biosynthesis of these compounds, no conclusions are possible. The synthesis of saponins in numerous species of Dioscorea suggests the phylogenetic affinity among these species. However, insight into genetic homology and the biosynthetic pathways of these compounds is much desired to make definite conclusions about the phylogeny within the genus.

PHYLOGENY AND EVOLUTION

The Dioscoreaceae undoubtedly belong to the order Liliales sensu lato (Cronquist 1981). However, due to extreme heterogeneity of the vegetative organs, the assignment of individual families and genera within this order has generated many discrepancies (de Jussieu 1789, Ventenat 1799, Endlicher 1836, Baillon 1895, Hutchinson 1973).

Solm-Laubach (1878), Baillon (1895), Uline (1898) and Knuth (1924) indicated the closeness of Dioscoreaceae and Amaryllidaceae to each other in their general morphology and embryology. Burkill (1960) did not accept this view and pointed out that Dioscoreaceae, Stemonaceae, and Taccaceae are phylogenetically linked. He further indicated that the origin of the Dioscoreaceae has its roots in the ancestry of the subfamily, Asparagoideae of the Liliaceae. The supposed inheritance of the rhizomes of the other Old World genera of Dioscoreaceae, namely, Averta, Stenomeris, and Trichopus, from the rhizomatous ancestors of "proto-Liliales" supports the link between the Dioscoreaceae and Asparagoideae (Fig. 18). Therefore, the rhizomatous section Stenophora of the genus Dioscorea is presumed to be archaic. As suggested by the distribution of this section and also the exclusively eastern distribution of Averta, Stenomeris, and Trichopus and allied families Taccaceae and Stemonaceae, an eastern origin of the Dioscoreaceae seems

Fig. 17. Phylogenetic diagram showing affinities of the
Dioscoreaceae (after Burkill 1960).



probable. This view is further supported, as genera of the Asparagoideae of closest affinity, such as Paris and Aspidistra, are also predominantly eastern.

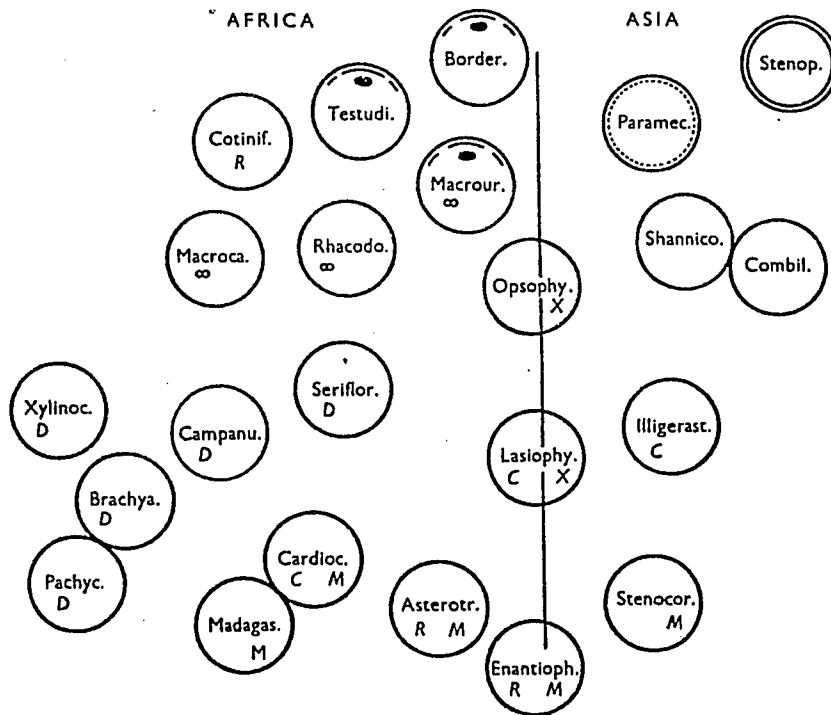
Phylogeny within the genus Dioscorea is evidently complicated. Burkill (1960) provided a diagrammatic presentation of the 23 Old World sections of the genus indicating the possible relationships between various sections (Fig. 19). He primarily separated the Asian and African sections with common ones in the center. The type of the seed-wing, deeply buried tubers, direction of twining and the presence of compound leaves were also indicated in the diagram.

It is believed that convergence occurred in some vegetative and reproductive organs within the genus and, such features, therefore, do not reliably indicate the phylogeny. Therefore, some taxonomic relationships and phylogenetic affinities, postulated by Kunth (1850), Uline (1897), Knuth (1924), and Burkill (1960), are not here accepted. For instance, the relationship between the sections Trieuphorostemon and Lasiophyton is much more distant than what was formerly believed. Although both sections have palmately compound leaves and proximally directed seed-wings, several other morphological, anatomical, and chemical features indicate their distance from each other. The direction of the seed-wing cannot be used to assemble subgenera due to possible parallelism (see Fruits and Seeds). Furthermore, the direction of twining is probably liable

to be reversed as species differing in this character exhibit uniformity in several other features, e. g. D. bulbifera and D. inopinata (sect. Opsophyton).

Fossils of Dioscoreaceae are meagerly known. The only Cretaceous fossil which is claimed to belong to this group is D. cretacea from Dakota, U.S.A. (Lesquereux 1874). However, its identity is questionable (Zittel 1890, Knowlton 1919, Burkill 1960). The Tertiary leaf impressions of Dioscorites resurgens and Dioscorides lyelli from western Europe are apparently dioscoreaceous (Potonie 1921), and the latter resembles the leaves of some extant species of Stenophora (Burkill 1960). Nevertheless, the Cretaceous age of the genus is evident from abundance of its extant species in Africa and S. America. Geologists and biographers believe that the Atlantic Rift parted the West Gondwanaland in the Upper Cretaceous, and direct overland migration between the resultant land masses, namely Africa and S. America, was possible until the Cenomanian Stage, i.e. 95-90 million years ago (Howarth 1981). After this initial division, the genus apparently evolved on either side of the S. Atlantic. This is clear by the absence of species or sections common to both regions. However, the validity of this view should be further reviewed by comparative systematic studies, especially in the light of enhanced knowledge of the neotropical species of the genus.

Fig. 18. Relationship of Old World sections of Dioscorea according to Burkill (1960). C, compound leaves; D, deeply buried tubers; M, mid-placenta; X, proximally-directed seed-wing.



The eastern Asian and N. American distribution of the section Stenophora indicates its Laurasian origin, and furthermore its diversity in Asia implies a Eurasian history. The antiquity of the section is supported by the Eocene fossil records (Potonie 1921, Burkill 1960), and its characteristic rhizome which most phylogenists consider to be more primitive than the tuber. Its extension into N. America most probably occurred when direct migration between Eurasia and N. America was possible throughout the Tertiary (Raven & Axelrod 1974).

It is postulated that the section Stenophora survived under subtemperate and temperate climates while other rhizomatous ancestors in the West Gondwanaland rapidly became extinct under tropical environments. The rare occurrence of one or a few rhizomatous species, e.g. D. perdicum, in S. America, under subtropical conditions, indicates possible relicts. The tuberous species are presumedly independently evolved and consequently the tuber, which is regarded to be an advanced feature, facilitated the great diversity and adaptive radiation of the genus. Burkill's (1960) view, that the rhizomatous Dioscorea migrated from Eurasia across a bulk of the West Gondwanaland during the Cretaceous, is apparently not plausible.

Burkill (1960) speculated that the sections of Dioscorea originated prior to the Miocene, but almost every extant species originated from the Miocene onwards. D. bulbifera, which is widely distributed in Asia and Africa, is supposed to be the only

extant species that occurred in the Miocene. Its success is attributed to the high rate of reproduction (both sexually and asexually), precocity, and small seeds which are shaped for efficient dispersal.

It is believed that in the Miocene the climate was mild, with adequate humidity and warmth, and it supported a rich growth of plant life in most parts of the earth (Raven & Axelrod 1974). Therefore the existence of a rich vegetational continuum between Africa and Asia was very probable. However, the events which followed the Miocene caused an increasing aridity in most parts of Africa and adjacent regions in Asia. Raven & Axelrod (1974) discuss events like the upwarp of the African continent which is continuing to the present as the rift valleys continue to grow, and the development of a volcanic field in the eastern Africa, which increased the rain-shadow effect and caused great drought and temperature extremes. The fluctuations of the Quaternary climate also had an important effect on the African tropical rainforest flora, with the drier phases being times of extinction of taxa that required more nearly ever-wet conditions. Dioscorea, among many other genera, became extinct in this region as indicated by the notable gap between India and Central Africa.

Relative high diversity of the flora and the endemism in Malagasy is associated with its separation from Africa as early as the Lower Cretaceous, probably during the Hauterivian Stage, ca. 110 million years ago (Howarth 1981). It was thus not

subjected to the effects of spreading aridity and mass extinction that occurred on mainland Africa. The peculiar genus Averta and several sections of Dioscorea, such as Brachyandra, Cardiocaspa and Madagascarienses are among many taxa endemic to Malagasy.

ECONOMIC IMPORTANCE AND DISTRIBUTION OF YAMS

Introduction

The term "yam" is often used for many nondioscoreaceous plants that produce edible starchy roots, tubers, corms, or rhizomes, e.g. Ipomoea batatas, Colocasia spp., Alocasia spp., Xanthosoma spp., Maranta arundinacea, Amorphophallus campanulatus etc. As all these crop plants have adequate common names to distinguish them, it seems that the use of "yam" to describe them is only a source of confusion. Guided by Coursey's (1967) definition, it is recommended that the use of the term "yam" be restricted to genera of Dioscoreaceae that produce economically useful tubers, rhizomes, or bulbils.

Of all the food crops of the tropics, few are quite so widespread as the yams. They provide the staple foodstuff for millions of people in many tropical and even some subtropical countries, and are an important secondary food for many millions more. Apart from yams that are cultivated for food crops, wild yams form a reliable standby to further large human populations in times of famine or scarcity. In recent years, some of the yams have also been providing useful pharmaceutically active compounds to modern medicine, as they have done to traditional medicine for centuries past. There is hardly any tropical country, apart from the most arid, where yams are not used to some extent, although their large-scale cultivation as food crops is

restricted largely to three main areas of the world, namely, W. Africa; S.E. Asia including adjacent parts of China, Japan, and Oceania; and the Caribbean (Coursey 1967).

Although the genus Dioscorea contains over 600 species (Knuth 1924), the edible yams are provided mainly by ten: D. alata (Greater Yam, Water Yam), D. bulbifera (Potato Yam, Aerial Yam), D. cayenensis (Yellow Yam), D. dumetorum (Bitter Yam), D. sativa (Lesser Yam, Chinese Sweet Potato), D. hispida, D. japonica, D. opposita (Chinese Yam), D. rotundata (White Yam), and D. trifida (Cush-cush Yam). Most of the edible species are tuberous, and in majority of them the tubers are renewed annually, but in some others they are perennial, and mature plants may even be woody. Above ground, the growth is almost invariably annual, and consists, in most species, of a twining stem which requires support from neighboring vegetation or from stakes.

Agriculturally, the edible yams are field crops, which, although perennial, are treated as annual plants. They are harvested every season, sometimes more than once in a season, and replanted every year. Invariably, small "seed-tubers" or pieces of tubers are used to regenerate the crop, rather than actual seed, in much the same manner as potatoes. Although they are essentially crops of humid to semiarid areas, they could be cultivated in climates in which the dry season is long, if a substantial amount of water is provided during their growing

season for the development of tubers. They are poorly adapted to modern techniques of mechanized agriculture and are essentially crops of peasant farmers, who cultivate entirely by manual methods. Such farmers individually cultivate small acreages, and very substantial proportions of their crops are consumed by themselves, or by their neighbors. The yams thus belong primarily to subsistence, rather than to commercial agriculture. Various aspects of agriculture including agronomy, economics, pests and diseases, production, utilization, storage, and processing of yams have been amply described by Coursey (1967).

Early cultivation and distribution by man

Yams certainly provided an important source of food to prehistoric man. However, the process by which the yams were introduced into cultivation must have been different from those which took place in the case of the familiar grain crops of the temperate and Mid-east countries. The dates at which yam-based agriculture evolved in various parts of the world are uncertain, as tuber crops, such as yams, leave no archeological evidence of their use comparable to the extensive traces of early grain use, in the form of pottery impressions and actual desiccated grains (Coursey 1967).

Coursey (1967) believed that there are four distinct centers of origin for the edible yams: (1) Somewhere in Indo-China, where D. alata, D. pentaphylla, and probably D. sativa,

D. bulbifera, and some other species of minor importance were brought to cultivation; (2) a center in southern China, where the more temperate-adapted species, D. opposita and D. japonica, and possibly D. sativa, originated; (3) a location on the fringe of the W. African forest belt where D. cayenensis, D. rotundata, and D. dumetorum originated, with perhaps a subsidiary center in or near the Congo basin; (4) The Caribbean area where D. trifida and probably some other less important species of Dioscorea and Rajania originated; there may have been a subsidiary center in S. America.

It is generally accepted that the cultivation of a number of food yams originated in S.E. Asia, probably Burma or Thailand. Burkill (1935) suggested that D. alata originated to the east of Bay of Bengal. Although this species is unknown in the wild state, its allied species, namely, D. hamiltonii occurs naturally in Burma, Assam, and in other neighboring regions. D. sativa reportedly occurs wild in Thailand (Prain & Burkill 1936).

The little historical evidence available shows that yam cultivation in S.E. Asia must be at least about 2000 years old. Although yams must have been grown in India at a considerably earlier period, the first traceable reference in classical Indian literature is in the Susruta Samhita of between 600 and 700 A.D. This work describes yams as being grown for food in the Ganges basin (Prain & Burkill 1936, Burkill 1951). Burkill (1960)

suggested that the yams, together with aroids such as Colocasia, were first domesticated by fishing communities in S.E. Asia.

It has been suggested that the yam cultivation may have begun in Africa as early as 5000 B.C. This suggestion is based on the view that at that time, a culture using heavy stone hoes, which would be well adapted for the digging of tubers, began to spread out of the equatorial Africa to other parts of sub-Saharan regions. As the northern parts of the continent became more desiccated, about 2000 B.C., the hoe-using people were forced southward into the forest zone of W. Africa, taking the now partially domesticated savanna species of yams with them.

The spread of D. alata from its original area of cultivation, through S.E. Asia and Indo-China and across the S. China sea to the Indonesian islands has been described by Burkill (1951). The wide distribution and the profusion of cultivators in the eastern parts of Indonesian Archipelgo, such as Borneo, Sulawesi (Celebes), and New Guinea indicates an establishment of a secondary center of distribution, from which yams spread to the more southern parts of Indonesia, and through New Guinea, the Solomon Islands, Fiji, and Samoa to Polynesia and the rest of the tropical Pacific. The date of the dispersion of the yam into the Pacific is uncertain, but is certainly earlier than European contact with the area (Coursey 1967).

It is believed that D. alata was introduced to Malagasy and the E. African mainland across the Indian Ocean by the

Indo-Malayan people (Burkill 1951). This migration occurred either in the first or second centuries A.D., or between the eleventh and fifteenth centuries, as supposed by different historians.

The origin of yam cultivation in the western hemisphere is obscure, except that it is almost certainly pre-Columbian, and probably dates back to the pre-Mayan period (Chevalier 1946). A number of species of Dioscorea and the closely related Rajania were used for food by the Amerindians of the Caribbean in pre-Hispanic times, though to what extent they were actually cultivated is not known. The cultivation of what is presumably D. trifida ('Aje') is referred to by Columbus, and this plant was certainly cultivated by the earliest Europeans and African immigrants in that region (Coursey 1967).

The cultivation of D. opposita and D. japonica is appropriately assigned to the Chinese center of origin, and it is known that the medicinal use of some members of Dioscorea has been mentioned in the earliest Chinese medical documents before 2000 B.C., as quoted by de Candolle (1886). The cultivation of D. sativa as a food plant in China in the third century A.D. is referred to by Ting & Chi (1948).

References to yams have not been identified among ancient Egyptian writings, or in those of the various Mesopotamian or Near Eastern civilizations; also there are no known references to edible yams in early Arabic literature (Coursey 1967). The

yams were unknown in the Mediterranean world of the classical era, as, indeed, they are still virtually unknown in that region to this day due to unsuitable climatic conditions.

Distribution by man in historic times

The distribution of D. alata in the world is amply described by Burkill (1951). Yams became soon familiar to the European mariners travelling to Africa, Asia, and the New World in the fifteenth and sixteenth centuries. The Portuguese introduced D. alata from Indo-Malaya to W. Africa. They also encountered D. rotundata and D. cayenensis, which were already in cultivation in Africa. It appears that these mariners preferred D. alata to the W. African species. With the establishment of Spanish colonies in the Caribbean and the concomitant slave-trade from Africa, D. rotundata and D. cayenensis were soon cultivated in the West Indies. By the end of the sixteenth century, D. alata was being grown in W. Africa to a sufficiently large extent to be used for the provisioning of the ships and it was thereby introduced to the New World. It was certainly widely cultivated there by the middle of the seventeenth century (Burkill 1938).

The spread of the other edible Dioscorea species is less well known. D. sativa is unlikely to have been used in early days, as it does not keep well during long journeys in the sea; nevertheless, it has become established in America. The African form of D. bulbifera also appears to have been carried to

America in the early days of the slave-trade. The inferior, and frequently toxic, D. dumetorum and D. hispida seem never to have left Africa and Asia respectively. D. trifida is the only American species to be cultivated outside that continent. At present it is grown on a small scale in the northern part of Sri Lanka, where it was possibly introduced by the Portuguese in the sixteenth century.

Relative decline of yam cultivation in certain areas

The discovery of America initially gave, in various ways, an impetus to the extension, on the global scale, of yam cultivation, but subsequently it has resulted in a relative decline in the importance of this crop. The introduction, from the New to the Old World, of food crops, such as potatoes (Solanum tuberosum and related species), sweet potatoes (Ipomoea batatas), taros or cocoyams (Xanthosoma sagittifolium), and, most important, manioc or cassava (Manihot utilissima) rapidly replaced the yams. All these crops were introduced to various parts of the world within a few decades of the discovery of America (Coursey 1967).

Potatoes are more important as temperate, rather than as tropical crops, and therefore have not provided much competition to yams, although in recent decades they have begun to do so in the cooler parts of India and Sri Lanka. However, sweet potatoes, cocoyams, and to a much greater extent cassava, were

responsible for the decline of yam cultivation in Asia, Africa, and Malagasy, especially during the present century (Burkill 1951).

Uses other than as food

Apart from the usefulness as a source of biologically active compounds or their precursors (see Chemistry), yams are mainly utilized as food in various ways. A number of minor applications, however, may be mentioned. Many members of Dioscorea are used in traditional medicine in Asia (Watt 1890, Burkill 1935) and Africa (Watt & Breyer-Brandwijk 1962). The N. American species D. villosa and possibly some others were used by early European settlers in the treatment of internal disorders, from which use their vernacular name in United States, "Colic Root", is derived (Bartlett 1910).

Various uses of Dioscorea spp. containing poisonous principles, such as saponins and alkaloids, have been mentioned by many other authors (Watt 1890, 1908; Prain & Burkill 1936, 1939, Coursey 1967). A decoction of rhizomes of D. deltoidea is used as a shampoo, in northern India and adjacent regions, to destroy lice, and it is also used to wash wool and silk. Similar insecticidal properties are found in D. piscatorum in Malaysia; it is also used as a fish poison and to destroy rice parasites in paddy fields. The high toxicity of D. hispida in Asia, and D. dumetorum, in Africa, has been used for criminal purposes and also to poison wild animals like tigers, monkeys, and fowls.

The use of these species in the preparation of arrow poison is also reported.

D. cirrhosa contains a high proportion of tannin (6.4 %) and hence is used by the fishing peoples of Indo-China for the preservation of fishing lines, nets and sails (Burkill 1935).

SYSTEMATIC TREATMENT

DIOSCOREA Linnaeus, Sp. pl. 1032. 1753; Endlicher, Gen. pl. 158. 1836; Kunth, Enum. pl. 5: 325. 1850; Bentham & Hooker, Gen. pl. 3: 742. 1883; Pax in Engler & Prantl, Nat. Pflanzenfam. II. 5: 133. 1888; Knuth in Engler, Pflanzenr. 87(IV. 43) 45. 1924, in Engler & Prantl, Nat. Pflanzenfam. II. 15a: 445. 1930; Prain & Burkill, Ann. Roy. Bot. Gard. Calcutta 14: 1. 1936; Burkill, Fl. Males. 4: 299. 1951. Lectotype: Dioscorea sativa Linnaeus, chosen by Britton & Brown, III. Fl. N. V. S. ed. 2. 1: 535. 1913.

Dioscoridesa Cothenius, Disp. veg. meth. 16. 1790 (orth. var.).

Ubium Cothenius, Ibid. 25. 1790. Type: not chosen.

Oncus Loureiro, Fl. Cochinch. 194. 1790. Type: Oncus esculentus Loureiro = Dioscorea sativa Linnaeus

Oncorrhiza Persoon, Syn. pl. 1: 374. 1805. Type: Oncorrhiza esculentum Persoon = Dioscorea sativa Linnaeus

Testudinaria Salisbury in Burchell, Travels S. Africa 2: 147. 1824. Lectotype: Testudinaria elephantipes Salisbury in Burchell, chosen by Phillips, Gen. S. Afr. Fl. Pl. ed. 2. 208. 1951 = Dioscorea elephantopus Sprengel

Botryosicyos Hochstetter, Flora 27 (Bes. Beil. Bd. 1): 3. 1844. Type: Botryosicyos pentaphyllus Hochstetter

Helmia Kunth, Enum. pl. 5: 414. 1850. Type: not chosen.

Sismondaea Delponte, Mem. Acad. Sci. Torino II. 14: 394.

1854. Type: Sismondaea dioscoreoides Delponte

Epipetrum Philippi, Linnaea 33: 253. 1864. Type: Epipetrum

humile (Bertero & Colla) Philippi = Dioscorea humile

Bertero & Colla

Borderea Miegville, Bull. Soc. Bot. Fr. 13: 374. 1866.

Type: Borderea pyrenaica (Bubani & Bodere in Grenier)

Miegville = Dioscorea pyrenaica Bubani & Bodere in

Grenier

Humatris Salisbury, Gen. pl. 11. 1866. Type: Dioscorea

triphylla Linnaeus

Merione Salisbury, Ibid., 12. 1866. Type: Dioscorea villosa

Linnaeus

Polynome Salisbury, Ibid., 12. 1866. Type: not chosen

Strophis Salisbury, Ibid., 12. 1866. Type: Discorea cirrhosa

Loureiro

Elephantodon Salisbury, Ibid., 12. 1866. Type: Dioscorea

eburnea Loureiro

? Androsyne Salisbury, Ibid., 61. 1866. Type: Dioscorea

gracilis Salisbury

Higinbothamia Uline, Publ. Field Columbian Mus. Bot. I. 412.

1899. Type: Higinbothamia synandra Uline

Nanarepenta Matuda, Anales Inst. Biol. Univ. Nac. Mexico 32:

142. 1962. Type: Nanarepenta toluicana Matuda

Perennial, twining or relatively dwarf or erect herbs, arising from a starchy rhizome or much more often from a hypogeous, or seldom epigeous tuber that grows due to annual increments from a continuous or discontinuous growth zone within; plants, especially the underground parts, often accumulating varying amounts of saponins and sometimes alkaloids and tannins, rarely containing terpenes. Stems annual to perennial, often suffrutescent, sometimes prickly; vascular bundles relatively few, in 2 dissimilar cycles, or in a single cycle of 2 alternating types; secondary growth lacking, except in the tuber; vessels present in all vegetative organs or sometimes absent in the leaf-blades and rhizomes, sometimes with scalariform perforations; plastids of the sieve tubes with cuneate proteinaceous inclusions; nodal anatomy complex due to the presence of xylem- and phloem glomeruli in the nodes. Leaves alternate or sometimes opposite, the petiole with a pulvinus at each end, twisted or jointed and often with stipule-like flanges on either side of the base; blade often broad, cordate at the base, entire to less often palmately lobed or cleft or even compound, sometimes with "superficial" or internal glands or nectaries, some of which harbor bacteria capable of fixing nitrogen; the primary veins 3-13, acrodromous or campylodromous (pinnate in leaflets of some compound leaves), curved-convergent, traversed by a network of smaller veins; stomates mostly anomocytic. Flowers small, unisexual (the plants dioecious),

variously in racemes, spikes, or panicles, arranged singly or in 2 or 3-flowered cymes, sessile or rarely pedicelled, regular, epigynous, trimerous; tepals 6 in 2 cycles, distinct or connate at base into a short tube; stamens 6 in 2 cycles, the inner set sometimes staminodial or obsolete; filaments free or adnate to the base of the perianth tube; anthers introrse or rarely extrorse, tetrasporangiate and dithecal, sometimes well separated on the broad connective; pollen grains binucleate, monosulcate to less often disulcate or trichotomosulcate; gynoecium tricarpellate, syncarpous; ovary inferior, trilocular, with axile placentation; styles short, distinct or connate with separate, usually lobed stigmas; ovules 2 (rarely more) in each locule, anatropous, bitegmic, crassinucellar; endosperm-development nuclear. Fruit capsular, often triangular and 3-winged, loculicidal; wings seldom reduced. Seeds variously winged; wing sometimes reduced; embryo small but well differentiated with a lateral or subterminal plumule, a broad, terminal cotyledon and a scale-like second cotyledon, axially embedded in the copious, very hard, medially split endosperm with food reserves of protein, oil, and hemicellulose, the latter in the thickened cell walls.

Distribution. Dioscorea, the largest genus of the Dioscoreaceae, consisting of over 600 species (sensu Knuth 1924), is cosmopolitan, being widespread in tropics and subtropics, with relatively few species extending into the North Temperate

regions. None of its species, however, is naturally common to the Old and the New Worlds, and there is only one member which is common, without the aid of man, to the continents of Africa and Asia. S. America, especially its tropical zone, is apparently the richest in species of Dioscorea. Several species have long been cultivated, especially in Africa and Asia, for their edible tubers and introduced to many other regions. Pharmaceutical interests, developed during recent decades, have prompted the cultivation of some species yielding appreciable amounts of steroid sapogenins.

Key to the sections of Dioscorea in the
Indian Subcontinent

1. Underground stem rhizomatous. Stem sinistrorse. Leaves simple. Staminate flowers in 2-4-flowered cymules (Reduced to one at apex). Tepals connate at the base to form a shallow to deep cup. Capsules reflexed; broader than long. Seed-wing usually circumferential. Stenophora

1. Underground stem tuberous. Stem sinistrorse or dextrorse. Leaves simple or compound. Staminate flowers arranged singly or very rarely in 2 or 3-flowered cymules. Tepals distinct or connate at the base. Capsules reflexed or erect, of variable shapes. Seeds-wing circumferential or from one side.

2. Stem sinistrorse. Hairs, if present, not of stiletto or or dendroid type. Leaves simple or compound. Capsule reflexed, longer than broad; wings \pm elliptic, dehiscing at apex. Seed-wing proximal and directed toward base or circumferential.

3. Tubers several, distinctly stalked. Leaves simple. Bulbils absent. T-shaped hairs present. Staminate flowers in spikes, arranged singly or rarely in cymules; tepals connate to form a cup-shaped base.

Dioscorea

3. Tubers one to few, not distinctly stalked. Leaves simple or compound. Bulbils present or absent. T-shaped hairs absent. Staminate flowers in spikes or commonly in panicles, arranged singly. Tepals distinct.

4. Leaves simple. Hairs 1-celled and finger-like or absent. Tepals over twice as long as wide.

Opsophyton

4. Leaves palmately compound. Hairs common, usually 2-celled, long and tapering. Tepals less than twice as long as wide.

5. Leaves 3-5-foliolate; primary veins eucamptodromous (acrodromous in outer halves of outermost leaflets). Staminate flowers pedicelled, generally loosely arranged on the axis of inflorescence without a distinct distal flowering zone; fertile stamens 3; anther lobes distinctly separated by connective. Capsule not exceeding 3 x 1.5 cm. Triephorostemon

5. Leaves 3-foliolate; primary veins acrodromous basal. Staminate flowers sessile, usually densely aggregated in the distal flowering zone along the inflorescence; fertile stamens 6; anther lobes not widely separated from each other. Capsule exceeding 3 x 2 cm. Lasiophyton

2. Stem dextrorse. Hairs, if present, of stiletto or dendroid type. Leaves simple. Capsule erect, broader than long; wing \pm round, dehiscing all round. Seed-wing circumferential. Enantiophyllum

Dioscorea sect. Stenophora Uline in Engler & Prantl, Nat.

Pflanzenfam. II. 5. 84. 1897, as subg. Helmia sect. Type:
Dioscorea tenuipes Franchet & Savatier (lectotype chosen
here).

Dioscorea subg. Eudioscorea sect. Macropoda Uline, Ibid.,

II. 5. 85. 1897. Type: Dioscorea villosa Linnaeus

Dioscorea subg. Testudinaria sect. Stenophora Uline in

Engler, Bot. Jahrb. 25: 157. 1898. Type: not chosen.

Dioscorea subg. Eudioscorea sect. Orientali-asiaticae Knuth,

in Engler, Pflanzenr. 87 (IV. 43): 252. 1924. Type:

Dioscorea gracillima Miquel

Dioscorea subg. Eudioscorea sect. Japonicae Knuth in Engler,

Ibid., 87 (IV. 43): 254. 1924. Type: Dioscorea

asclepiadea Prain & Bukill

Rhizome creeping horizontally beneath the surface of the soil, poisonous due to appreciable quantities of saponins. Stem sinistrorse. Leaves alternate, simple, entire or lobed. Hairs, if present, unicellular. Staminate flowers sessile or pedicelled, in 2-4-flowered cymes (reduced to one toward apex) arranged on long spikes; tepals connate the base, forming a distinct perianth tube, extrorse in outer cycle and, if present, introrse in inner cycle. Capsule reflexed, usually broader than long, dehiscent only at apex leaving a trifurcate aperture. Seeds winged circumferentially, and often, unequally broadened.

Distribution. This section includes about 30 species which are predominantly temperate and subtropical in distribution. They occur mainly in eastern Asia, extending westward along the Himalaya, with 2 adjunct species in eastern Europe. A few species are found in eastern N. America, and hence this is the only section of Dioscorea that is common to both the Old and the New Worlds.

The chief salient feature of this section is its rhizomatous underground stem which grows horizontally beneath the surface of the soil. The presence of cymules and the connate tepals are also important distinguishing features. Uline's sections, namely, Stenophora and Macropoda do not differ from each other to any considerable degree and should be united. Knuth (1924), while combining them into Macropoda, created a subgenus Stenophora in which the section Eustenophora was placed to accomodate those species with oblong capsules. and seeds whose wings are directed toward the apex of the capsule. Knuth's idea is essentially accepted here, although these two sections should have been united into Stenophora, while the necessity of creating a new subgenus is being challenged. Knuth also proposed 2 additional sections, namely, Orietali-asaiaticae and Japonicae. As the charater used to differentiate them from Macropoda, namely, the shape of the capsule, is variable within these sections, their union into Stenophora is suggested.

Key to the species of Dioscorea sect. Stenophora
in the Indian Subcontinent

1. Petiole longer than half the length of the blade; blade truncate to cordate or hastate at base, green above, glaucous-green and pubescent on veins below. Staminate flowers sessile; perianth lobes scarcely longer than tube, membranous, reflexed at anthesis, drying whitish to fawn.

1. D. deltoidea

1. Petiole shorter than half the length of the blade; blade cordate at base, glossy green and glabrous on both surfaces. Staminate flowers pedicelled; perianth lobes at least twice as long as the tube, firm, ± erect, drying brown.

D. prazeri

1. *Dioscorea deltoidea* Wallich [Cat. no. 5110. 1832. nomen nudum] ex Kunth, Enum. pl. 5: 340. 1850; Hooker f., Fl. Br. India 6: 291. 1892; Prain & Burkill, J. Asiat. Soc. Bengal, pt. 2, nat. hist. 73, suppl.: 5. 1904; Knuth in Engler, Pflanzenr. 87 (IV. 43): 174. 1924; Prain & Burkill, Ann. Roy. Bot. Gard. Calcutta 14: 25, pl. 4. 1936. Type: Nepal, Sankas, 1821, Wallich 5110 (holotype K; isotypes B, E, K, US; photo of B-isotype, NY, neg. 4668). Fig. 19A, B.

Rhizome horizontal, lying near the surface of the soil, up to 20 cm long, the surface chesnut brown, with scattered roots. Stem up to 5 m long, up to 5 mm in diam., shallowly striate when dry, green, turning straw-colored when mature or dry, glabrous. Bulbils absent. Leaves alternate, occasionally subopposite; blade ovate to cordiform, basally truncate to hastate, apically long-acuminate 4-14 x 3-9 cm, green and glabrous above, glaucous-green and pubescent on veins below; hairs white, unicellular, papillose to cylindric, 0.1-0.7 mm long, sparse and short on primary veins, relatively dense and long on other veins; primary veins campylodromous, 7(-9), the outer ones very widely arcuate in hastate leaves; secondary veins branched toward outside; reticulation distinct on both sides; margin distinct, yellowish, usually finely revolute; petiole \pm as long as the blade, 3-13 cm long, channelled above, glabrous or puberulent near the base; stipules absent. Staminate inflorescence axillary, solitary or

rarely 2-3 per axil, spicate or occasionally compound due to a few lateral branches, the axis \pm firm, flexuous, ascending to horizontal, up to 30 cm long, angled, glabrous or sometimes puberulent especially at the base. Flowers 6-35 per spike, in lax, 2 or 3 flowered cymules (reduced to one toward apex), sessile, 1.8-2.5 x 2.5-3 mm, completely open at anthesis; bract very widely ovate, acute to obtuse, ca. 1.2 x 1.2 mm, \pm irregularly or sometimes lobed at the margin, glabrous, membranous; bracteole as bract or smaller; perianth campanulate with ca. 0.5 mm-deep tube, the lobes scarcely longer than the tube, ascending to reflexed, ovate, acute to obtuse, 1-1.3 mm long; stamens 6, inserted at the base of the perianth tube, the filament 0.4-0.5 mm long, the anthers extrorse in the outer cycle, introrse in the inner cycle, 0.2-0.4 mm long, the connective not expanded beyond the width of the filament; pistillode inconspicuous, sometimes obscurely 3-lobed. Pistillate inflorescence axillary, solitary, spicate, erect to ascending in flower, pendent in fruit, the axis 5-17 cm long, glabrous or puberulent at base. Flowers up to 12 per spike, lax, sessile or very shortly pedicelled; bract ovate, acuminate to obtuse, 1.2-1.5 x 0.8-1 mm, glabrous, membranous; bracteole oblong-ovate, 0.8-1.2 x 0.5-0.7 mm, acuminate, glabrous, membranous; perianth as in staminate flower, but smaller and fleshy, the lobes 0.5-0.8 mm long; staminodes 0.2-0.3 mm long, inserted at the margin of the perianth tube; ovary 2-6 mm long,

with wings bordered by a distinct margin, glabrous; styles connate nearly to the top, columnar, ca. 1 mm long; stigmas clavate, shallowly lobed terminally. Capsules 2-6 per spike, reflexed, loosely imbricate, usually broader than long, widely depressed-obovate, usually rounded basally, truncate or cleft apically, 1.5-3 x 1.8-3.3 cm, reddish or tan with transverse striations; wings somewhat broad, firmly bordered by a distinct margin, stipe 2-4 mm long. Seed wing circumferential, but laterally broader, 5.5-12 x 8.5-18 mm including the wing, the wing 2.5-9 mm wide at the widest, fawn.

Distribution. Occurs in the Himalayan range at altitudes of 1000-3000 m, and in south western China up to 3600 m.

Representative specimens. PAKISTAN. Hazara Dist.: Kagan, Duthie 22609 (JEPS), Burt 957 (E); Rawalpindi Dist.: Murree, Changla gali, Stewart 13901 (GH, JEPS, NY).

JAMMU & KASHMIR STATE. Gurez, Koelz 9292 (GH, NY); Pahlgam, Stewart 21617 (NY, US).

INDIA. Himachal Pradesh State, Chamba Dist.: Kulal Forest, Lace 1669 (E); Khajar, Koelz 8826 (GH, NY); Kangra Dist.: Kulu, Koelz 4680 (GH, NY, US); Dharmsala, Stewart 2005 (NY, PH); Mahasu Dist.: Kunawar, Drummond 22192 (E); Simla, Thomson s.n. (E); Uttar Pradesh State, Dehra Dun Dist.: Chakrata, Raizada 41 (E); Mussooree, Anderson s.n. (E); Almora Dist.: Strachy & Winterbottom 1 (GH); Uttarkashi Dist.: Stewart s.n. (E).

NEPAL. Titre, Kali Gandaki Valley, Stainton et al. 5471 (E); Sialgarhi, Polunin et al. 110 (K); Phulchoki, Banerjee 1801 (E); Godaway, Kath Valley, Shrestha 1020 (US); s.loc, Wallich 5110 (E, K, PH, US). BHUTAN. Lhuntse Dzong, Ludlow et al. 20162 (E).

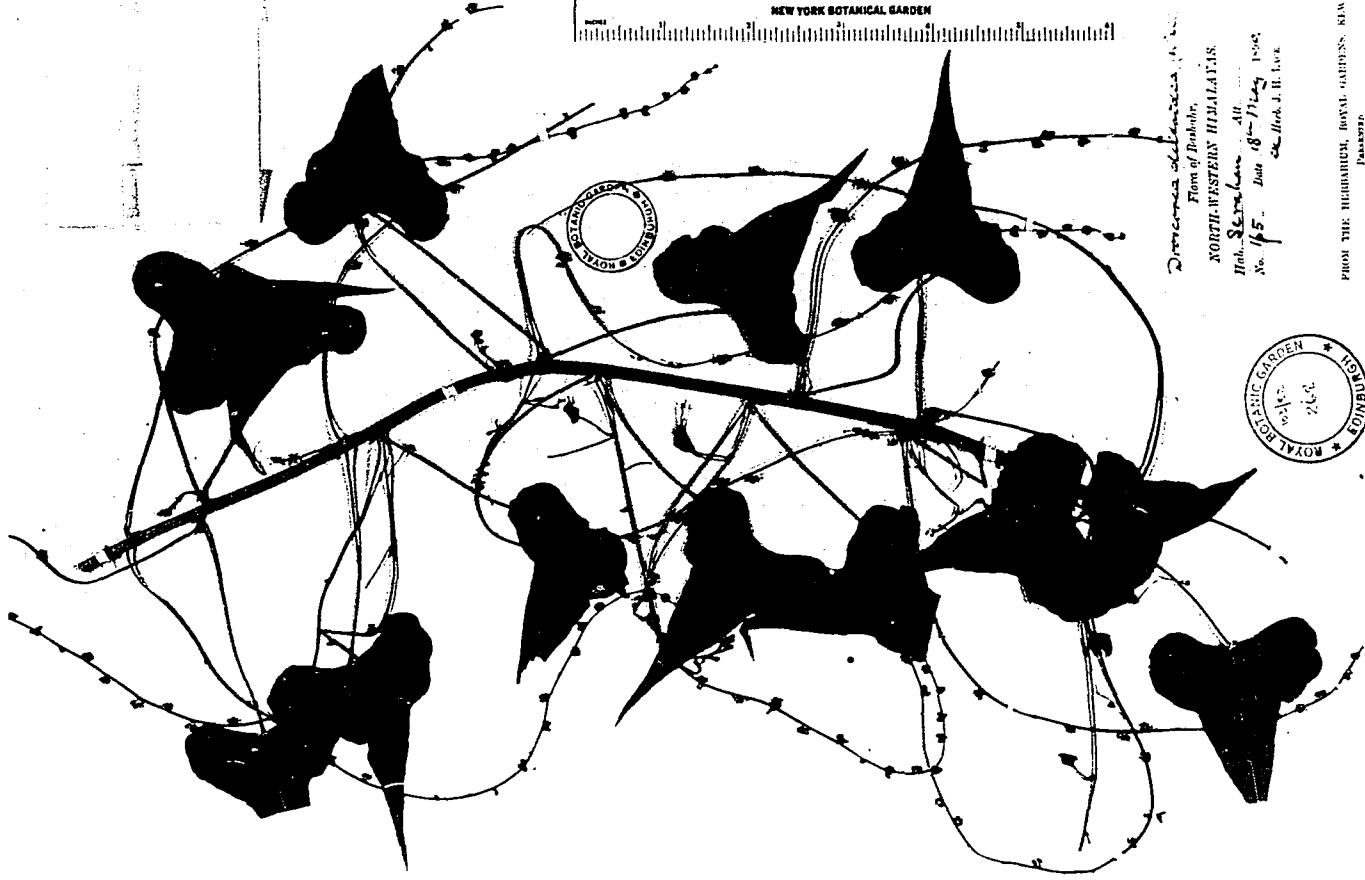
Common names and uses. India & Pakistan: Kildi, Krithi. The rhizomes contain a toxic saponin and preparations of these are used by some people in the northern states of India and Nepal for killing lice in hair and clothing (Burkill 1935). It is also a source of diosgenin.

Easily distinguished from its allied species, namely, D. prazeri, by unicellular hairs on the veins of the leaf-surface.

Fig. 19. Dioscorea deltoidea

A. Staminate plant (Lace 165, E)

B. Pistillate plant (Stewart s.n., A).



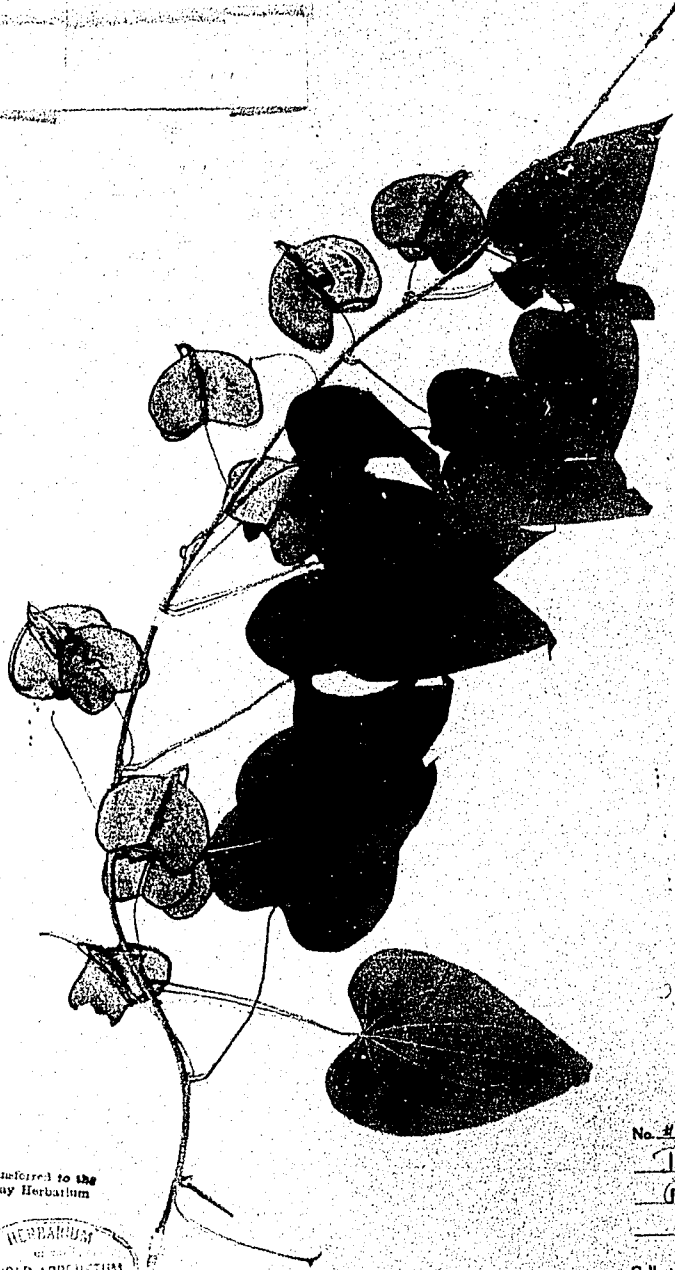
NEW YORK BOTANICAL GARDEN

Dioscorea deltoidea L.
 Form of *Dioscorea*
 NORTH-WESTERN HIMALAYAS
 Hb. Sargentian All.
 No. 145. Jan 18-May 1904.
 ex Herb. J. H. Rose

FROM THE HERBARIUM, ROYAL GARDENS, NEW
 PALACE



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HERBARIUM OF THE UNIVERSITY OF CALIFORNIA
JAN 10 1921

Dioscorea deltoidea, Walp.

Determinavit *M. S. G. Baker*

Plants of Kashmir

No. 4

Dioscorea deltoidea Wall. ex

Bahlyan

7700

Collected by R. R. Stewart Aug. 18, 1920

Transferred to the
Gray Herbarium

HERBARIUM
OF
ARNOLD ARBORETUM
HARVARD UNIVERSITY

2. *Dioscorea prazeri* Prain & Burkill, J. Asiat. Soc. Bengal, pt. 2, nat. hist. 73, suppl.: 2. 1904; Knuth in Engler, Pflanzenr. 87 (IV. 43): 175. 1924; Prain & Burkill, Ann. Roy. Bot. Gard. Calcutta 14: 29, pl. 5 & 6. 1936; Burkill, Fl. Males. 4: 304. 1951. Type: Burma. Upper Chindwin Dist.: Sittaung, Prazer s.n.; Bhamo Dist.: Bhamo, Burkill 21537; Mamouk, east of Bhamo, Burkill 21507, 21509, 21514; Katha Dist.: Katha, Burkill 21557, 22493, 22494, 22495, 22496, 22652, 22658, 22664, 22665 (syntype, n.v.). Fig. 20A, B.

Dioscorea sikkimensis Prain & Burkill, J. Asiat. Soc.

Bengal, Pt. 2, nat. hist. 73, suppl.: 3. 1904. Type: India. W. Bengal State, Darjeeling Dist.: Darjeeling, Griffith 5555 (lectotype chosen here, K; isolectotype, NY).

Dioscorea clarkei Prain & Burkill, J. & Proc. Asiat. Soc.

Bengal 10: 15. 1914. Type: India. Nagaland State, Kohima Dist.: Naga Hills, Kohima, Clarke 41018 (holotype, CAL, n.v.; isotype, K).

Rhizome horizontal, short, somewhat stout, creeping beneath the soil-surface, freely branched, the branches up to 10 x 12 cm, each producing usually one shoot near its apex, the surface greyish brown or nearly black, with many scattered roots, the tissue white to cream-colored, poisonous due to saponins. Stem slender, up 4 m long, smooth or shallowly striate, green or speckled with brownish purple, often chesnut-brown when dry,

glabrous. Bulbils rare. Leaves alternate or rarely opposite toward the base of the stem; blade ovate, basally cordate, apically long- or abruptly acuminate, 8-18 x 4.5-12 cm, glabrous, glossy and usually green on both surfaces; primary veins campylodromous, 7(-9); secondary veins branched toward the margin; reticulation distinct on both sides; margin distinct, brown or yellowish, usually finely revolute; petiole shorter than half the length of the blade, 3-8 cm long, channelled above, glabrous; stipules absent. Staminate inflorescence axillary or terminal, paniculate or spicate; panicles solitary in axils, with 5-25 cm-long rachis; spikes 1-3 per axil, the axis \pm firm, somewhat flexuous, 4-20 cm long, angled or narrowly alate, glabrous or pubescent especially at the base. Flowers 25-70 per spike or branch of panicle, lax, in 2-4-flowered cymules (reduced to one toward apex), 1.5 x 2.5-3 mm, completely open at anthesis, pedicelled; pedicel 0.3-0.6 mm long broadened toward the apex; bract ovate to widely ovate, acuminate, 1-2 x 0.8-1.2 mm, glabrous; bracteole as bract but smaller, 0.7-1 x 0.6-0.8 mm; perianth campanulate or rotate with ca. 0.5 mm-deep tube, the lobes over twice as long as tube, ovate, acute to rounded, ca. 1.2 x 1 mm, flaring or divergent; stamens 6, inserted at base of the perianth, the filament twice as long as the anther, ca. 0.4 mm long, reflexed at anthesis, the anthers extrorse in outer cycle and introrse in inner cycle, ca. 0.2 mm long, the connective not expanded beyond the width of the filament; pistillode humpy,

0.1-0.2 mm high. Pistillate inflorescence axillary, solitary, spicate, erect to ascending in flower, pendent in fruit; axis 3-20 cm long, angled or narrowly alate, glabrous or puberulent at base. Flowers up to 10 per spike, lax, very shortly pedicelled; bract ovate to widely ovate, acuminate, 1.2-1.5 x 1.2 mm, glabrous; bracteole as bract but smaller, ca, 1 x 0.8 mm; perianth as in staminate flower but relatively fleshy; staminodes ca. 0.2 mm long, inserted at base of the perianth; ovary 5-7 x 2-3 mm, with wings bordered by a distinct margin, glabrous; styles connate to top, columnar, ca. 0.5 mm long; stigmas clavate, shallowly lobed terminally. Capsules up to 6 per spike, reflexed, loosely imbricate, broader than long, widely depressed obovate, basally rounded, apically obtuse to truncate, 1.5-2.5 x 2-3 cm, glossy-tan with transverse striations; stipe 2-3 mm long, Seed winged circumferentially but laterally broader, 9-12 x 5-11 mm including wing, the wing 4-6.5 mm wide at the widest, fawn.

Distribution. Moist eastern parts of the Himalaya, mountains between Assam State in India and Burma, extending into the Malay Peninsula; usually occurs below altitudes of ca. 1200 m, although it has been gathered at ca. 1675 m.

Representative specimens. INDIA. Sikkim State: s.loc., Hooker s.n. (GH, K), Treutler 307 (K); W. Bengal State, Darjeeling

Dist.: Darjeeling, Griffith 5555 (K, NY), 5538 (K); Chunbat, Clarke 26512-A (BM), Cowan 21 (E); Assam State, Jalpaiguri Dist.: Duars, Haines 487 (E); Bihar State, Champaran Dist.: s.loc. Hieronyms 375-b (K); Nagaland State, Kohima Dist.: Kohima, Clarke 41018 (K).

NEPAL. Kacheong, Ribu & Ramoo s.n. (E), Stainton et al. 6826 (E); Rungeet, s. coll. s.n. (GH, NY, US); Naumala, Bis Ram 67 (JEPS).

BHUTAN. Ngaramp, Cooper 4623 (E); Nivichoma Timpu, Cooper 1145 (E)

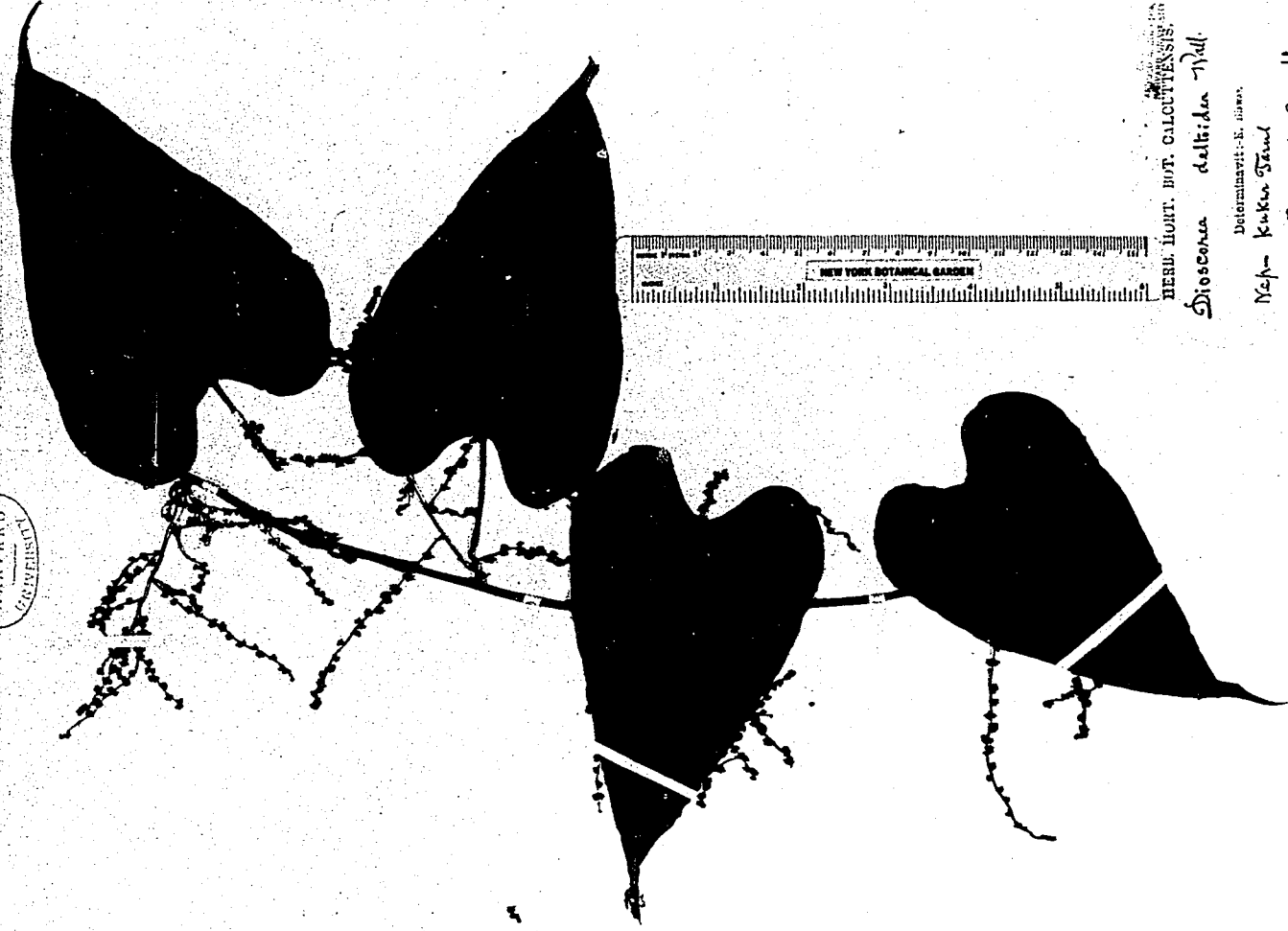
Common names and uses. NEPAL: Kukur torul. In northern India, a shampoo made from the rhizomes is used to kill head-lice.

Fig. 20. Dioscorea prazeri

A. Staminate plant (s.coll. s.n., GH).

B. Pistillate plant (Clarke 26512-A, BM).

UNIVERSITY OF CALIFORNIA



HERB. MORT. BOT. CALCUTTENSIS

Sioscora deltoidea Nutt.

Determinavit: E. Sieww.

Nep- Kaku Samul

Bungast-Looff

Frank.

4/1/1935.



NEW YORK BOTANICAL GARDEN
GEORGE ENGELMANN PAPERS

Dioscorea sect. *Dioscorea*

Type: *Dioscorea sativa* Linnaeus

Dioscorea sect. *Combilium* Prain & Burkill, J. & Proc.

Asiat. Soc. Bengal 10: 19. 1914. Type: *Dioscorea aculeata*
sensu Linnaeus 1754, non Linnaeus 1753 = *Dioscorea sativa*
Linnaeus

Tubers several, stalked, arising from a woody base of the stem, protected by thorny roots in wild plants. Plants abundantly pubescent with T-shaped hairs. Stem annual, sinistrorse, armed. Bulbils absent. Leaves alternate, simple, cordiform, the apex extending to a distinct leaf-tip gland. Staminate flowers in long spikes, solitary or cymosely aggregated, pedicelled; perianth connate at base. Capsule reflexed.

Distribution. This monotypic section (= *Combilium* sensu Prain & Burkill, 1914), consisting of *D. esculenta*, is indigenous to Indo-china, although it seldom occurs wild.

The affinities of this section are somewhat obscure, although Prain & Burkill (1936) placed it along with *Stenophora*. Arrangement of staminate flowers in simple spikes and the connate perianth suggest their resemblances, but the nature of the underground storage organs differ greatly and hence they are considered phylogenetically distant from each other.

3. *Dioscorea sativa* Linnaeus, Sp. pl. 1033. 1753. Type: Rheede, Hort. malab. 8: 97. pl. 51. 1688 (lectotype chosen here). Fig. 21.

Dioscorea aculeata sensu Linnaeus, Herb. Amb. 23. 1754, non Linnaeus 1753.

Oncus esculentus Loureiro, Fl. cochinch. 194. 1790. Type: Vietnam (Cochinchina), Loureiro s.n. (holotype, BM, n.v.).

Convolvulus mammosus Loureiro, Ibid. 108. 1790. Type: from Vietnam, no specimen cited.

Dioscorea cliffortiana Poiret, Tabl. encycl. 3: 409. 1796, based on Lamarck, Ibid. pl. 818 (upper figure). 1793.

Dioscorea fasciculata Roxburgh [Hort. Bengal. 72. 1814, nomen nudum] Roxburgh, Fl. Ind. 3: 801. 1832. Type: from cultivation in India, no specimen cited.

Dioscorea tugui Blanco, Fl. Filip. 800. 1837. Type: from Philippines, no specimen cited.

Dioscorea tiliaefolia Kunth, Enum. pl. 5: 401. 1850. Type: Philippines, Tayabas Prov., 1841, Cuming 781 (B, n.v.).

Dioscorea papuana Warburgh in Engler, Bot. Jahrb. 13: 273. 1891. Type: from cultivation, no specimen cited.

Dioscorea spinosa Wallich [Cat. no. 5103. 1832, nomen nudum] ex Hooker f. Fl. Brit. India 6: 291. 1892. Type: India, Bihar State, Monghyr Dist.: ? Nathpur, 21 Sept. 1810, Buchanan-Hamilton in Wallich, Cat. no. 5103-D (lectotype chosen here, E).

Dioscorea aculeata Linnaeus var. tiliaefolia Prain & Burkill,
J. & Proc. Asiat. Soc. Bengal 10: 20. 1914. Type: from
cultivation in Philippines, no specimen cited.

Dioscorea aculeata Linnaeus var. spinosa Prain & Burkill,
ibid. 10:20. 1914. Type: from cultivation in India, no
specimen cited.

Dioscorea aculeata Linnaeus var. fasciculata Prain & Burkill,
ibid. 10: 20. 1914. Type: from cultivation in India,
Java, and Malay peninsula, no specimen cited.

Dioscorea esculenta (Loureiro) Burkill, Gard. Bull. Straits
Settl. 1: 396, pl. 7. 1917. Basionym. Oncus esculentus
Loureiro

Dioscorea esculenta (Loureiro) Burkill var. spinosa Knuth in
Engler, Pflanzenr. 87 (IV. 43): 189. 1924. Basionym.

Dioscorea spinosa Wallich ex Hooker f.

Dioscorea esculenta (Loureiro) Burkill var. fulvido-
tomentosa Knuth in Engler, Ibid. 87 (IV. 43): 190. 1924.
Type: 14 specimens from various localities cited.

Dioscorea esculenta (Loureiro) Burkill var. fasciculata
Knuth in Engler, Ibid. 87 (IV. 43): 189. 1924. Basionym.

Dioscorea fasciculata Roxburgh ex Roxburgh

Tubers several, arising from woody base of the stem lying beneath the soil-surface, shortly stalked and closely aggregated or long-stalked and lax, globose to oblong or flattened and lobed, usually up to 12 cm long and weighing up to 3 kg, the surface fawn to brown or greyish brown, smooth or with soft or minutely thorny rootlets, the tissue soft, white, edible; long roots arising near origin of the tubers, some becoming branched, indurated, and thorny (protective roots absent in most cultigens due to selection), the upwardly directed thorns usually larger than others. Stems one or rarely more than one, green, sometimes tinged with purple toward base, pubescent, becoming glabrescent with age, armed with prickles, often densely at base; prickles up to 3 mm long, straight or slightly deflected downward. Bulbils absent. Leaves alternate; blade cordiform, acuminate or mucronate with 5-10 mm-long apex, 6-13 x 7-15 cm, glabrescent above, pubescent below; primary veins campylodromous, 9-13, the inner 5 veins reaching apex, the outer ones increasingly arcuate toward outside, becoming submarginally obscure, the outermost pair suprabasal; secondary veins widely acute or right angled or obtuse, almost parallel; reticulation \pm distinct on both sides; margin distinct; petiole almost as long as blade, 4-12 (14) cm long, pubescent; stipules prickle-like, longer than internodal prickles, up to 7 mm long, directed downward. Staminate inflorescence axillary, solitary or occasionally 2 per axil, spicate, the axis \pm firm, ascending, 10-45 cm long, somewhat

angled, pubescent. Flowers usually up to 70 per spike, solitary or in 2-3-flowered cymules, opening irregularly along axis, 2.5-3.5 x 3.5-5 mm, shortly pedicelled; bract ovate, 1.5-3.2 x 1-1.5 mm, long-acuminate to cuspidate, densely pubescent without; bracteole as bract 1-1.5 x 0.4-0.6 mm; pedicel 0.2-0.8 mm long, broadened toward apex, fleshy; perianth campanulate, densely pubescent without, the tube 0.8-1.5 x 1.5-3 mm, the lobes oblong-ovate, acute, 1-1.7 x 1-1.2 mm, ascending; stamens 6, rarely one or more in outer cycle become sterile, inserted at the rim or halfway up the perianth tube, the filament 0.2-0.6 mm long, inflexed, the anther 0.4-0.6 mm long with lobes closely held by narrow connective; pistillode humpy or conical, obscurely 3-lobed. Pistillate inflorescence axillary, solitary, spicate, the axis up to 40 cm long, pendent, bluntly angled, pubescent. Flowers up to 60 per spike, shortly pedicelled; bract ovate, acuminate at apex, ca. 2 mm long, pubescent without; bracteole as bract, ca. 0.8 mm long; perianth tube distinctly shorter than lobes, the lobes narrowly ovate, ca. 1.5 x 0.5 mm, rotate to somewhat reflexed, pubescent without, the outer lobes obtuse, the inner lobes acute; staminodes 6; ovary densely pubescent; styles connate nearly to the top, the stigmas terminally reflexed. Capsule (immature) reflexed, oblong-obovate, basally rounded to truncate, apically retuse, ca. 2.7 x 2.5 cm, becoming glabrescent. Seeds (mature) not known.

Distribution. Originally from western Indo-china; cultivated in India, China, and Malaysia during very early times; subsequently introduced into Pacific Islands and Africa.

Representative specimens. INDIA. W. Bengal State, Howrah Dist.: Calcutta, Helper s.n. (GH); Bihar State, Monghyr Dist.: Nathpur, Buchanan-Hamilton in Wallich no. 5103-D (E); Kerala State, Quilon Dist.: Quilon, Wight 1087 (E); State unknown: Wight 2828 (GH); Buchanan-Hamilton in Wallich no. 5103-E (E).

BANGLADESH. Rangpur Dist.: Gangachora, Buchanan-Hamilton in Wallich no. 5103-A (E).

SRI LANKA. Kandy Dist.: Peradeniya (cultivated) s. coll. s.n. (PDA); District unknown: Walker 1195 (E).

Common names and uses. Lesser Yam, Asiatic Yam, Potato Yam, Chinese Yam; India: Mau alu, Gora alu; Sri Lanka: Panu konda, Hin kukul ala. Provide edible yams that are soft in texture and containing less fiber; also free from toxicity and are of good palatability and, therefore, considered superior to other species of yams.

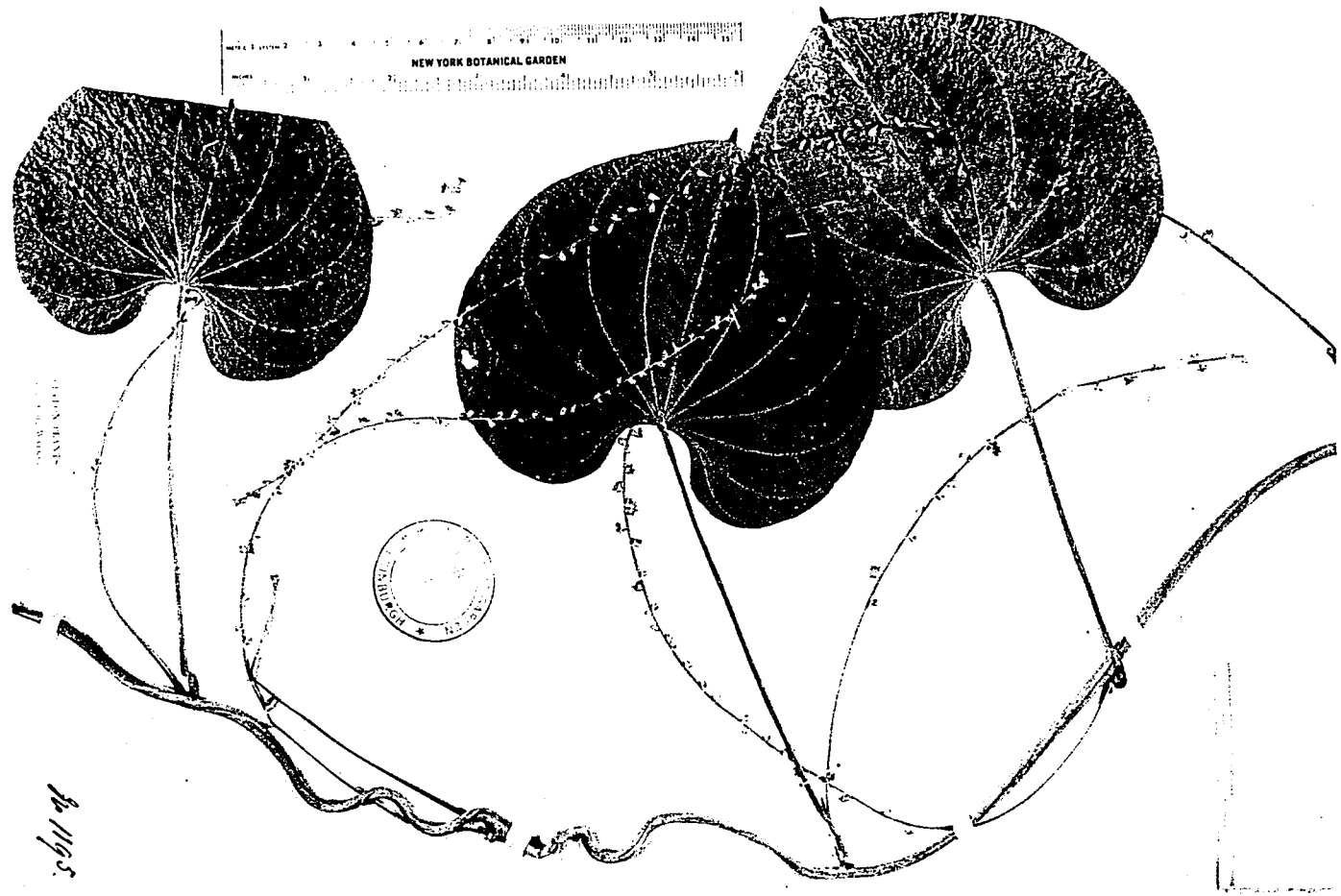
Linnaeus (1753) based D. sativa on several elements apparently including 4 species of Dioscorea and a menispermaceous plant. Prain & Burkill (1919) analysed these components and abandoned that the name as ambiguous. The present international Code of Botanical Nomenclature (1983) does not provide for the

rejection of names merely because they have been diversely applied. Rheede's plate no. 51 (1688), included in Linnaeus' protologue, clearly represents the species here considered, and the name has often been used in this sense. Therefore, it is proposed that D. sativa be retained and the Rheede's plate is chosen as its lectotype.

The varieties recognized by Prain & Burkill (1914, 1936), on the presence and absence of spiny roots, are not accepted as the absence of spiny roots is associated with cultivated plants. The loss of these protective roots is certainly due to selection by man. Knuth (1924) proposed the variety fulvido-tomentosa due to the somewhat tawny tomentose nature of the lower leaf-surface. Such variation in the nature of pubescence is not regarded as sufficient in distinguishing varieties within this species.

Fig. 21. Dioscorea sativa

Staminate plant (Walker 1195, E).



NEW YORK BOTANICAL GARDEN

No. 1195.

Dioscorea sect. Opsophyton Uline in Engler & Prantl, Nat.

Pflanzenfam. II. 5: 84. 1897, as subg. Helmia sect.

Lectotype: Dioscorea bulbifera Linnaeus, chosen by Prain & Burkill, Ann. Roy. Bot. Gard. Calcutta 14: 109. 1936).

Tuber annual, vertical, produced beneath the soil surface, nauseous and somewhat poisonous in wild plants due to saponins. Plants generally glabrous, the hairs unicellular and finger-like when present. Leaves alternate, simple, cordiform, the apex extending to a distinct leaf-tip gland; stipules often present. Staminate flowers in panicles or spikes, solitary, sessile, fully open at anthesis; tepals free, long and narrow. Capsule reflexed, longer than broad, dehiscent at the apex along shoulders and partially along placentas leaving a trifurcate aperture. Seed-wing distal, directed toward base of the capsule, adapted to swirl in gusty wind.

Distribution. This section consist of over 20 species (sensu Knuth, 1924) of which all, but one, are restricted to the tropical Africa and Malagasy.

Knuth (1924) subdivided this section into 3 subsections, namely, Euopsophyton, Macrourea, and Isocantha, the former consisting of D. bulbifera and the latter two accomodating several species in Africa and Malagasy. The relationships of the constituent species have to be critically evaluated to verify Knuth's classification.

4. *Dioscorea bulbifera* Linnaeus, Sp. pl. 1033. 1753, excluding reference to Rheede, Hort. malab. 7: 69, pl. 36. 1688; Knuth in Engler, Pflanzenr. 87 (IV. 43): 88. 1924; Prain & Burkill, Ann. Roy. Bot. Gard. Calcutta 14: 111, pl. 49-51. 1936; Burkill, Fl. Males. 4: 311. 1951. Type: Hermann, Parad. bat. pl. 217. 1698 (lectotype chosen here). Fig. 22A, B.

Dioscorea sativa sensu Thunberg, Fl. Jap. 151. 1784, non Linnaeus

Dioscorea tamnifolia Salisbury, Parad. lond. pl. 17. 1806.

Dioscorea pulchella Roxburgh [Hort. Bengal 72. 1814, nomen nudum] ex Roxburgh, Fl. Ind. 3: 801. 1832. Type: from Bangladesh, Chittagong, no specimen cited.

Dioscorea crispata Roxburgh [Hort. Bengal 72. 1814, nomen nudum] ex Roxburgh, Fl. Ind. 3: 802. 1832. Type: from cultivation in India, no specimen cited.

Dioscorea latifolia Benth in Hooker, Niger Fl. 535. 1849. Type: Nigeria, Nun River, Niger Delta, Vogel s.n. (K, lectotype chosen here).

Helmia bulbifera Kunth, Enum. pl. 5: 435. 1850. Basionym.

Dioscorea bulbifera Linnaeus

Dioscorea anthropophagorum A. Chevalier [in Jumelle, Pl. tuberc. aliment. 172. 1910, nomen nudum] ex A. Chevalier, Veg. ut. de l'Afr. trop. Fr. 8: 357. 1913. Type: from Africa, no specimen cited.

Dioscorea sativa Linnaeus var. anthropophagorum (A. Chevalier)

Baudon, Ann. Inst. Bot.-Geol. Colon. Marseille III. 1:
236. 1913. Basionym. Dioscorea anthropophagorum
A. Chevalier ex A. Chevalier

Dioscorea violacea Baudon, *ibid.* III. 1: 242, fig. 5. 1913.

Type: Central African Republic, Kemo Grinbingui Dist.,
M'Bres, Tomo, 4 Jul. 1912, Baudon 1723 (n.v.).

Dioscorea longipetiolata Baudon, *ibid.* III. 1: 242, fig. 6.

Type: Central African Republic, Kemo Grinbingui Dist.,
Kaga M'Bra, 13 Aug. 1912, Baudon 1853 (n.v.).

Dioscorea bulbifera Linnaeus var. vera Prain & Burkill, J. &

Proc. Asiat. Soc. Bengal 10: 26. 1914. Type: no specimen
cited.

Dioscorea bulbifera Linnaeus var. simbha Prain & Burkill, J.

ibid. 10: 26. 1914. Type: from India, Sikkim State, no
specimen cited.

Dioscorea bulbifera Linnaeus var. cacheo Prain & Burkill,

ibid. 10: 26. 1914. Type: from India, Sikkim State, no
specimen cited.

Dioscorea bulbifera Linnaeus var. suavior Prain & Burkill,

ibid. 10: 26. 1914. Type: cultivated in India, no
specimen cited.

Dioscorea bulbifera Linnaeus var. birmanica Prain & Burkill,

ibid. 10: 26. 1914. Type: cultivated India and Burma, no
specimen cited.

Dioscorea bulbifera Linnaeus var. sativa Prain & Burkill,
 ibid. 10: 26. 1914. Type: from Pacific Islands and India,
 no specimen cited.

Dioscorea bulbifera Linnaeus var. elongata Prain & Burkill,
 ibid. 10: 26. 1914. Type: from Australia, no specimen
 cited.

Dioscorea bulbifera Linnaeus var. deltoidea Prain & Burkill,
 ibid. 10: 26. 1914. Type: Hong Kong, Bodinier 1310(n.v.).

Dioscorea bulbifera Linnaeus var. heterophylla Prain &
 Burkill, Ann. Roy. Bot. Gard. Calcutta 14: 117. 1936.
 Type: Malaysia, Malay Peninsula, Penang State, Bukit
 Penara, Burkill 1469, 1471; Negri Sembilan State, Kendong,
Burkill 2203 (syntype, n.v.).

Tuber (absent in some cultigens in favor of bulbils) usually solitary, globose to pyriform or somewhat lobed when large, weighing up to 1 kg, nauseous due to various quantities of saponins (edible in some cultigens), the surface purplish black or earth-colored, covered abundantly by small feeding roots (smooth in some cultigens), the tissue white to lemon-yellow and somewhat flecked with purple, mucilaginous, becoming brown or orange on exposure; long roots produced above the tuber. Stem solitary or rarely 2, up to 30 m long and 1 cm in diam., usually flecked with purple brown, terete or narrowly alate, glabrous. Bulbils abundant, axillary or among staminate inflorescences or

rarely between petiole and leaf blade, globose (flattened in some African forms), weighing up to 0.5(2) kg, warty, or smooth when large, the tissue as in tuber. Leaves alternate; blade cordiform, often broader than long, abruptly- or long-acuminate with up to 3.5 cm-long apex, 5-25 x 5-26 cm, glabrous, slightly glossy or dull on both surfaces; primary veins campylodromous, 5-11, the inner 5 reaching the apex, the outermost pair suprabasal; secondary veins widely acute to right angled, almost straight, parallel; reticulation faintly distinct or obscure; margin distinct; petiole usually slightly shorter than the blade, 3-21 cm long, channelled above, glabrous; stipules lunate, auriculate, 2-8 x 1.5-4 mm, membranous, sometimes absent. Staminate inflorescence axillary or terminal, usually solitary, paniculate or spicate; panicles pendent when long, the rachis 5-70 cm long, glabrous; spikes up to 6 per axil of leaf or inflorescence bract, the axis \pm firm, 3-20 cm long, shaply angled or narrowly alate, glabrous. Flowers 10-80 per spike, sessile, 1.8-6.5 mm long, completely open at anthesis, glabrous, whitish to pale pink, fragrant; bract ovate to widely ovate, long-acuminate, 1-2.5 x 0.7-1.4 mm; bracteole ovate, acuminate to caudate, 0.7-1.5 x 0.4-0.7 mm; outer tepals lanceolate, 1.5-6 x 0.5-1.2 mm, somewhat fleshy, spreading; inner tepals as outer tepals but narrower; stamens 6, free or adnate at base of tepals, the filament 0.1-0.4 mm long, the anther 0.2-0.4 mm long, the connective not expanded beyond the width of the filament;

pistillode represented by 3 conical lobes, up to 0.3 mm long. Pistillate inflorescence axillary, up to 6 per axil, spicate, usually pendent, the axis 8-40 cm long, sharply angled or narrowly alate, glabrous. Flowers up to 50 per spike, sessile at anthesis, glabrous, white or greenish white; bract ovate, long-acuminate or caudate, 1.2-2.8 x 1-2 mm; bracteole as in bract, 0.8-2.2 x 0.6-1 mm; tepals as in staminate flower but slightly shorter, 1.8-4.3 x 0.5-0.8 mm; staminodes 6, adnate to base of tepals, ca. 0.5 mm long; ovary 2.5-8 x 1.5-3 mm; styles connate nearly to top, the stigmas reflexed and shortly divided into two lateral lobes and one lower median lobe. Capsules 10-35 per spike, closely imbricate, longer than broad, oblong, basally rounded or obtuse, apically truncate to rounded or obtuse, 1.8-2.8 x 1-1.5 cm, glossy, often bronzed or flecked with red, glabrous. Seed 12-20 x 5-7 mm including the wing, cuneate at base, smoky brown.

Distribution. The most prolific and the most widespread of all species of the genus; eastward from the Atlantic coast of Africa to the furthest islands of the Pacific with a marked gap of its absence from northern Africa to northwestern India; introduced to tropical America probably from Africa.

Representative specimens. INDIA. Himachal Pradesh State, Chamba Dist.: Sao Valley Lace 799 (E); between Kalel and Masrund, Lace 2066 (E); Uttar Pradesh State, Dehra Dun Dist.: Mussooree,

Stewart 15019 (GH, JEPS, NY); W. Bengal State, Darjeeling Dist.: Kalimpong, Cowan s.n. (E); Howrah Dist.: Calcutta Helper s.n. (US); Assam State, Goalpara Dist.: Buchanan-hamilton in Wallich no. 5106-A (E); Meghalaya State: Khasia, Thomson s.n. (E, K), Griffith s.n. (E); Bihar State, Darbhanga Dist.: Buchanan-Hamilton in Wallich no. 5107-D (E); Monghyr Dist.: Monghyr, Buchanan-Hamilton in Wallich 5106-B (E); Maharashtra State, Kolaba Dist.: Uran, Divikar 1230 (MO), 1232 (MO); Mysore State, Hassan Dist.: between Biccode and Arehalli, Saldanha 15045 (E, MO, NY, US); Belgaum Dist.: Belgaum, Ritchie 728 (E).
 NEPAL. Bongakhani, Stainton et al. 3966 (E); Suranti Khola, Stainton et al 6857 (E).
 BHUTAN. Chukka Timpu, Cooper 1260 (E); between Sarbhang & Chirang, Grierson & Long 1543 (E); Mirichoma Timpu, Cooper 1136 (E).
 BANGLADESH. Sylhet Dist.: Sylhet, Wallich 5106-H (E); Rungpur Dist.: Gongachora, Buchanan-Hamilton in Wallich no. 5106-B (E); Chittagong Dist.: Ganjanina, Cowan 1007 (E).
 SRI LANKA. Mannar Dist.: Kovi kulam, Kundu & Balakrishnan 582 (PDA, US), 583 (PDA, US); Kandy Dist.: Hantane, Thwaites C.P. 2977 (PDA); Hambantota Distr.: Ruhuna National Park, Block I, Müller-Dombois & Cooray 69011502R (GH, JEPS, MO, NY, PDA, US).

Common names and uses. Potato Yam, Aerial Yam; India: Genthī, Karu, Kanda, Karanda; Sri Lanka: Udala, Panu kondol. Used as food to some extent; tuber is normally small compared with

that in most other species and sometimes it is entirely absent; even when sizable, it is usually bitter, hard, and unpalatable; bulbils, however, are freely produced and attain large sizes, sometimes as large as 2 kg; it is these bulbils that are usually used as food; some forms reportedly contain appreciable amounts of saponins.

Linnaeus (1753) based D. bulbifera on three plates. However, Rheede's plate (Hort. malab. 7: pl. 36. 1688) does not depict D. bulbifera, as generally understood. Of the rest, Hermann's plate no. 217 (1698) is chosen as lectotype of D. bulbifera because it portrays features such as tubers, bulbils, direction of twining of the stem, and leaves more explicitly than Plukenet's figure (Phytographia 2: pl. 220. fig. 6. 1691). Thunberg's (1784) misapplication of the Linnaean epithet, sativa, to this species led to further confusion of the identity of D. sativa, as several authors, such as Kunth (1850) and Hooker (1892), followed Thunberg applying D. sativa to D. bulbifera.

Prain & Burkill (1914, 1936) recognized several varieties, primarily on the variations in shape, size, color, acidity, and nature of the surface of tubers and bulbils; the minor variations in leaf-shape and the length of staminate tepals also were taken into account. The variability in the aforementioned characters of tubers and bulbils is influenced by whether the plants are wild or cultivated, and the degree of selection by man and hence the

subdivision of the taxon using such variable characters is not recommended. The minor variations in leaf-shape are also not sufficient to establish varieties. Examination of a large number of specimens showed that the length of staminate tepals varies between 1.5-6 mm, and no sharp distinctions into varieties, as proposed by Prain & Burkill (1914), can be made on this character.

Fig. 22. Dioscorea bulbifera

A. Staminate plant (Jaffray s.n., E).

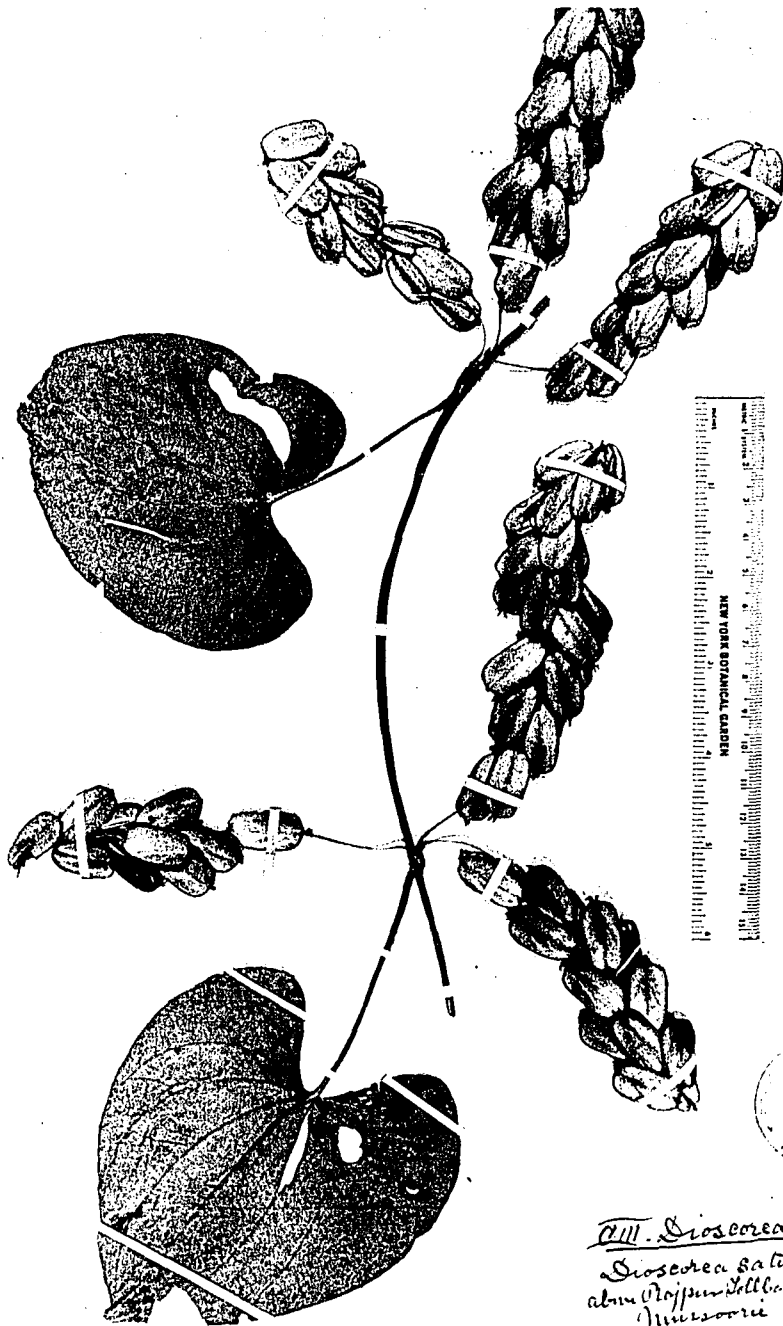
B. Pistillate plant (Anderson s.n., E).



Adiantum sp.
Davallia sp.
 W. C. Cresson
 N. Y. Bot. Gard.
 1884.



Herbar. N. Y. Bot. Gard.
 1884.



III. Dioscoreaceae
Dioscorea sativa
 abn. Poppundellbar - 3500
 Missouri
 Coll. Anderson Oct. 1916

Dioscorea sect. *Triumphorstemon* Uline in Engler & Prantl, Nat. Pflanzenfam. 11. 5: 84. 1897, as subg. Helmia sect. Type Dioscorea pentaphylla Linnaeus

Tubers one to few, unarmed, long-cylindrical, penetrating deeply into the soil, and then nonpoisonous, or \pm ovoid, lying beneath the soil-surface, and then somewhat nauseous and poisonous due to varying amounts of saponins. Plants commonly pubescent; hairs 2-celled with a short basal cell and a long tapering cell. Stem sinistrorse. Leaves alternate, generally palmately compound with 3-5 leaflets; primary veins eucamptodromous (acrodromous in outer halves of outermost leaflets). Staminate flowers arranged in a raceme or a panicle, pedicelled with bract and bracteole arising at apex of pedicel; Perianth open upto halfway at anthesis; stamens 3, free or adnate to the outer tepals, the filaments distinctly shorter than anther; anther lobes widely separated by broadened connective; staminodes 3, free or adnate to the inner tepal. Pistillate flowers in spikes; ovules produced closer to apex of the ovary. Capsule reflexed, longer than broad, dehiscent only at apex along shoulders and partially along placentas leaving a trifurcate aperture. Seeds winged distally and directed toward the base of capsule, adapted to swirl in gusty wind.

Distribution. Consisting of over 25 species (sensu Knuth, 1924), this section is widespread in southern Asia from western

India eastward to some Pacific regions, such as New Guinea, but absent in Australia.

Union of this section with Lasiophyton, as proposed by Prain & Burkill (1914, 1936), is not acceptable on account of numerous morphological, anatomical and chemical features that differ among these sections. In addition to the characters mentioned in the key to the sections, the separation of these two sections is supported by the anatomical differences in the fruit walls (see Fruits and seeds) and the unique presence of large amounts of alkaloids in the Lasiophyton (see Chemistry). A striking feature which enables the recognition of Triephorostemon is its compound leaves, in which at least middle leaflets show eucamptodromous venation, a unique and specialized character in the genus in Asia.

Key to the species of Dioscorea sect. Triephorostemon
in the Indian Subcontinent

1. Leaves tomentose below. Staminate flowers less than 1.5 mm across; stamens distinctly epitepalous. Capsule tomentose at maturity. 5. D. tomentosa
1. Leaves glabrous to hirsute below. Staminate flowers more than 1.5 mm across; stamens free or adnate to bases of outer tepals. Capsule glabrate with maturity.
2. Stem usually armed with prickles. Reticulation distinct on lower surface of leaves; stipules absent. Staminate racemes 1.5-6.5 cm; staminate flower flattened at base; pistillode stumpy or conical. Capsule glossy, blackish or brown. 6. D. pentaphylla
2. Stem unarmed. Reticulation obscure on lower surface of leaves; stipules common or occasional. Staminate racemes 2-9 cm long; staminate flower cuneate at base; pistillode columnar with a slightly broadened apex. Capsule tawny or straw-colored.
3. Stem pubescent, becoming glabrate with maturity.
Bulbils greyish brown. Leaves pubescent to glabrescent above, pubescent at least on veins below; middle leaflet up to three times as long as broad; petiole usually pubescent; stipules occasional, 0.8-1.5 mm long.
Staminate flower 1.5-2.5 x 1.5-2.5 mm; bract 2.5-3.5 mm

long, with a 0.5-1.5 mm-long tip overtopping the flower;

bracteole 1.5-2 mm long.

7. D. kamoensis

3. Stem glabrous at maturity. Bulbils glossy, black.

Leaves glabrous on both sides; middle leaflet ca. four

times as long as broad; petiole glabrous; stipules

common, 1-3 mm long. Staminate flower 1.3-1.5 x 1.5-1.8

mm; bract 1.6-2 mm long, with a blackened, ca. 0.5

mm-long tip not overtopping the flower; bracteole 1-1.2

mm long.

8. D. melanophyma

5. *Dioscorea tomentosa* Koenig [ms., nomen nudum] ex Sprengel,
 Pl. pugil. secund. 92. 1815; Wight, Ic. pl. ind. or. 3: pl.
 815. 1840; Kunth, Enum. pl. 5: 391. 1850; Hooker f. in
 Trimen, Handb. Fl. Ceylon 4: 275. 1898; Knuth in Engler,
 Pflanzenr. 87 (IV. 43): 139. 1924; Prain & Burkill, Ann.
 Roy. Bot. Gard. Calcutta 14: 156, pl. 54(8), 56, 57. Type:
 from India, no specimen cited. Fig. 23A, B.

Helmia ? tomentosa Kunth, Enum. pl. 5: 439. 1850. Basionym.

Dioscorea tomentosa Koenig ex Sprengel

Tubers several, arising from woody base of stem, deeply penetrating up to 2 m, \pm cylindrical, up to 4 cm diam., sometimes branched, with short roots arising from upper parts and long feeding roots near soil-surface, the surface brown, \pm granular, the tissue soft, white, traversed by fibers. Stem usually solitary, up to 20 m long and 5 cm in diam., densely pubescent, becoming less intensely pubescent or rarely glabrate with maturity, commonly somewhat prickly, the prickles straight or slightly upcurved, glossy, yellow-brown, 0.3-2 mm long. Bulbils not seen. Leaves 3 or 5 foliate, rarely simple (juvenile), pubescent to glabrescent above, tomentose below with white to yellowish hairs, sometimes becoming ferrugineous on veins and margins, drying greenish to brownish above; middle leaflet \pm elliptic, 5-15 x 2.5-6.5 cm, apiculate with a blackish, 2-10 mm-long forerunner leaf tip., the secondary veins-3-4 pairs, the

reticulation obscure on both surfaces; lateral leaflets 3-15 x 2-8 cm, inequilateral, the inner half resembling a half of a middle leaflet, the outer half broader with a rounded base and 2-3, primary veins; intermediate leaflets when present intermediate in size, resembling middle leaflet in shape; simple leaves when present broadly ovate to cordiform, with 5-7 primary veins from base; petiole usually shorter than middle leaflet, 3-12 cm long, tomentose commonly with ferrugineous hairs, occasionally prickly near apex or base or both; petioles up to 0.7 mm long, tomentose; stipules absent. Staminate inflorescence paniculate or racemose or both; panicles terminal or axillary, 1-4 per axil, the rachis up to 35 cm long, tomentose; racemes fascicled up to 10 per axil, 20-70-flowered, the axis 1.5-6.5 cm long, tomentose. Flower, 1-1.4 x 1-1.5 mm; bract cordiform to widely depressed ovate, obtuse to acute, 1-1.8 x 1.2-1.8 mm, densely pubescent without; bracteole similar to bract, sometimes narrower, often oblique at base, 0.8-1.4 x 0.7-1.4 mm; pedicel 0.2-1 mm long; torus expanded into a fleshy cuneiform or obdeltoid base of flower; tepals \pm erect but slightly incumbent at apices, often scarious on margin, the outer tepals ovate or triangular, rounded or acute apically, 0.8-1.5 x 0.4-1 mm, membranous to fleshy, pubescent without and on margins, the inner tepals smaller, oblong ovate, rounded apically, 0.7-1.2 x 0.3-0.6 mm, glabrous; stamens distinctly epitepalous, inserted above base of outer tepals, the filaments ca. 0.1 mm long, the anther

0.2-0.3 mm long; staminodes epitepalous, inserted nearly halfway within inner tepals; pistillode 0.4-0.6 mm long, columnar, 3-ridged. Pistillate inflorescence axillary, 1-3 per axil, spicate, pendent, the axis 4-38 cm long, tomentose. Flowers up to 40 per spike, lax; pedicel very short at anthesis; bract and bracteole narrowly ovate to oblong-ovate, acute to acuminate, pubescent without, the bract 1.5-3.7 x 1-1.5 mm, the bracteole 2-2.4 x 0.8-1 mm; tepals almost as in staminate flower but more fleshy, the outer tepals 1-1.5 x 0.6-1 mm, the inner tepals 1-1.4 x 0.5-0.8 mm, pubescent without; staminodes ca 0.1 mm long, inserted at base of tepals; ovary 3-5 x 2-4 mm, densely tomentose; styles connate to halfway, up to 0.5 mm high; stigmas recurved at apex and grooved above. Capsules loosely imbricate, oblong to elliptic, rounded basally, truncate to rounded apically, 1.3-2.2 x 1-1.2 cm, brownish to blackish, densely pubescent to tomentose; wings semi-elliptic, 0.4-0.5 mm broad. Seed 9-14 x 3.5-6 mm including wing, basally cuneate; wing 6.5-12 mm long, yellowish brown.

Distribution. South of the Gangetic plains in India, and in Sri Lanka; occurs chiefly in dry lowlands although occasionally it has been observed in moist regions and at altitudes of ca. 1300 m.

Representative specimens. India. Mysore State, Belgaum Dist: Belgaum, Ritchie 1238 (E); S. Canara Dist. : Mangalore,

Hohenacker 286 (E, GH); Mysore Dist. : Kollegal, Narayanaswami 3457 (GH); Kerala State, Trivandram Dist. : Ponmudi, Ridsdale 136 (K, Mo); Malabar, Wight 1098 (E); Tamil Nadu State, S. Arcot Dist. : Melpat, Barber 1040 (NY); Coimbatore Dist.: Coimbatore, Pullanchy, Cleghoru s.n. (E); Thanjavur Dist.: Nagappattinam, Wight s.n. (E); Mudura Dist.: Periankulam road, Anglade 129 (Jeps); 529 (JEPS); Kanniyakumeri Dist.: Cape Comorin. Wight 943 (E).

SRI LANKA. Anuradhapura Dist.: Mihintale, Sohmer 8138 (GH, MO, US); Polonnaruwa Dist.: between Giritale and Minneriya, Sohmer 8211 (MO, PDA, US); Matale Dist.: between Naula and Dambulla, Jayasuriya et al. 565 (MO, PDA, US); Amparai Dist.: Kokagala, Bernardi 15683 (MO, NY, PDA, US); Padagoda, Fosberg & Sachet 53093 (GH, MO, NY, PDA, US); Colombo Dist.: Urapola, Senaratna s.n. (PDA); Kandy Dist.: Hakkinda, Alston 839 (NY, PDA); W. of Mahiyangana, Davidse & Jayasuriya 8434 (MO, PDA, US); Hambantota Dist.: Ruhuna National Park, Block I, Cooray 69111723 (GH, JEPS, MO, NY, PDA, US); Wirawan 684 (PDA, US).

Common names and uses. India: Suta alu, Nula dampu, Nulvalli kilangu, Eenthi Kacchel, Kalu Kilangu; Sri Lanka: Uyala.

This species is easily recognized by the densely tomentose under-surface of the leaves.

Fig. 23. Dioscorea tomentosa

A. Staminate plant (Davidse & Jayasuriya 8434, MO).

B. Pistillate plant (Jayasuriya et al. 565, MO).

PREPARATION OF SPECIMENS SUPPORTED BY A GRANT FROM THE SUNNEN FOUNDATION, ST. LOUIS.

MISSOURI
BOTANICAL GARDEN
HERBARIUM

No 2425445



NEW YORK BOTANICAL GARDEN
 HERBARIUM

PLANTS of CEYLON

Dioscorea tomentosa Heyne
(Dioscoreaceae)

Locality: 2200 ft. elevation, Kandy District, 20
miles N of Kandy, on the road to
the Kandy Forest.

Occurrence: Forest, 2200 ft.

Date: 14 Nov 1974

Alt: 2200 m

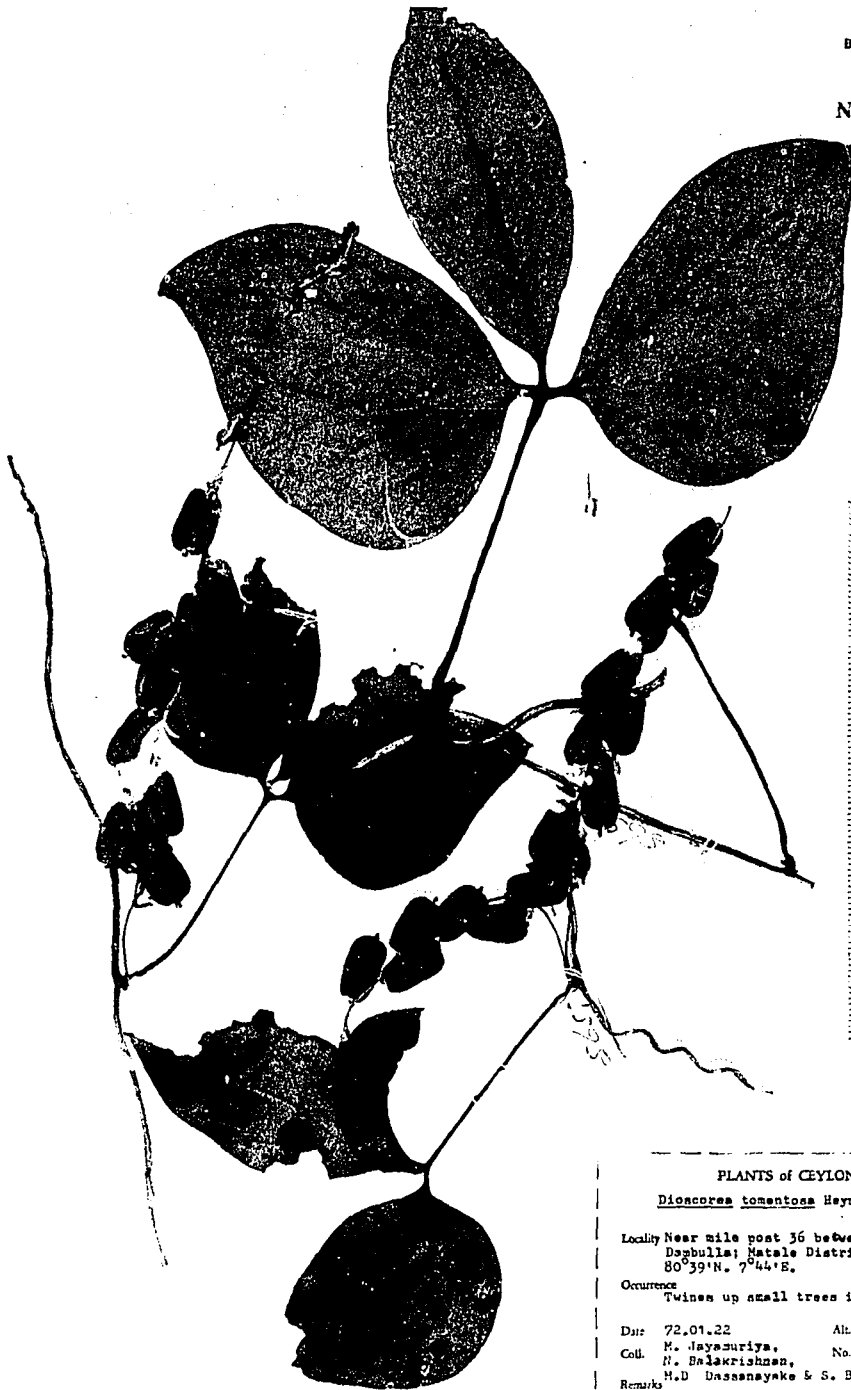
Coll: Gerrit Davidse
A.H.H. Jayawardeniya

No: 6125

Remarks: Vase; inflorescence 1/2 in.

MISSOURI
BOTANICAL GARDEN
HERBARIUM

No 2298333



PLANTS of CEYLON

Dioscorea tomentosa Heyne ex RothLocality Near mile post 36 between Naula-
Dagbulla; Matale District;
80°39'N. 7°44'E.Occurrence
Twines up small trees in scrub.

Date 72.01.22 Alt. Low m

Coll. M. Jayasuriya, No. 565

Remarks H.D. Dassanayake & S. Balasubramani

Dioscoreaceae;

6. *Dioscorea pentaphylla* Linnaeus, Sp. pl 1032. 1753; Kunth, Enum. pl. 5: 396. 1850; Hooker f. in Trimen, Handb. Fl. Ceylon 4: 276. 1898; Knuth in Engler, Pflanzenr. 87 (IV. 43): 145. 1924; Prain & Burkill, Ann. Roy. Bot. Gard. Calcutta 14: 160, pl. 66-68. 1936; Burkill, Fl. Males. 4: 315. 1951. Type : Rheede, Hort. malab. 7: pl. 35. 1688. (lectotype chosen here). Fig. 24.

Dioscorea triphylla Linnaeus, Sp. pl. 1032. 1753. Type: Rheede, Hort. malab. 7: pl. 33. 1688 (lectotype chosen here).

Dioscorea digitata Miller, Gard. dict. abr. ed.8. 1768, in part. Type: description in Rheede, Hort. malab. 7. 67. 1688.

Dioscorea spinosa Burman, Fl. malab. 5. 1769. Type: Rheede, Hort. malab. 7: pl. 34. 1688

Ubiom scandens Jaume Saint-Hilaire, Expos. fam. nat. 1: 106. 1805. Type: Rumphius, Herb. amboin. 5. pl. 127. 1750

Botryosicyos pentaphyllum Hochstetter, Flora 27 (Bes. Beil. Bd. 1): 3. 1844. Basionym. *Dioscorea pentaphylla* Linnaeus

Dioscorea kleiniana Kunth, Enum. pl. 5: 394. 1850. Type: India, Willdenow Herb. no. 18411 (B, n.v.).

Humatris triphylla Salisbury, Gen. pl. 12 1866. Basionym. *Dioscorea triphylla* Linnaeus

Dioscorea jacquemontia Hooker f., Fl. Brit. India 6: 290.

1892. Type: India, Maharashtra State: Concan, between Poona and Carli, Jacquemont s.n. (syntype, n.v.); Mysore State, Belgaum Dist. : Belgaum, Ritchie s.n. (syntype, E).

Dioscorea arachnida Prain & Burkill, J. & Proc. Asiat. Soc.

Bengal 10: 21. 1914. Type: India, Assam State, Nowgong Dist. : near Lumding, Lungfer, Kalka-pershad 35581 (holotype, K; isotype, CAL).

Dioscorea pentaphylla Linnaeus var. linnaei Prain & Burkill,

ibid. 10: 23. 1914. Type: India, Wight in Wallich Cat. no. 5102-C (lectotype chosen here, K; isolectotype, E).

Dioscorea pentaphylla Linnaeus var. thwaitesii Prain &

Burkill, Ibid. 10:23. 1914. Type: Sri Lanka, Kandy Dist.: Hantane, Thawaites C.P. 2869, in part (holotype, K, n.v., isotype, PDA).

Dioscorea pentaphylla Linnaeus var. suli Prain & Burkill,

Ibid. 10: 23. 1914. Type: India, W. Bengal State, Darjeeling Dist.: Bakharikot, Cowan 93 (lectotype chosen here, E).

Dioscorea pentaphylla Linnaeus var. jacquemontii Prain &

Burkill, Ibid. 10: 23. 1914. Basionym. Dioscorea jacquemontii Hooker f.

Dioscorea pentaphylla Linnaeus var. cardonii Prain & Burkill,

ibid. 10: 23. 1914. Type: from India, Bihar State, Chota Nagpur region, no specimen cited.

Dioscorea pentaphylla Linnaeus var. simplicifolia Prain & Burkill, Ibid. 10: 23. 1914. Type: from India, Maharashtra State, Amraoti Dist.: Melghat Hills, no specimen cited.

Dioscorea pentaphylla Linnaeus var. rheedii Prain & Burkill, Ibid. 10: 23. 1914. Type: India, Tamil Nadu State, Tirunelvely Dist.: Kuttalam, Wight 2823 (lectotype chosen here, NY).

Dioscorea pentaphylla Linnaeus var. malaica Prain & Burkill, Ibid. 10: 23. 1914. Type: from Malay Peninsula, no specimen cited.

Dioscorea pentaphylla Linnaeus var. hortorum Prain & Burkill, Ibid. 10:23. 1914. Type: from cultivation in India, no specimen cited.

Dioscorea pentaphylla Linnaeus var. communis Prain & Burkill, Ibid. 10: 23. 1914. Type: Bangladesh, Sylhet Dist.: Sylhet, Wallich 5098-F (lectotype chosen here, K; isolectotype, male plant (a), K, E).

Dioscorea pentaphylla Linnaeus var. kussok Prain & Burkill, Ibid. 10: 23. 1914. Type: from India, Sikkim State, no specimen cited.

Dioscorea kalkapershadii Prain & Burkill, Ibid. 10: 23. 1914. Syntype: India, Bihar State, Ranchi Dist.: Rangarit Cardon 12 (K), Kalaka-pershad 34389 (n.v.), 34390 (n.v.); Orissa State, Mayurbhanj Dist.: Baripada, Holmes 33185

(n.v.), 33825 (n.v.); Balasore Dist.: Patharchaki,
Kalka pershad 34323 (K); Tamil Nadu State, Salem Dist.:
 Shevaroy Hills, Perrottet 1 (n.v.), 334 (n.v.)

Dioscorea pentaphylla Linnaeus var. cyathiformis Haines,
 Bot. Bihar & Orissa 3: 1124. 1922. Type: from India,
 Bihar State, Ranchi Dist.: Angul, no specimen cited.

Dioscorea pentaphylla Linnaeus var. unifoliolata Uline
 [ms.] ex Knuth in Engler, Pflanzenr. 87 (IV. 43): 146.
 1924. Type: ? Java, Moll s.n. (holotype, BR, n.v.).

Dioscorea pentaphylla Linnaeus var. papuana Burkill, Gard.
 Bull. Straits Settl. 3: 258. 1924. Type: from Papua- New
 Guinea, near Port Morseby, no specimen cited.

Dioscorea pentaphylla Linnaeus var. javaniva Burkill, Ibid.
 3: 258. 1924. Type: from Java, no specimen cited.

Dioscorea pentaphylla Linnaeus var. palmata Burkill, Ibid.
 3: 258. 1924. Type: from cultivation in Philippines, no
 specimen cited.

Dioscorea pentaphylla Linnaeus var. sacerdotalis Burkill,
 Ibid. 3: 258. 1924. Type: from cultivation in Java, no
 specimen cited.

Dioscorea pentaphylla Linnaeus var. siamica Prain & Burkill,
 Ann Roy. Bot. Gard. Calcutta 14: 165. 1936. Type: from
 cultivation in Thailand, no specimen cited.

Tuber usually single, annual, globose to palmately lobed and creeping beneath the soil-surface, or elongated up to 1.3 m and 4 cm in diam. and penetrating deeply, or of intermediate in nature, with almost none to abundant bristly roots arising from upper parts and long roots produced near the soil-surface, the tissue whitish or lemon-yellow, sometimes with purple flecks, tender and esculent in deep-burying forms and usually firm and nauseous in others. Stem solitary, up to 10 m long and 7 mm in diam., pubescent with white or rarely ferrugineous hairs, glabrate with maturity, usually armed with prickles, mostly toward the lower internodes, the prickles up to 4 mm long, usually directed or curved upward. Bulbils abundant, globose or shortly ellipsoid, rarely 8-10 cm long and cylindrical with numerous rootlets directed downward, the tissue yellowish to purple. Leaves alternate, 3-5-foliolate, rarely simple or 2-foliolate, variously pubescent on both surfaces with usually whitish hairs, often glabrescent above, rarely completely glabrous, gland-dotted below, drying green or yellowish or brownish; middle leaflet elliptic to oblanceolate to broadly obovate, basally acute, apically cuspidate or shortly acuminate, 4-18 x 2-8 cm; secondary veins 3-4 pairs, the reticulation obscure above, distinct below; lateral leaflets relatively smaller, 2.5-14 x 1.5-7.5 cm, usually inequilateral, the inner half resembling a half of middle leaflet, the outer half broader with a rounded base and 2 primary veins; intermediate leaflets when present intermediate in size,

resembling middle leaflet in shape; petiole usually shorter than middle leaflet, 2-15 cm long, channelled above, glabrous to pubescent with white or more often ferrugineous hairs, occasionally with few small prickles; petiolules up to 1.5 cm long, glabrous or relatively more pubescent than petiole, rarely scarcely prickly; stipules absent, sometimes replaced by prickles. Staminate inflorescence paniculate or racemose or both in same or separate axils; panicles terminal or 1-3 per axil, the rachis up to 50 cm long, densely pubescent with white or ferrugineous hairs; racemes fascicled up to 11 per axil, 1.5-6.5 cm long, 10-75-flowered, the axis densely pubescent. Flower 1.2-1.8 x 1.8-2.2 mm ; bract cordiform to widely depressed ovate, basally truncate to cordate or oblique, acuminate to cuspidate, 1.2-2.3 x 1.4-2.4 mm, usually densely pubescent without or atleast on the margins, rarely completely glabrous; bracteole \pm similar to bract but slightly smaller, 1-2 x 0.7-2 mm; pedicel 0.2-1.7 mm long, densely pubescent; torus expanded into flat base of the flower; tepals \pm erect but slightly incumbent at apices, often scarious on margins, the outer tepals ovate or triangular, 0.8-1.4 x 0.7-1.3 mm, membranous to fleshy, usually pubescent without near the margins, rarely completely glabrous, the inner tepals \pm similar to outer tepals, glabrous, rarely pubescent at apices; stamens free or inserted at base of the outer tepals, the filaments 0.2 mm long, the anther 0.2-0.4 mm long; staminodes up to 0.4(0.8) mm. long, free or inserted at base of the inner

tepals; pistillode 0.4-0.8 mm long, stumpy or conical. Pistillate inflorescence axillary, 1-3 per axil, spicate, pendent, the axis 5-30 cm long, angled, densely pubescent with whitish or yellowish or ferrugineous hairs. Flowers up to 50 per spike, lax; pedicel very short at anthesis; bract ovate to oblong-ovate, acuminate to cuspidate 1.5-2.8 x 1-2.3 mm, decurrent on the axis, pubescent without; bracteole similar to bract but smaller, 1-2.3 x 0.5-1.4 mm; tepals \pm as in staminate but slightly larger, fleshy, the outer tepals 1-2.3 x 0.5-1.4 mm, the inner tepals 1-2 x 0.5-1.4 mm; staminodes ca 0.1 mm long, inserted at base of the tepals; ovary 2-8 x 0.7-5 mm, densely or often wooly pubescent, with a short or indistinct neck; styles connate, 0.3-0.4 mm high; stigmas recurved at apex and parted into 2 lobes. Capsules loosely imbricate, oblong, basally rounded, apically truncate to retuse, 2-3 x 1-1.5 cm, becoming glossy blackish and glabrate with maturity; wings \pm semi-elliptic, 6-7 mm broad; stipe 2-3 mm long. Seed ca. 10 x 5 mm including the wing, basally cuneate; wing 5-7.5 mm long, smoky brown.

Distribution. Throughout the moist tropical Asia and eastward to the furthest islands of the Pacific; also cultivated in Indonesia and Pacific Islands; occurs from low altitudes to ca. 1750 m.

Representative specimens. INDIA. Himachal Pradesh State, Mahasu Dist. : Simla, Lace s.n.(E); Dehra Dun Dist. : Dehra Dun, Ravzada s.n. (GH); Uttar Pradesh State, Allahabad Dist. : Allahabad, Chatham Limes, Prasad 1365 (Mo); Saharanpur Dist., Saharanpur, Jameson s.n. (E); Sikkim State, Sikkim, long s.n.(E); W. Bengal State, Howrah Dist.: Calcutta, Helper s.n. (E, GH, NY, US); Hooghly Dist, Hooghly Watt 44 (E); Darjeeling Dist. : s.loc., Cowan s.n. (E); Assam State, S.loc. Masters s.n. (E); Jenkin s.n.(E); Nowgong Dist. : Luming, Kalka-pershad 35581 (K); Bihar State, Monghyr Dist. : Monghyr, Buchanan-Hamilton in Wallich 5098-A (E); Manipur State, Makru, Meebold 6025 (E); Orissa State, Dhenkanal Dist. : between Raigoda and Labangi, Lace 2566 (E); Maharashtra State, Kolaba State, Khandala, Santapau 13854 (E); 13948 (Mo); Andhra Pradesh State, Hyderabad, Cambell s.n. (E); Mysore State, Belgaum Dist. : Belgaum, Ritchie 1238 (E); Dharwar Dist. : Dharwar, s.coll, s.n. (E) Bellary Dist. : Kotturu, Barnes 992 (GH) Hassan Dist. : Hebbsale, Saldanha 14449 (E, MO, US) North Canara Dist. : Angadi, Meebold 10634 (E); Mysore Dist. : Biligiri Rangan Hills, Barnes 719 (GH); Kerala State, Trichur Dist. : Travancore Cardamon Hills, Fernandes 349 (GH); Tamil Nadu State, Chingleput Dist. : Madras Thomson s.n. (NY); Salem Dist. : Hosur Taluk, Yeshoda 296 (GH) Coimbatore Dist. : Ootacamund, Cleghora s.n. (E); Thanjavur Dist. : s.loc., Wight s.n. (E); Madurai Dist. : Palni Hills, Wight 3093 (E).

NEPAL. N of Chainpur, Stainton 1523 (E); Sitalpati, Polunin et al. 5828 (E).

Bhutan. Chukka Timpu, Cooper 1217 (E); Punakha, Cooper 2816 (E).

BANGLADESH. Chittagony Dist. : Teknaf, Khan 589 (E); Cox's Bazar, Sinclair 3259 (E).

SRI LANKA. Jaffna Dist.: Keerimalai, Kankesanturai, Kundu & Balakrishnan 661 (PDA, US); Matale Dist.: between Dambulla and Anuradhapura Cooray 70013101R (JEPS, Mo, NY, PDA, US); Kandy Dist.: Madugoda, Jayasuriya et al. 506 (PDA, US); 509 (PDA, US); Nuwara-Eliya Dist.: Hakgala, Balakrishnan 427 (MO, US); Monaragala Dist.: Monaragala, Cramer 5041 (MO, PDA, US); Kalutara Dist.: Kalutara, Kundu & Balakrishnan 479 (MO, PDA, US); Matara Dist.: between Deniyaya and Kotapola, Huber 599 (E, PDA, US); Hambantota Dist.: Ruhuna National Park, Block 1 Müeller-Dombois 69010706 (GH, JEPS, NY, PDA).

Common names and uses. India: Suli bok, Begur, Alshi, Gabadu, Shendwel, Chataveli, Gha jir, Kussok ding; Indonesia: Ubi pasir, Ubi devata, Rabet sosoan, Hata. Tubers are edible, although with some tendency to be nauseous; more palatable forms have been evolved by selective cultivation.

As the basis for D. pentaphylla, Linnaeus cited 4 references which include one illustration, namely, Rheede's plate no. 35, the lectotype chosen for the species. Rheede's plate no. 33,

which Linnaeus cited under D. triphylla, is clearly the same as D. pentaphylla and is used to lectotypify the former.

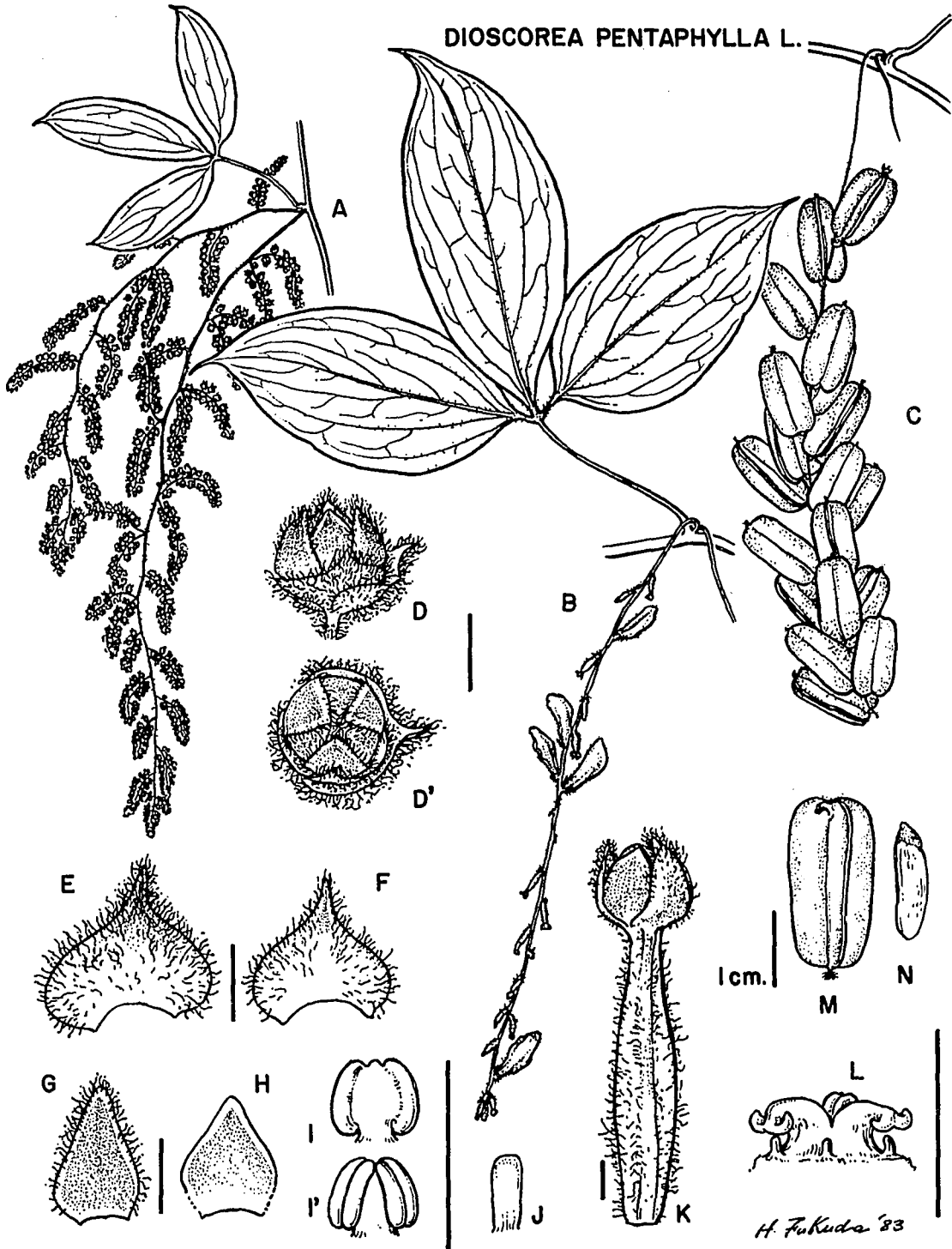
Due to the widespread distribution of the species, remarkable interpopulational variations are seen in the shape and size of the leaflets, degree of pubescence, and the nature of tubers. The latter is also affected to a great extent by cultivation. These variations led Prain & Burkill (1914, 1936) to split the taxon into 2 species and 16 varieties which are reduced to D. pentaphylla in this treatment.

Fig. 24. Dioscorea pentaphylla

- A. Staminate plant showing panicles and upper surface of leaf (x 2/3, from Cowan s.n., E).
- B. Pistillate plant showing a spike and lower surface of leaf (x 2/3, from Jayasuriya et al. 507, PDA).
- C. A spike with mature capsules (x 2/3, from Lace 2566, E).
- D, D'. Side view and top view respectively of staminate flower (from Ramamoorthy 317, US)
- E. Outer surface of bract.
- F. Outer surface of bracteole.
- G. Outer surface of outer tepal.
- H. Outer surface of inner tepal.
- I, I'. Outer view and inner view respectively of anther.
- J. Staminode.
- K. Pistillate flower (from Jayasuriya et al. 507, PDA).
- L. Upper part of pistil showing stigmas and staminodes.
- M. Capsule showing recurved stipe.
- N. Seed.

(scales = 1 mm, except for M & N).

DIOSCOREA PENTAPHYLLA L.



7. *Dioscorea kamoensis* Kunth, Enum. pl. 5: 395.

1850; Prain & Burkill, Ann. Roy. Bot. Gard. Calcutta 14: 146, pl. 62-64. 1936. Type: India, Uttar Pradesh, Kumaun Division, Wallich 5098-E (holotype, K; isotype, BM). Fig. 25A, B).

Dioscorea kumaonensis Hooker f., Fl. Brit. India 6: 290.

1892 (orth. var.).

Dioscorea fargesii Franchet, Rev. Hort. Agric. Afrique N.

68: 541. 1896. Syntype (n.v.): China, Sze-chuan Prov.:

Tchen-keou-tin, Farges 227 ; Hu-peh Prov.: near

Ichang, Henry 2666, 7501

Dioscorea delavay Franchet, Ibid. 68: 541. 1896.

Syntype(n.v.): China, Yun-nan Prov.: ta-pin-tze,

Delavay 1825, 1828.

Dioscorea kamoensis Kunth var. *vera* Prain & Burkill,

J. & Proc. Asiat. Soc. Bengal 10: 21. 1914. Type:

India Uttar Pradesh, Kumaon Div.: Lohathal, Strachy &

Winterbottom 6 (lectotype chosen here, K;

isolectotype, GH).

Dioscorea kamoensis Kunth var. *straminea* Prain &

Burkill Ibid. 10: 21. 1914. Syntype: China, Yun-nan

Prov. Meng-tze, Henry 9495-C (n.v.), 11301 (US).

Dioscorea kamoensis Kunth var. *fargesii* Prain &

Burkill Ibid. 10: 21. 1914. Type: China, Sze-chuan

Prov.: N. Wushan, Henry 7103 (lectotype chosen here).

Dioscorea kamoensis Kunth var. delavay Prain & Burkill,
 Ibid. 10: 22. 1914. Syntype (n.v.): China, Yun-nan Prov.:
Delavay 563, 1825, 1828, 3318, 3833; Sze-chuan Prov.:
Farges 227; Kwei-chow Prov.: Chaffanjou & Bodinier 2408;
 Hup-eh Prov.: Henry 6419 .

Dioscorea kamoensis Kunth var. henryi Prain & Burkill,
 Ibid. 10: 22. 1914. Syntype: China, Yun-nan Prov.: Henry
9495 (n.v.), 9715 (isosyntype, NY); Kwei-chow Prov.:
Chaffanjon & Bodinier s.n. (n.v.).

Dioscorea kamaonensis Knuth in Engler, Pflanzenr. 87
 (IV. 43): 140. 1924 (orth. var.).

Dioscorea engleriana Knuth in Engler, Ibid. 87(IV. 43): 140.
 1924. Type: China, Yun-nan Prov.: Meng-tze, Henry 9495-B
 (n.v.).

Dioscorea firma Knuth in Engler, Ibid. 87(IV. 43): 141. 1924.
 China, Yun-nan Prov.: Lakou, Maire 7340 (holotype, B, n.v.).

Dioscorea rotundifolia Knuth in Engler, Ibid. 87 (IV. 43):
 142. 1924. Type: China, Yun-nan Prov. : Pan-long-tse,
Maire 6704 (holotype, B, n.v.)

Dioscorea mengtzeana Kunth in Engler, Ibid. 87 (IV. 43):
 142. 1924. Type: China, Yun-nan Prov.: Meng-tze, Henry
11301 (holotype, B, n.v.; isotype, US).

Dioscorea subfusca Knuth in Engler, Ibid. 87 (IV. 43): 143.
 1924. Type: China, Hu-peh Prov.: Henry 4486 (holotype, B,
 (n.v.).

Dioscorea delavayi (Prain & Burkill) Knuth in Engler, Ibid.

87 (IV. 43): 143. 1924. Basionym. Dioscorea kamoensis
Kunth var. delavayi Prain & Burkill.

Dioscorea burkillii (Prain & Burkill) Knuth in Engler, Ibid.

87 (IV. 43): 143. 1924. Basionym. Dioscorea kamoensis
Kunth var. henryi Prain & Burkill.

Dioscorea mairei Knuth in Engler, Ibid. 87 (IV. 43): 144.

1924, non Leveille, 1913. Type: China, Yun-nan Prov.:
Lou-ki-tuin, Maire 6805 (holotype, B, n.v.).

Dioscorea dissecta Knuth in Engler, Ibid. 87 (IV. 43): 355.

1924. Basionym. Dioscorea mairei Knuth in Engler.

Dioscorea kamoensis Kunth var. engleriana Prain & Burkill,

Ann. Roy. Bot. Gard. Calcutta 14: 148, pl. 62 (fig. 12).
1936. Syntype (n.v.): China, Yun-nan Prov.: Teng-yueh
Valley, Forrest 8865; Meng-tze, Henry 11301.

Dioscorea kamoensis Kunth var. praecox Prain & Burkill,

Ibid. 14: 148, pl. 63 (fig. 1-4). 1936. Syntype (n.v.):
China, Yun-nan Prov.: Rock 5081 in part; Tschang-tschun-
shan, Schoch 134.

Dioscorea kamoensis Kunth var. media Prain & Burkill,

Ibid. 14: 148, pl. 64 (fig. 8, 9). 1936. Syntype (n.v.):
China, Yun-nan Prov.: Maire 3577, 3598.

Dioscorea kamoensis Kunth var. brevifolia Prain & Burkill,

Ibid. 14: 148, pl. 64 (fig. 10, 11). 1936. Syntype (n.v.):
China, Yun-nan Prov.: Rock 5081 in part; Lou-ki-tuin,
Maire 6805-b.

Tuber usually single, annual, \pm ellipsoidal, usually penetrating deeply into the soil, densely covered with small roots. Stem up to 4 mm in diam., densely pubescent when young with whitish or tawny or ferrugineous hairs, glabrate with age, unarmed. Bulbils abundant, depressed glabose, greyish brown, pubescent when young. Leaves alternate, 3(-5)- foliate or rarely simple among inflorescences, glabrescent to pubescent above with whitish hairs, pubescent at least on the veins below, drying green; middle leaflet narrowly elliptic to elliptic, basally acute, apically acuminate to finely acuminate, 3.5-13.5 x 1.5-4.5 cm; secondary veins 4-6-pairs, the reticulation obscure on both sides; lateral leaflets relatively small, 2-10 x 1-4.3 cm, often inequilateral with a broader outer half with a rounded base and 1 or 2 acrodromous basal primary veins; petiole shorter than the middle leaflet, 1.5-12.5 cm long, channelled above, usually pubescent with tawny or often ferrugineous hairs; petioles up to 2 mm long, densely pubescent; stipules occasional, oblong or flipper-shaped, 0.8-1.5 x 0.4-1 mm. Staminate inflorescence paniculate or racemose or both in same or separate axils, usually ascending, densely pubescent with tawny or ferrugineous hairs; panicles few, solitary in axils or often terminal, 4-15 cm long; racemes abundant, fascicled up to 6 per axil, 2-9 cm long with 1-2 (-4) cm long sterile zone at base, 10-65-flowered. Flower 1.5-2.5 x 1.5-2.5 mm ; bract ovate to widely ovate, sometimes basally oblique, apically acuminate or commonly apiculate or

caudate, 2.5-3.5 x 1.5-2.5 mm, with a 0.5-1.5 mm-long acumen which usually overtops the flower, densely or rarely sparingly pubescent without and on margins; bracteole similar to bract but smaller with relatively short acumen, 1.5-2 x 1-2 mm; pedicel 0.5-2 mm long, pubescent; torus broadly cuneate at base; tepals ovate, the outer tepals 1.3-2 x 0.8-1.4 mm, slightly fleshy, pubescent without, rarely glabrous, the inner tepals 1.2-2 x 0.7-1.2 mm, often incurved apically, glabrous or sparsely pubescent without; stamens free or inserted at the base of outer tepals, the filament ca. 0.1 mm long, the anther 0.2-0.4 mm long; staminodes 0.5-1.2 mm long, free or inserted at base of the inner tepals; pistillode 0.7-1.2 mm long, columnar, broadened at apex. Pistillate inflorescence axillary, 1 or 2 per axil, spicate, pendent, the axis 5-25 cm long, densely pubescent with white to ferrugineous hairs. Flowers 10-40 per spike, lax; pedicel very short at anthesis; bract and bracteole as in staminate flower; tepals as in staminate flower but relatively small, the outer tepal 1-1.8 x 0.6-1 mm, the inner tepals 1-1.7 x 0.5-0.8 mm, often pubescent without; staminodes 0.2-0.4 mm long, dimorphic, the outer cycle resembling stamens, the inner cycle clavate; ovary 3-6 x 2-2.8 mm, densely pubescent with tawny or ferrugineous hairs, with a very short neck; styles free or connate at base, 0.2-0.5 mm long, stigmas recurved apically and 2-parted or ridged above. Capsules imbricate, oblong, basally rounded to truncate, apically truncate, ca. 2 x 1.5 cm, becoming glossy, tawny, and

glabrate with maturity; wing ca. 0.7 mm broad; stipe up to 3 mm long. Seeds ca. 12x5 mm including the wing, basally cuneate; wing 8-9 mm long, pale brown.

Distribution. Himalaya and eastward to south-western China and northern Thailand; usually occurs between 1200-3000 m, although collections have been gathered at much higher altitudes, for instance, at ca. 4200 m in southwestern China.

Representative specimens. INDIA. Uttar Pradesh State, Kumaon Division, Lohathal, Strachy & Winterbottom 6 (GH, K); Meghalaya State, Khasia Hills, Hooker & Thomson s.n. (BM, E, GH); Manipur State, Ukhrul, Kingdon-Ward 17897 (BM); 18290 (NY).

NEPAL. Barikot, Polunin et al. 472 (E); Lalitpur Dist.: Bagmati zone, Godavari Botanical Garden, Nicolson 2281 (US).

BHUTAN. Tashiyangsi chu valley, Cooper 4470 (E).

BANGLADESH. Sylhet Dist. : Sylhet, Wallich 5102-D (K).

Common names and uses. India, Sikkim State: Tukjhok. The nature of the tubers is not well known, but it would seem to be only rarely used as food.

Knuth proposed several species differing in the relative lengths of staminate bracts, color of pubescence, and minor variations in leaf shape and size. Prain & Burkill divided this species into several varieties using more or less the same characters. Examination of several specimens, including types,

revealed that leaf-shape is very variable that varieties cannot be delimited using this character. The delayed leaf-formation, which Prain & Burkill used to distinguish var. praecox, is probably due to unusual aridity, and it is possibly an ecological modification rather than a variety, as they have even suggested (Prain & Burkill 1936). The relative lengths of staminate bracts vary even within a individual and the color of the pubescence, as is well known, differs in intensity with the changes of altitudes, and therefore the use of such variations to split the species is not recommended. Prain & Burkill (1936) indicated that varieties of D. kamoensis occur intermixed, which suggests that the aforementioned morphological differences, at least to some extent, are intrapopulational. They also based different varieties on different sexes, which is inadmissible.

Fig. 25. Dioscorea kamoensis

A. Staminate plant (Henry 11301, US).

B. Pistillate plant (Steward et al. 465, NY).



UNITED STATES NATIONAL MUSEUM

PLANTS OF CHINA

Risneria

Meng-tze

S. 11301 A. HENKEL

CHINA

11301

Meng-tze

Risneria

Risneria
11301

Meng-tze

Risneria

HERBARIUM, UNIVERSITY OF TORONTO

Chinese name _____
 P. N. _____

Locality *To Ho Shan, S. of Hsin Yang*

Habitat _____

Altitude above the sea _____ Meters

Tree or shrub; bush; vine; herb _____

Height of plant _____ cm

Flower _____

Special notes _____

Field No. *447* Herbarium No. _____

Collector *S. H. H. & H. C. Chou*

Date *Sept 25 1931*



SEP 25 1931

Dioscorea kamomensis
 Kunth

Var. *largesii*

Determinavit *Rehder*

PLANTS OF KWEICHOW PROVINCE, CHINA

Dioscorea pentaphylla?

Brushy slope Alt. 1100 m.
 Twining herb
 Capsule light green To Ho Shan
 FAN CHING SHAN

COLLECTED IN COOPERATION BETWEEN THE ARNOLD ARBORETUM OF HARVARD UNIVERSITY, THE NEW YORK BOTANICAL GARDEN, AND THE UNIVERSITY OF TORONTO
 By Albert N. Seward, C. Y. Chiao, and H. C. Chou
 No. 465 IX/25 1931

NEW YORK BOTANICAL GARDEN

8. Dioscorea melanophyma Prain & Burkill, J. & Proc. Asiat. Soc. Bengal, 4: 452, 1902; Knuth in Engler, Pflanzenr. 87 (IV. 43): 139. 1924; Parker, Forrest, Fl. Punjab 519. 1924; Prain & Burkill, Ann. Roy. Bot. Gard. Calcutta 14 : 143. 1936.
 Type: Bangladesh, Sylhet Dist. : Sylhet, de Silva in Wallich no. 9032 (holotype, K). Fig. 26A, B.

Tubers ovoid, up to 5 x 3.5 cm, covered with numerous roots. Stem solitary, arising from a woody base on top of the tuber, up to 4 mm in diam., glabrous at maturity, usually finely ridged and straw-colored when dry, unarmed. Bulbils abundant, in axils of leaves and among inflorescences, glabose, up to 1 cm wide, glossy, black, sparingly pubescent when young. Leaves alternate, 3-5 (6)-foliolate, rarely simple among inflorescences, glabrous on both surfaces, green or ochre to brown when dry; middle leaflet narrowly elliptic, ca. four times as long as as broad, 5-14 x 1-3 cm, basally narrow-cuneate, apically apiculate with a fine 1.5-5 mm-long tip; secondary veins 5-6 pairs, the reticulation obscure on both surfaces; lateral leaflets similar to middle leaflets or oblique due to a slightly broader outer half with 1-2 acrodromous, basal primary veins, 4-8 x 1-2.5 cm; intermediate leaflets when present \pm similar to the middle leaflet; petiole shorter than the middle leaflet, 2-7 cm long, channelled above, glabrous; petiolules 1-4 mm long, glabrous; stipules common, bluntly triangular or flipper-shaped, 1-3 x 0.7-2 mm. Staminate

inflorescence paniculate or racemose or both in same or separate axils, pubescent; panicles terminal or 1-2 per axil, 3-30 cm long; racemes 1-3 per axil, 2-8 cm long, with ca. 1 cm-long, basal, sterile zone, 15-40-flowered. Flower 1.3-1.5 x 1.5-1.8 mm; bract depressed-ovate, 1.6-2 x 1.6-2 mm, with a apiculate to aristate, ca. 0.5 mm-long, blackened apex, pubescent without; bracteole widely depressed-ovate, mucronate at apex, 1-1.2 x 1.4 mm, pubescent without; pedicel 0.6-10 mm long, pubescent; torus expanded into a cuneate base of the flower; tepals ovate to widely ovate, apically acute, 0.7-1 x 0.5-0.8 mm, the outer tepals pubescent especially on the margins, the inner tepals glabrous or with few hairs without; stamens free or inserted at base of the outer tepals, the filament ca. 0.1 mm long, the anther ca. 0.3 mm long; staminodes 0.4-0.6 mm long, free or inserted at base of the inner tepals; pistillode 0.4-0.6 mm high, columnar, broadened at apex, \pm 3-ridged. Pistillate inflorescence axillary, 1-2 per axil, spicate, pendent, the axis 8-20 cm long, pubescent. Flowers 25-40 per spike, somewhat compact; bract obovate, ca. 2.5 x 1.3 mm, with a apiculate to aristate, ca. 0.5 mm- long tip, pubescent without; bracteole narrowly ovate, acute to acuminate, ca. 1.5 x 0.5 mm long, pubescent without; pedicel very short at anthesis; outer tepals widely deltate, ca. 1.2 x 1 mm, pubescent without, the inner tepals similar to outer tepals, elliptic, apically rounded; staminodes 0.1-0.2 mm long; ovary 3-4 x 1.5-1.8 mm, densely or wooly

pubescent, with a very short neck; styles connate to ca. halfway, ca. 0.3 mm long; stigmas slightly reflexed and ridged above. Capsules strongly imbricate, oblong to elliptic, basally rounded, apically truncate or rounded or obtuse, 1.5-2 x 1 cm, straw-colored, glabrate at maturity; wings \pm semielliptic, 4-5 mm broad, firm-chartaceous. Seed 13-15 x 4-5 mm including wing, the wing ca 10 x 4.5 mm, ochre.

Distribution. Himalaya, from the eastern border of Kashmir State to Nepal, southern parts of Khasia Hills in Assam State in India, and south-western China; occurs generally between 1200 and 2200 m, although it has been collected at altitudes of ca. 675 m in India, and at ca. 3000 m in China.

Representative specimens. INDIA. Himachal Pradesh State, Chamba Dist.: Sao Valley, Lace 1201 (E); Kangra Dist.: Kulu Cooper 5677 (E), Koelz 1410 (NY); Mahasu Dist.: Simla, Drummond 1885 (E, JEPS); Uttar Pradesh State, Dehra Dun Dist.: Mussoorie, Stewart 11288 (NY); Almora Dist.: Strachy & Winterbottom 5 (GH).

NEPAL. Samela, Polunin et al 507 (E); Mugu Karnali Valley, Polunin et al 3025 (E).

BHUTAN. Chalimarpha Timpu, Cooper 1479 (E).

BANGLADESH. Sylhet Dist. Sylhet, De Silva in Wallich 9032 (K).

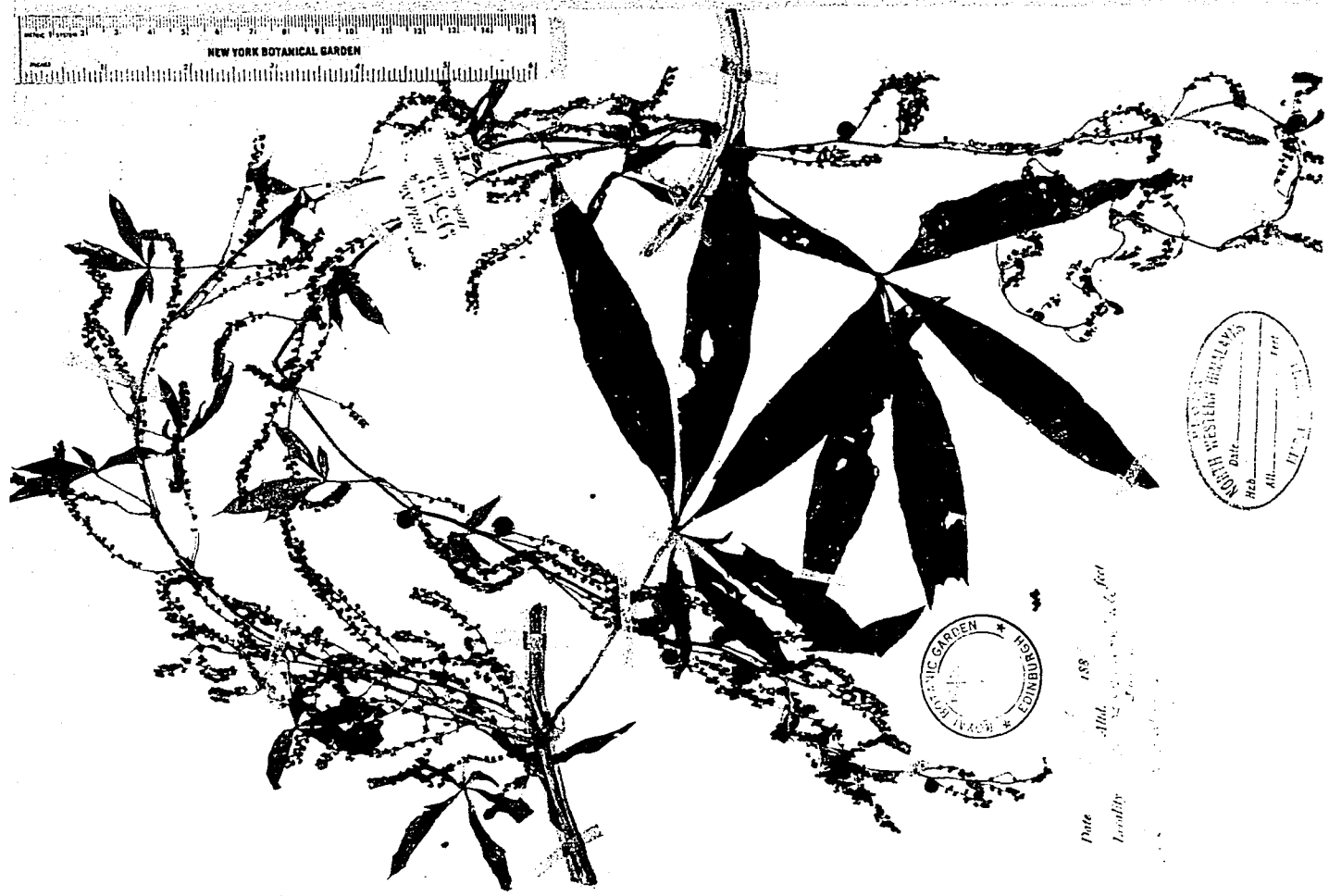
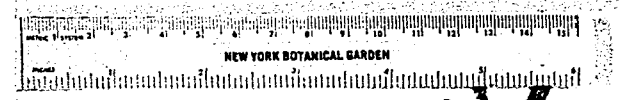
Local names and uses. India: Mungaya, Mengwa, Phan klau; China: Tsie-chou-hoa. Tubers are edible.

Closely allied to D. kamoensis but easily distinguished from it by the glabrous nature of the plant and glossy black bulbils.

Fig. 26. Dioscorea melanophyma

A. Staminate plant (Watt 9543)

B. Pistillate plant (Henry 10253)

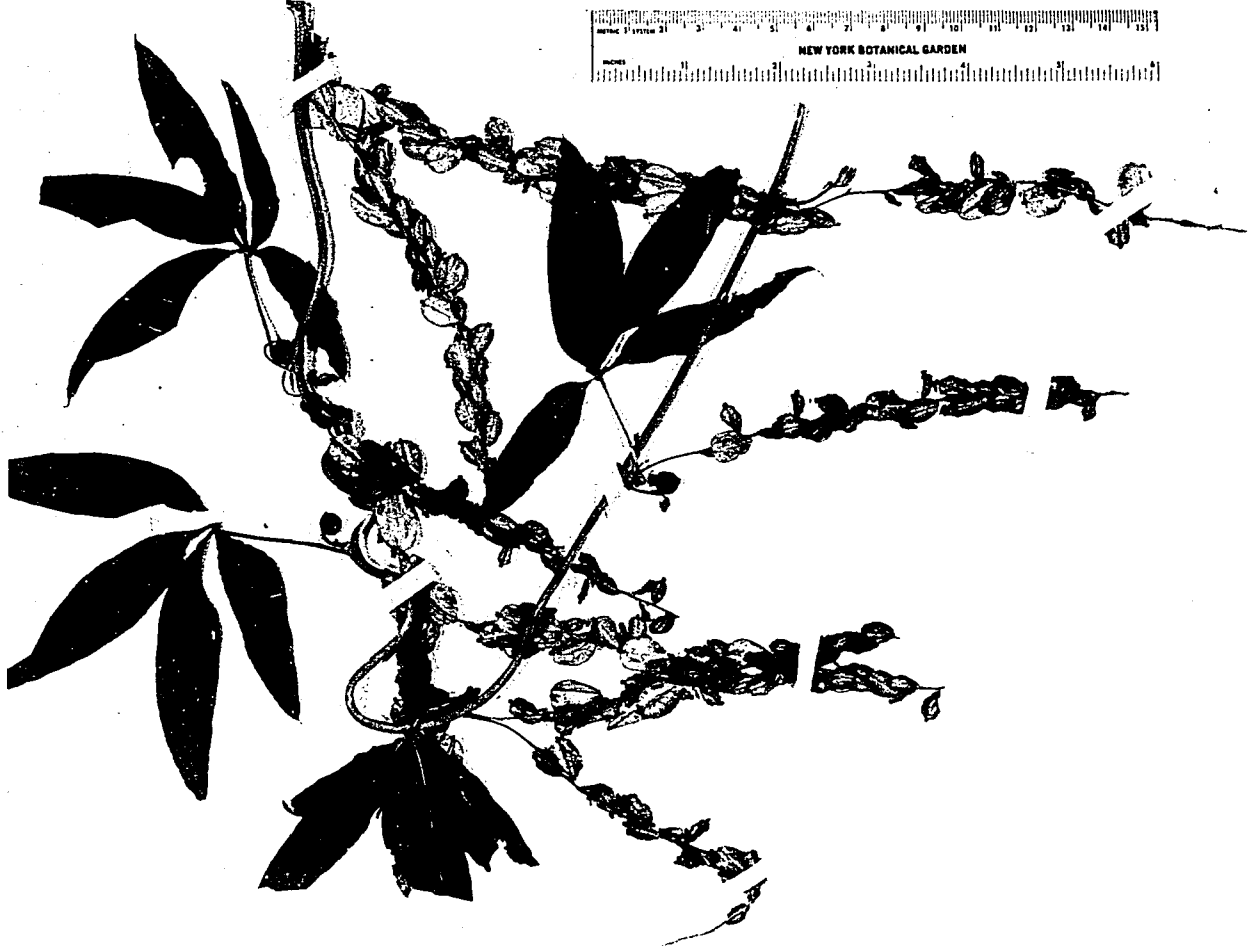


189
1888
189



Date 1888
Locality





A. HENRY.

TYPE No. 10 253

from Purple
Deserts

Ciscomia melanophylla

Determinavit *A. H. S. W.*

NEW YORK BOTANICAL GARDEN
HERBARIUM OF A. HENRY
PUBLISHED BY WARREN IN THE GARDEN, 1901

Dioscorea sect. Lasiophyton Uline in Engler & Prantl, Nat. Pflanzenfam. II.5:84. 1897, as subg. Helmia sect. Type Dioscorea hispida Dennstedt (lectotype chosen here).

Tubers ovoid to elongated, often lobed, large and produced at or near the soil-surface, very poisonous due to large quantities of alkaloids. Plants pubescent; hairs unicellular or bicellular with a short basal cell and a long tapering cell. Stem sinistrorse. Leaves alternate, trifoliolate; primary veins acrodromous basal. Staminate flowers in panicles, usually densely aggregated, sessile; stamens 6; filaments distinctly shorter than anther; connective not distinctly broadened. Capsule reflexed, longer than broad, large, woody, dehiscing only at apex leaving a trifurcate aperture. Seeds winged distally and directed toward base of capsule, adapted to swirl in gusty wind.

Distribution. This section accomodates 4 species (sensu Knuth, 1924) of which all, but one, are tropical African. D. hispida is the only Asian species.

This section is clearly distinct from Triephorostemon, as already indicated, and can be easily distinguished by its trifoliolate leaves in which leaflets show acrodromous basal venation. It is believed that compound leaves and seeds with proximal wings in the two sections are due to parallel evolution.

9. *Dioscorea hispida* Dennstedt, Schlusel Hortus malab. 15. 1818;
Prain & Burkill, Ann. Roy. Bot. Gard. Culcutta 14:188. 1936;
Burkill, Fl. Meles 4:318. 1951. Type: Rheede, Hort. malab.
7:pl. 51. 1688 (lectotype chosen here). Fig. 27A, B.

Dioscorea triphylla sensu Linnaeus, Herb. Amb. 23. 1754,
non Linnaeus 1753.

Dioscorea lunata Roth, Nov. pl. sp. 370.1821. Type. no
specimen cited.

Dioscorea hirsuta Blume, Enum. pl. Javae 21. 1827.

Type: Rumphius, Herb. amboin. 5: 361, pl. 128. 1750
(lectotype chosen here).

Dioscorea mollissima Blume, ibid. 21. 1827. Type. no
specimen cited.

Dioscorea daemona Roxburgh [Hort. Bengal 72. 1814, nomen
nudum] ex Roxburgh, Fl. Ind. 3: 805. 1832, excluding
reference to *Ubiu silvestre* Rumphius, Herb. amboin. 5:
pl. 127. 1750. Type: no specimen cited.

Dioscorea amoena Wight, Icon. pl. ind. or. 3: pl. 811. 1840
(orth. var.).

Helmia hirsuta Kunth, Enum. pl. 438. 1850. Basionym.

Dioscorea hirsuta Blume

Helmia ? *daemona* Kunth, Enum. pl. 439. 1850. Basionym.

Dioscorea daemona Roxburgh

Dioscorea daemona Roxburgh var. reticulata Hooker f., Fl.

Brit. India 6: 289. 1892. Type: s. loc., Wallich 5100

Dioscorea triphylla Linnaeus var. daemona Prain & Burkill,

J. & Proc. Asiat. Soc. Bengal, 10: 26. 1914. Type: from

India and Java, no specimen cited.

Dioscorea triphylla Linnaeus var. reticulata Prain &

Burkill, Ibid. 10: 26. 1914. Type: from Malay Peninsula,

no specimen cited.

Dioscorea triphylla Linnaeus var. mollissima Prain & Burkill,

Type: from Burma, Thailand, and Malay Peninsula, no

specimen cited.

Dioscorea hispida Dennstedt var. reticulata (Hooker f.)

Prain & Burkill, Bull. Misc. Inform. 237. 1927. Basionym.

Dioscorea daemona Roxburgh var. reticulata Hooker f.

Dioscorea hispida Dennstedt var. mollissima (Prain &

Burkill) Prain & Burkill, Ibid. 237. 1927. Basionym.

Dioscorea triphylla Linnaeus var. mollissima Prain &

Burkill.

Dioscorea hispida Dennstedt var. scaphoides Prain & Burkill,

Ibid. 237. 1927. Type: Thailand, Puket, Pangnga, Pulau

Tebun, Haniff & Nur 3596 (holotype, K, n.v.).

Dioscorea hispida Dennstedt var. neo-scaphoides Prain &

Burkill, Ibid. 237. 1927. Type: Thailand, Payap,

Chiangmai, Kerr 5650 (holotype, K, n.v.).

Tuber \pm depressed-globose, often lobed, sometimes slightly elongated, produced at or near the soil-surface, weighing up to 35 kg, sparsely covered by small roots, the surface straw-colored or grey, the tissue white to lemon-yellow, very poisonous due to dioscorine. Stem up to 30 m long and 1 cm in diam., green to straw-colored, pubescent, glabrate with maturity, usually prickly, the prickles broad at base, horizontal or somewhat curved downward. Bulbils not seen. Leaves 3-foliolate, rarely simple among inflorescences, pubescent to glabrous above, relatively more pubescent to glabrous above, relatively more pubescent below especially on veins, drying green or straw-colored, paler beneath, somewhat chartaceous; middle leaflet elliptic to obovate, basally acute, apically acuminate, 5-30 x 3-22 cm; primary veins usually 5, the secondary veins \pm parallel, the reticulation distinct on both sides; lateral leaflets inequilateral, the inner half resembling a half of middle leaflet but usually narrower, with 1 or 2 primary veins, the outer half broader with a rounded base, with usually 3 primary veins; petiole shorter or longer than leaflets, 7-27 cm long, channelled above, pubescent, sometimes prickly; petiolules 4-20 mm long, relatively more pubescent than petioles; stipules absent. Staminate panicles 1 or 2 per axil, the rachis 3.5-40 cm long, usually firm, ascending, densely pubescent, the branches spicate, alternate, 1-4 per axil of a bract, 7-15 mm long, 15-30-flowered usually with a distal, 3-8 mm-long flowering zone

and a proximal, 3-10 mm-long sterile zone. Flowers densely aggregated, ca. 1.5 mm across, \pm fully open at anthesis; bract cordiform or depressed ovate, nearly rounded but abruptly acuminate apically, subsaccate encircling and overtopping the flower, 1-1.5 x 1.5-1.8 mm, pubescent without; bracteole \pm orbicular, 0.7-1 x 0.5-0.9 mm, sparingly pubescent without; torus not distinctly expanded; outer tepal \pm orbicular, 0.6-0.8 x 0.7-0.9 mm, glabrous to sparingly pubescent without, membranous, the inner tepals \pm orbicular, 0.7-1 x 0.8-1.1 mm, thicker than outer ones, glabrous; stamens free or slightly adnate to the tepals, the filament indistinct or ca. 0.1 mm long, the anther 0.2-0.3 mm long, the connective not expanded beyond the width of the filament; pistillode indistinct, humpy. Pistillate inflorescence axillary, solitary or rarely 2 per axil, spicate, pendent, the axis 15-50 cm long, pubescent. Flowers 10-25 per spike, lax, sessile at anthesis; bract lanceolate-ovate, acute, ca 2.5 x 1 mm, pubescent without; bracteole ovate, apically rounded, 0.8-1.5 x 0.5-1 mm, pubescent without; tepals ovate to widely depressed ovate, apically \pm rounded, pubescent without, fleshy, the outer tepals 0.8-1 x 0.6-0.8 mm, the inner tepals 1-1.2 x 0.7-1.3 mm; staminodes 6, adnate to the tepals at base; ovary ca. 10 x 25 mm, densely pubescent, with a short neck; styles free to base, stigmas lobed into two upper lateral lobes and one lower median lobe. Capsules up to 25 per spike, loosely imbricate, oblong-elliptic, basally truncate to rounded or

retuse, apically truncate to obtuse and sometimes slightly broadened, 3.5 - 7 x 2.4-2.8 cm, glabrate with maturity, shiny, straw-colored to honey-brown, woody; wings semi-elliptic, 1-1.2 mm broad. Seed 3.2 - 3.8 cm long including wing, obliquely cuneate at base; wing 2.7-3 x 0.9-1.2 cm, dark brown.

Distribution. Tropical Asia, from India eastward to Taiwan, Philippine Islands, and New Guinea; absent in Sri Lanka; generally occurs in dry regions at low altitudes.

Representative specimens. BANGLADESH. Rangpur Dist.: Koroyiban, Buchanan-Hamilton in Wallich 5099-E (E).

INDIA. Uttar Pradesh, Dehra-Dun Dist.: Mussooree, Stewart 15002 (GH, JEPS, MO, NY, PH, US); Garwal Dist.: Pauri-Hills, Bamra, Mooney 3344 (A); Almora Dist.: Sarju river, Strachy & Winterbottom 7 (GH); Sikkim State, Sikkim, Hooker s.n.(GH); Cave s.n. (A, E); W. Bengal State, Jalpaiguri Dist.: W. Duars, Tondu Forest, Haines 690 (E). Howrah Dist.: Calcutta, Voigt s.n. (NY). Assam State, s.loc. Hooker s.n. (NY); Meghalaya State, Khasia Hills, Hooker & Thomson s.n. (GH); Maharashtra State, Usoda forest, Fernandes 2449 (A); Kerala State, Malabar, Wight 1100 (E).

NEPAL. Karelung, Madi Khola, Stainton et al. 5903 (A, E); between Simra and Amlekhgang, Gardner 1585 (E); s.loc. Buchanan-Hamilton in Wallich 5099-A (E), 5099-B (E).

BHUTAN. Devangiri, Griffith 5536 (NY); Shonger Chu Valley above Lingmethang Grierson & Long 2428 (E);

Local names and uses. India: Chai, Kolo kand, Kulu sanga, Kulika, Ruglu; Burma: Kywe; Thailand: Koi, Kloi; Malay Peninsula: Bekoi. Due to the presence of a highly poisonous alkaloid, dioscorine, the tubers are not normally used for food. However, during famines in India, the tubers are reportedly eaten after an elaborate process of detoxication.

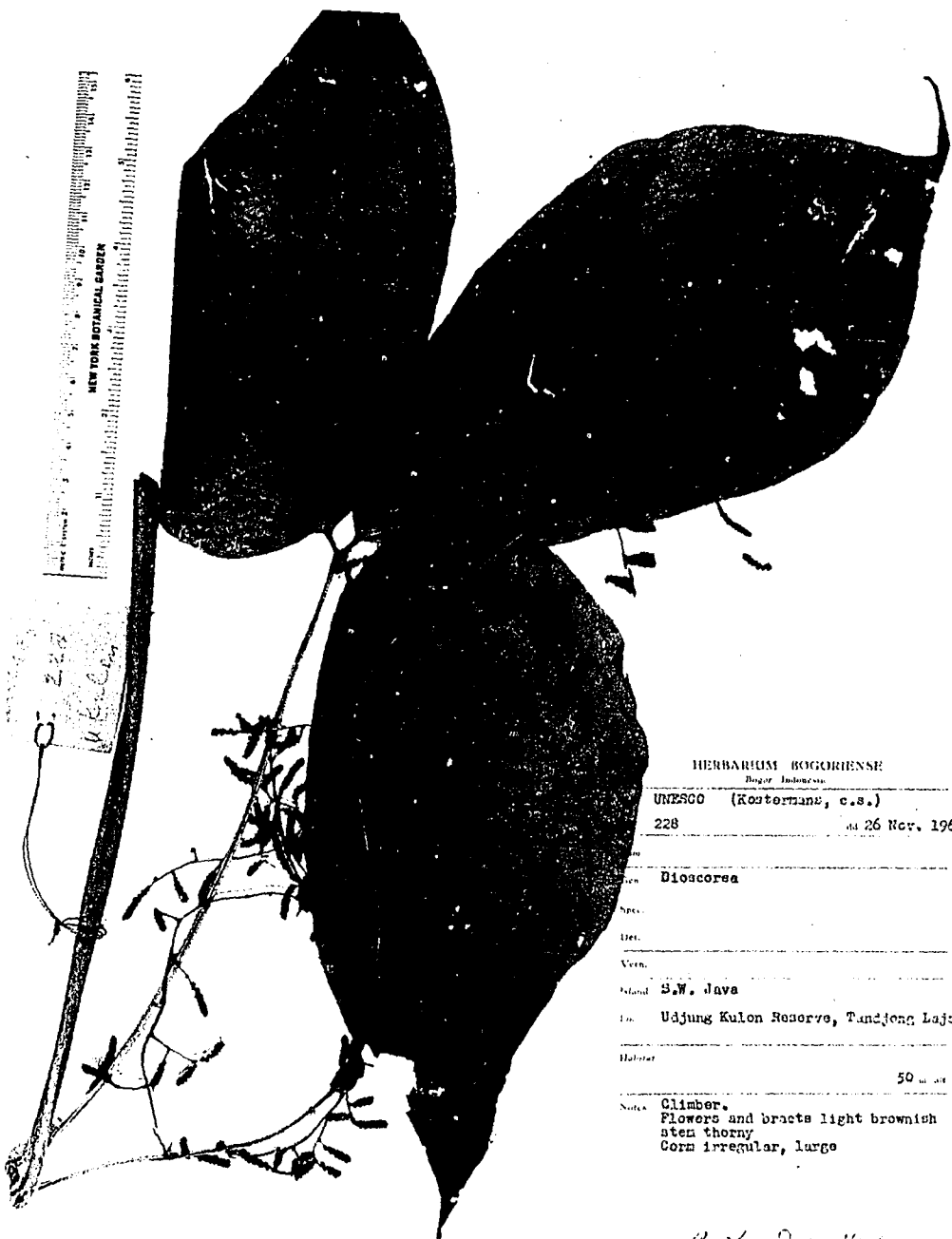
Dennstedt based D. hispida, on Rheede's description and plates no. 51 and 52 (1688). The latter is apparently based on discordant elements, including vegetative parts of D. hispida and fruits of a ranunculaceous plant. Therefore plate no. 51 is chosen as the lectotype of the species. Subsequently Blume described D. hirsuta based on Rumphius' plate no. 128 (1759) and Rheede's plates no. 51 and 52 of which Rumphius' plate no.51 is chosen as the lectotype.

The varieties proposed by Prain & Burkill (1914, 1927), based on minor variations in the nature of pubescence and staminate inflorescences, do not merit taxonomic recognition because these variations are not consistent.

Fig. 27. Dioscorea hispida

A. Staminate plant (Kostermans 228, NY).

B. Pistillate plant (Tsang 842, NY).



NEW YORK BOTANICAL GARDEN
 200th Street, New York 24, N.Y.

228
 W. B. C. 1960

HERBARIUM BOGORIENSE
 Bogor, Indonesia

UNERGO (Kostermans, c.s.)

228

at 26 Nov. 1960

Dioscorea

Spec.

Det.

Vern.

Island S.W. Java

Loc. Ujung Kulon Reserve, Tandjong Laja

Habitat

50 m alt

Notes

Climber.
 Flowers and bracts light brownish
 stem thorny
 Corn irregular, large

Genus, Palm, etc.

Dupl sent to Herb. at: London, Bogor, Ariz. Acad. Sciences, Manila
 Pacific Inst. Studies, New York, Bot. Mus. Harvard, University of
 Michigan, Cambridge, Stanford, Chinese Academy of Sciences, Beijing
 Please notify Bogor Herbarium of any identification of this specimen

NEW YORK
 BOTANICAL GARDEN



NEW YORK BOTANICAL GARDEN

FLORA OF HAINAN
 HERBARIUM OF HAINAN UNIVERSITY
 3rd Hainan Expedition

Disconea trijida, DuRoi.
 var. *reticulata*
 Determinavit: *M. H. H. H.*



Det. E. D. Merrill
 Coll. Tsang, Wai-Tak

NOH PONG SHAN, 南屏山
 (Tamschau District, 潭洲)

Dioscorea sect. *Enantiophyllum* Uline in Engler & Prantl, Nat.

Pflanzenfam. II. 5: 87. 1897, as subg. Eudioscorea sect.

Type: Dioscorea alata Linnaeus (lectotype chosen here).

Tubers one to few, unarmed, long-cylindrical, penetrating deeply into the soil (polymorphic in Dioscorea alata due to cultivation), nonpoisonous. Plants pubescent or glabrous, the hairs chiefly of stiletto type if present. Staminate flowers arranged in spikes or panicles, usually sessile; perianth open up to halfway at anthesis, the tepals ovate, erect to incurved, distinct or shortly connate at base; stamens 6 (inner cycle rarely sterile), ± free; connective not broadened beyond the width of the filament. Pistillate flowers in spikes or panicles. Capsule erect to ascending, broader than long; wings ± rounded, dehiscent all round. Seed winged all round, adapted to glide in the air.

Distribution. This is the largest section of the genus, accommodating ca. 120 species (sensu Knuth, 1924). They are distributed in tropical Africa and in Asia, eastward of India, extending to Australia and Pacific Islands including Tahiti.

It is clearly seen that no Asian section of the genus is more distinct than the Enantiophyllum. The dextrorse twining of the stems is apparently unique in the genus in Asia. Seeds with relatively large circumferential wings accommodated in similarly

shaped wings of a erect capsule are also characteristic. Such seeds, being capable of gliding in still air or gentle wind, make this section suitable to survive in rainforest habitats.

Uline (1897), made special reference to D. alata, D. glabra, and D. oppositifolia. D. alata is here considered the best to be chosen as the lectotype of the section Enantiophyllum.

Key to the section Enantiophyllum
in the Indian Subcontinent

1. Staminate inflorescence paniculate (sometimes spikes also present), the branches or spikes usually shorter than 5 cm.
2. Stem, inflorescence axes, and veins reddish brown to coppery red when dried. Secondary veins strongly distinct from reticulation. Branches of staminate inflorescence zigzag.
3. Tubers deeply penetrating and gradually swelling from base. Stem smooth or angular or very narrowly alate. Stipules absent, or if present less than 1 mm wide. Staminate rachis 4-angled; flowers less than 1.2 mm across; bract widely ovate, 0.5-0.7 x 0.5-0.7 mm; inner tepals obovate; pistillode humpy, ca. 0.1 mm high. Stigmatic arms in pistillate flower not recurved.

10. D. hamiltonii

3. Tubers polymorphic due to cultivation. Stem distinctly 4 (6-8 at base)-winged. Stipules auriculiform, 1-4 mm wide. Staminate rachis 4-winged. Staminate flowers up to 1.5 mm across; bracts deltate-ovate, 0.9-1 x 0.7-0.8 mm; inner tepals nearly spatulate; pistillode conical, ca. 0.2 mm high. Stigmatic arms in the pistillate flower distinctly recurved. 11. D. alata

2. Stem, inflorescence axes, and veins not reddish when dried. Secondary veins not strongly distinct from reticulation. Branches of staminate inflorescence not zigzag.

4. Leaves basally acute to rounded (except lowest leaves in D. wattii); petiole less than 1/3 the length of blade.
5. Leaves glabrous; reticulation distinctly elevated on both surfaces, with fine areoles. Capsules 2.7-3.5 x 4.2-5.5 cm. Seed more than 20 mm across.

12. D. wattii

5. Leaves glabrous or pubescent; reticulation obscure on both surfaces. Capsule 1.2-2.2 x 2-4 cm. Seed less than 20 mm across.

6. Plants variously pubescent, at least on inflorescence axes.

13 a. D. oppositifolia var. oppositifolia

6. Plants glabrous.

13 b. D. oppositifolia var. dukhunensis

4. Leaves basally cordate; petiole more than 1/3 the length of blade.

7. Stem and under surfaces of leaves pubescent.

14. D. pubera

7. Stem and leaves glabrous.

8. Stem often ridged or very narrowly alate. Bulbils abundant. Leaves commonly coriaceous, deeply cordate to sagittate basally with obtuse lobes; reticulation distinct above, strongly elevated below; stipules narrow, up to 1 mm wide. Ovary with a distinct, 0.7-2 mm-long neck; styles distinct.

15. D. belophylla

8. Stem terete. Bulbils rare or absent. Leaves chartaceous, truncate or cordate with rounded lobes; reticulation obscure above, not strongly elevated below; stipules absent. Ovary without a distinct neck; stigmas connate.

9. Leaves ovate, basally truncate to shallowly cordate; reticulation obscure below; petiole $\pm \frac{1}{2}$ the length of blade. Staminate spikes opposite to subopposite, less than 3.5 mm long. Pistillate inflorescence spicate.

16. D. glabra

9. Leaves cordiform, deeply cordate basally; reticulation prominent below; petiole \pm as long as blade. Staminate spikes alternate, up to 5 cm long. Pistillate inflorescence paniculate.

17. D. wallichii

1. Staminate inflorescence spicate (rarely with a few alternate branches); spikes usually longer than 5 cm.
10. Mature leaves cordiform, deeply cordate basally ; primary veins 7-9; petiole more than $\frac{1}{2}$ the length of blade.

18. D. wightii

10. Mature leaves ovate to obovate or elliptic to lanceolate, basally acute or shallowly cordate; primary veins 3-5(7); petiole less than $\frac{1}{2}$ the length of blade.
11. Leaves membranous, shallowly cordate basally; petiole more than $\frac{1}{3}$ the length of blade. Inner staminate tepals distinctly smaller than outer tepals. Capsules 1.8-2.5 x 2.4-3.2 cm, chesnut brown. Seed 10-15 mm across.

19. D. trimenii

11. Leaves chartaceous or coriaceous, basally acute or rounded or occasionally shallowly cordate; petiole less than $\frac{1}{4}$ the length of blade. Staminate tepals \pm similar. Capsules 1.8-3.2 x 3.3-6 cm, greyish to brownish. Seed 15-30 mm across.

12. Leaves chartaceous; reticulation prominent above, strongly prominent and elevated below, the areoles fine. Staminate spikes usually solitary, 5-23 cm long. Staminate flowers sessile, solitary or in cymes of 2-4 flowers; anther 0.3-0.5 mm long, $\pm \frac{1}{2}$ the length of filament. Ovary with a distinct neck.

20. D. spicata

12. Leaves coriaceous; reticulation usually obscure on both surfaces. Staminate spikes fascicled up to 10 per axil or arranged on a short rachis, 2-8.5 cm long. Staminate flowers solitary, shortly pedicelled; anther ca. 0.2 mm long, ca. $\frac{1}{3}$ the length of filament. Ovary without a distinct neck.

21. D. koyamae

10. *Dioscorea hamiltonii* Hooker f., Fl. Brit. India 6: 295. 1892; Knuth in Engler, Pflanzenr. 87 (IV. 43): 266. 1924; Prain & Burkill, Ann. Roy. Bot. Gard. Calcutta 14: 299, pl. 122, 1939. Type: India. Assam State, Goalpara Dist., Goalpara, Buchanan-Hamilton in Wallich no. 5108-D (lectotype chosen here, K; isolectotype, E). Fig. 28A, B.

Dioscorea lepcharum Prain & Burkill, J. & Proc. Asiatic Soc. Bengal 10: 36. 1914. Type: India. W. Bengal, Darjeeling Dist.: Mungpu, Sureil, Ribu in Gage no. 34207 (lectotype chosen here, K).

Dioscorea lepcharum Prain & Burkill var. *vera* Prain & Burkill, Ibid. 10: 36. 1914. Basionym. *Dioscorea lepcharum* Prain & Burkill

Dioscorea lepcharum Prain & Burkill var. *bhamoica* Prain & Burkill, Ibid. 10: 36. 1914. Type: Burma, Bhamo, Burkill 22828 (lectotype chosen here).

Tubers deeply penetrating, long-stalked or gradually swelling from base, up to 1 m long and 2 cm in diam., the surface brown or black, sometimes rather uneven or rough, the tissue white. Stem terete or somewhat angular or slightly alate, turning copper-red at maturity, glabrous to pubescent, unarmed. Bulbils often in large numbers, globose. Leaves opposite to subopposite or alternate, the phyllotaxy often varying within a individual; blade ovate or rarely deltate-ovate, basally cordate

to subsagittate, apically acuminate, 6.5-14 x 2.5-12 cm, glabrous, ± reddish brown when dried; primary veins campylodromous, 7, the inner 5 reaching apex, prominent above, strongly elevated and copper-red below; secondary veins almost straight, ± perpendicular to primary veins; reticulation somewhat prominent below; margin very slightly thickened; petiole 3.5-11 cm long, ± 4-angled, somewhat grooved and narrowly winged above, glabrous to puberulent; stipules absent or represented by narrow extensions of petiolar wings at base, up to 1 mm wide. Staminate inflorescence axillary, 1-2(3) per axil, paniculate, the rachis 5-50 cm long, usually sharply 4-angled, copper-red, puberulent, the branches 2-4 per axil, opposite to alternate, 5-22-flowered, the axis 0.5-1.5 cm long, zigzag, angled. Flowers 0.7-1.2 x 0.7-1.6 mm, partially open at anthesis; bract very widely ovate, acuminate, 0.5-0.7 x 0.5-0.7 mm, glabrous, divergent; bracteole as bract, 0.4-0.5 x 0.4-0.5 mm; tepals glabrous, the outer ones widely oblong-ovate, obtuse, 1-1.3 x 0.7-1.1 mm, the inner ones obovate, obtuse to rounded, 0.8-1 x 0.6-0.7 mm; stamens free, the filament 0.1 mm long, basally widened, the anther 0.2-0.3 mm long, the connective narrow; pistillode very small, 3-lobed. Pistillate inflorescence axillary, 1-3 per axil, spicate, up to 20-flowered, the rachis 2.5-25 cm long, angular, glabrous. Flowers laxly arranged, almost sessile at anthesis; bracts widely ovate, acuminate to caudate, 1.1-1.7 x 1.1-1.5 mm, glabrous; bracteole as bract,

1-1.2 x 0.8-0.9 mm; tepals larger and fleshier than those in staminate flower, the outer ones 1.3-2 x 1.5-1.7 mm, the inner ones 1.1-1.5 x 0.8-1.1 mm; staminodes 6, 0.2-0.3 mm long; ovary 3-7 x 2-3 mm, glabrous, with a 0.5-1 mm-long neck; styles connate basally, ca. 0.4 mm long; stigmas 2-parted at apex. Capsules up to 7 per spike, basally rounded, apically obcordate, 2-3 x 2.5-4 cm, reddish; wings wider than semicircular; stipe obdeltate, ca. 4 mm long. Seed 14-20 mm in diam.; wing 3-6 mm wide.

Distribution. Northeastern India to S. E. Asia, with disjunct distribution in western S. India; occurs in moist hilly regions, up to ca. 750 m.

Representative specimens. INDIA. Sikkim State, Mungpu, Clarke 36176-B (K); s.loc., Cave s.n. (BM); Bihar State, Santal Parganas Dist.: Korchu Hills, Haines 2464-C (K); Hazaribagh Dist.: Kerr 2540 (BM); Ranchi Dist.: Horhap Forest, Haines 5115 (K); Singbaum Dist.: Saitba Forest, Haines 5108 (K); W. Bengal State, Purulia Dist.: Purulia, Clarke 20789 (K); Hooghly Dist.: Calcutta, Voigt s.n. (GH,US); Assam State, Goalpara Dist.: Goalpara, Buchanan-Hamilton 2205 (E); Cachar Dist.: Bostelah, Keenan s.n. (K); Meghalaya State, Khasia Hills, Hooker & Thomson 14 (BM); Manipur State, Ukhrul, Kingdon-Ward 17752 (BM, NY); Mysore State, N. Kanara Dist.: Birchy, Talbot 2244 (K); S. Kanara Dist.: Mangalore, Hohenacker 699-a (BM, E, K); Kerala State, Ernakulam Dist.: Malayatur, Bourdillon 1444 (K).

Common names and uses. India: Pu-um bok, Pa-sok bok, Rui-vat, Ta-rum, Rana hak; Thailand: Man nok, Man rak; Laos: Khita manh. Tubers are reportedly excellent for food; not known in cultivation, although much soughted by people where it naturally occurs.

Examination of the types of D. lepcharum and its varieties indicates that these proposed taxa are intermediate between D. hamiltonii and D. glabra. They may prove to be hybrids between these two species, but cytological study is necessary to confirm this idea. The names are here for convenience listed under D. hamiltonii.

Fig. 28. Dioscorea hamiltonii

A. Staminate plant (Cave s.n., BM).

B. Pistillate plant (Hooker & Thomson s.n., K).

EX HERB. HORT. REG. BOT. EDIN.

PLANTS OF SIKKIM

COLL. CAVE

Winters 1925

Dioscorea



Dioscorea Hamiltonii, Hook. f.

NEW YORK BOTANICAL GARDEN

NEW YORK BOTANICAL GARDEN
R. W. G. & Co. 100 101 102 103 104 105 106 107 108 109 110 111 112 113 114 115 116 117 118 119 120 121 122 123 124 125 126 127 128 129 130 131 132 133 134 135 136 137 138 139 140 141 142 143 144 145 146 147 148 149 150 151 152 153 154 155 156 157 158 159 160 161 162 163 164 165 166 167 168 169 170 171 172 173 174 175 176 177 178 179 180 181 182 183 184 185 186 187 188 189 190 191 192 193 194 195 196 197 198 199 200

lent D. Flava
lent D. Yamilltonii
Mithras



Phaseolus vulgaris

W. H. ...
1862
1865

11. *Dioscorea alata* Linnaeus, Sp. pl. 1033. 1753; Haines, Bot. Bihar & Orissa 4: 1122. 1922; Knuth in Engler, Pflanzenr. 87 (IV. 43): 265. 1924; Prain & Burkill, Ann. Roy. Bot. Gard. Calcutta 14: 302, pl. 123-125. 1939; Burkill, Fl. Males. 4 : 330. 1951. Type: Rheede, Hort. malab. 7: pl. 38. 1688. (lectotype chosen here). Fig. 29A, B.

Dioscorea oppositifolia sensu Linnaeus, Herb. Amb. 22.

1754, non Linnaeus 1753.

Dioscorea eburina Loureiro, Fl. Cochinch. 625. 1790. Type: Cochinchina, no specimen cited.

Dioscorea eburnea Willdenow in Loureiro, Fl. Cochinch. ed. Willdenow, 767. 1793, excluding reference to Rheede, Hort. malab. 7: pl. 50. 1688. Type: from Cochinchina, no specimen cited.

Dioscorea spiculata Blume, Enum. pl. Javae, 1:22. 1827.

Type: Rumphius, Herb. Amboin. 5: pl. 123. 1747.

Dioscorea globosa Roxburgh [Hort. Bengal 72. 1814, nomen nudum] ex Roxburgh, Fl. Ind. 3: 797. 1832. Type: from cultivation in India, no specimen cited.

Dioscorea rubella Roxburgh [Hort. Bengal 72. 1814, nomen nudum] ex Roxburgh, Fl. Ind. 3: 798. 1832. Type:

Rumphius, Herb. Amboin. 5: pl. 121. 1747.

Dioscorea purpurea Roxburgh [Hort. Bengal 72. 1814, nomen nudum] ex Roxburgh, Fl. Ind. 3: 799. 1832. Type: from cultivation in India no specimen cited.

Dioscorea atropurpurea Roxburgh [Hort. Bengal 72. 1814,
nomen nudum] ex Roxburgh, Fl. Ind. 3: 800. 1832. Type: from
cultivation in Asia, no specimen cited.

Disocorea vulgaris iquel, Fl. Ned. Ind. 3: 572. 1859.
Type: Rumphius, Herb. amboin. 5. pl. 120. 1747.

Tubers one to several, polymorphic, long, slender, somewhat clavate, up to 1.5 m long, or globose, or intermediate in shape, variously branched or lobed, or more often unbranched, circular to flattened in section, the long tubers descending vertically into the soil or sometimes curving toward the soil-surface, the surface brown, sometimes cracking or flaking, the tissue tender, white or cream-white, sometimes with magenta sap partly or throughout under the surface, becoming rusty brown when exposed, proximally hard producing long roots, the short roots produced distally in decreasing numbers. Stem up to 15 m long and 1 cm in diam., prominently 4-winged or ridged (sometimes 6 or 8 at base), green to purplish, ± reddish brown when dried, glabrous, unarmed or rarely with weak blunt prickles at base. Bulbils sparse to abundant, globose, ovoid or obpyriform, sometimes flattened or elongated to ca 4 cm, usually astringent, occasionally with rootlets. Leaves opposite or rarely subopposite; blade ovate, or deltate-ovate, basally cordate or subsagittate or subhastate, apically acuminate, 6-16 x 4-13.5 cm, glabrous; primary veins campylodromous, 7, the inner 5 reaching apex, prominent below, secondary veins almost straight ± perpendicular to primary veins;

reticulation somewhat distinct below; margin distinct, often yellowish; petiole 3-12 cm long, grooved above, winged, the wings relatively more prominent proximally and distally, continued with stem-wings proximally and primary veins of blade distally; stipules extended from petiolar wings at base, auriculiform, 0.1-0.4 mm wide. Staminate inflorescence axillary, 1-2 per axil, occasionally terminal, paniculate, the rachis 4.5-27 cm long, proximally alate, reddish brown when dry, glabrous, the branches 1-3 (6) per axil, subtended by opposite to alternate inflorescence bract, 8-25-flowered, the axis 0.8-2.5 cm long, zigzag, angled or narrowly alate, glabrous. Flowers ca. 1.5 x 1.5 mm, partially open at anthesis; bract deltate-ovate, acuminate, 0.9-1 x 0.7-0.8 mm, glabrous, divergent; bracteole as bract 0.5-0.8 x 0.3-0.7 mm; tepals glabrous, the inner tepals widely ovate, obtuse, 1.1-1.3 x 0.9-1.3 mm, the inner tepals distinctly smaller, widely abovate, basally narrower, apically obtuse to rounded, 0.8-1 x 0.7-0.9 mm; stamens free, the filament 0.1-0.2 mm long, the anther 0.3-0.4 mm long, the connective narrow; pistillode conical, ca. 0.2 mm long, 3-lobed. Pistillate inflorescence solitary in axils, spicate, up to 20-flowered, the axis 6-35 cm long, angled, glabrous. Flowers laxly arranged, almost sessile at anthesis; bract ovate, acute, 1.1-1.4 x 1 mm; bracteole as bract, ca. 1 x 0.8 mm; tepals very fleshy, the outer tepals very widely ovate, apically obtuse to rounded, ca. 1.1 x 1.1 mm, the inner tepals oblong-obovate, apically obtuse, 1-1.1 x

0.8-1 mm, staminodes 6, very small; ovary ca. 3.5 x 1.8 mm, glabrous, with ca. 0.5 mm-long neck; styles connate, ca. 0.5 mm long, stigmas 2-parted with long sickle-shaped arms. Capsules up to 8 per spike, ca. 2.3 x 3.7 mm, basally tinged with red, stipe obdeltate, ca. 3 mm long Seed not seen.

Distribution. Not known in wild; the affinity with D. hamiltonii suggests that it originated in S.E. Asia; widely cultivated in all moist tropics and in subtropical China.

Representative specimens. INDIA. Bihar State, Santal Parganas Dist. : Santali, Watt 8106 (E); Monghyr Dist. : Monghyr, Buchanan-Hamilton 2213 (E); Assam State, Goalpara Dist., Mangaldai to foot of Bhutan Himalaya, Schlagintweit 13412 (US); Meghalaya State, Khasia hills, Hooker & Thomson 14 (GH).

NEPAL. s. loc. Wallich 5106-C (K).

Common names and uses. Greater yam, Water yam, Winged yam; India: Pem bok, Periyeh bok, Fena alu, Pat alu, Batharpatia alu; Sri Lanka: Kiri kondal, Vel ala; W. Malasia: Ubi, Ovi, Huwi. Most widely used of all food-yams.

Readily recognized by its 4(-8)-winged stem and opposite, deeply cordate leaves; due to cultivation, tubers have evolved into numerous shapes and sizes. Linnaeus (1753) based D. alata on two descriptions and one illustration. The latter, Rheedee's plate no. 38, is chosen as the lectotype of this species.

Fig. 29. Dioscorea alata

A. Staminate plant (Lace 4449, E).

B. Pistillate plant (Lace 2206, E)

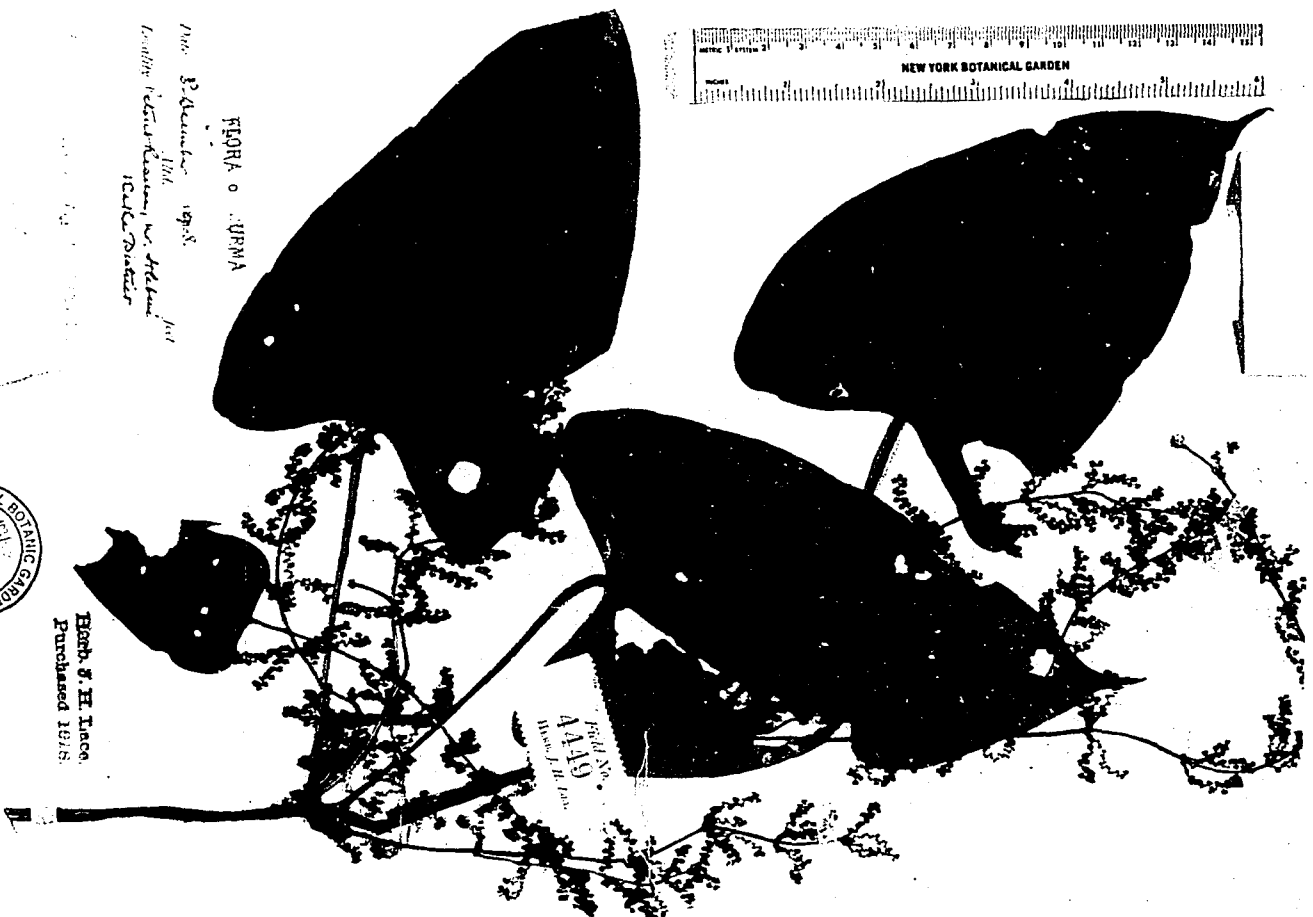
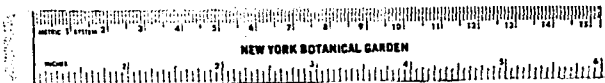


FIGURA 0. URWA

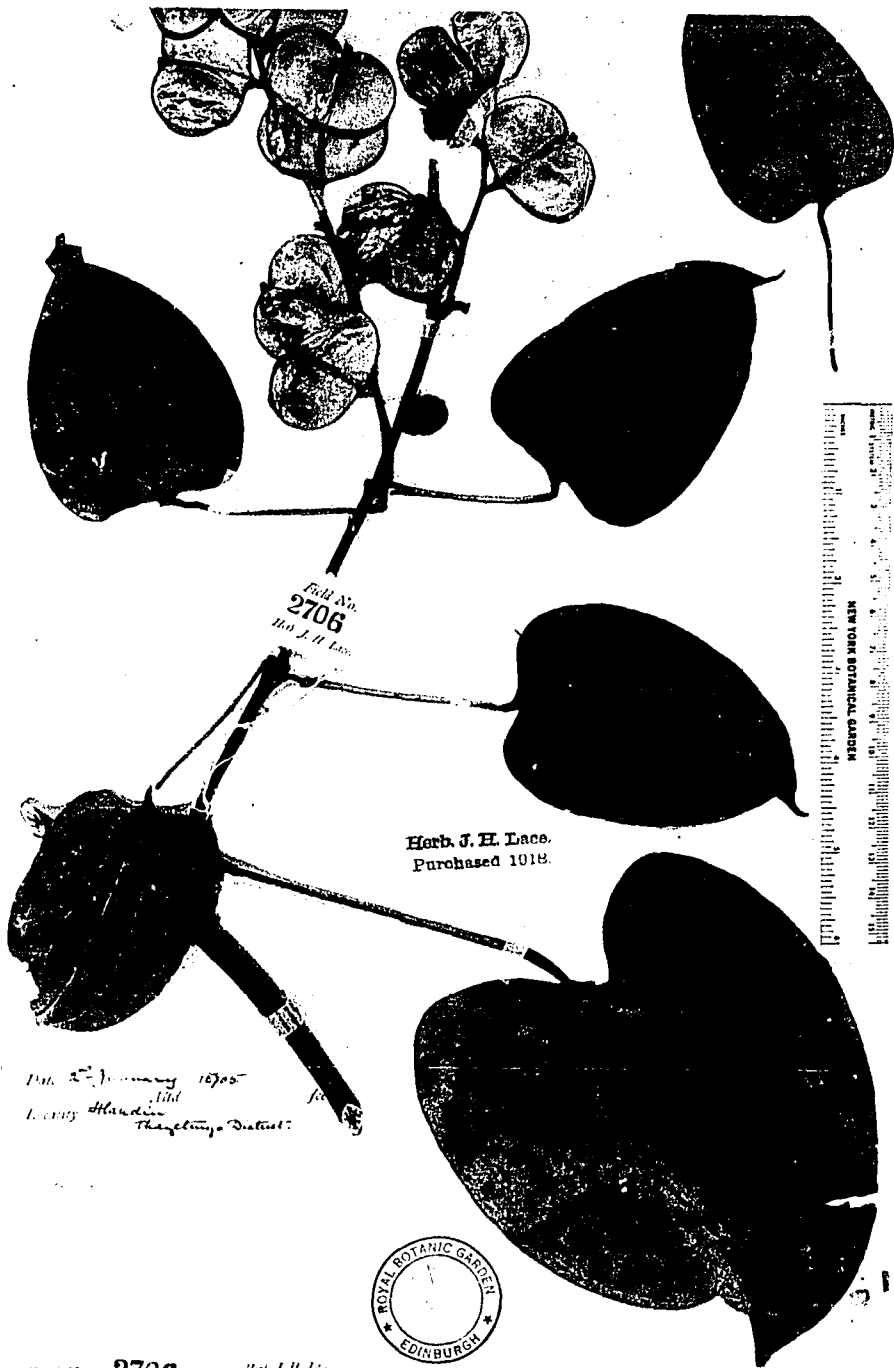
Prov. S. Americae 1878.

1878.

Locality: Viceroy's Residence, Rio de Janeiro, Brazil
 Collected by
 J. C. R. P. de S. J.

Herb. G. H. Lacey
 Purchased 1878.





Field No.
2706
 Hb. J. H. L.

Herb. J. H. Lace.
 Purchased 1918.

Dist. 2nd January 1875
Locality: Hradec, Bohemia
Thunberg's District



Field No. **2706** Hb. J. H. L.



12. *Dioscorea wattii* Prain & Burkill, J. & Proc. Asiat. Soc. Bengal, 4: 457. 1908; Knuth in Engler, Pflanzenr. 87 (IV. 43): 273. 1924; Prain & Burkill, Ann. Roy. Bot. Gard. Calcutta 14: 271, pl. 112, 1939. Type: India, Nagaland State: Khasia, Mambo, 12 May 1886, Clarke 43801 (lectotype K; isolectotype, CAL, n.v.).

Tubers deeply penetrating, the tissue rather fibrous, becoming reddish on exposure. Stem up to 20 m long and 7 mm in diam, with scattered prickles especially at base. Bulbils not seen. Leaves opposite to subopposite or alternate, the phyllotaxy often varying within a individual; blade commonly lanceolate to ovate or elliptic, basally obtuse to rounded, apically acuminate, 7-13.5 x 2-7.5 cm (the blade in basal leaves widely ovate, cordate at base, abruptly acuminate at apex, up to 30 x 24 cm), glabrous, coriaceous, drying greenish or reddish brown above and greenish below; primary veins acrodromous basal in upper leaves or campylodromous in basal leaves, 5(7), the inner 3-5 veins reaching apex, slightly distinct above, strongly prominent below; secondary veins only slightly distinct from reticulation, the areoles well-developed, very prominent below, 5-6-sided, 0.5-1 mm across; margin distinct, cartilaginous yellowish; petiole 1/4-1/3 the length of blade, 2-3.5 cm long. Stipules absent. Staminate inflorescence axillary or terminal, 1-2 per axil, paniculate, the rachis 3-25 (33) cm long, angled,

glabrous; branches alternate or less often subopposite or opposite, 1-2 per axil of a inflorescence bract, 2-4.5 cm long. Flower 5-22 per spike, lax, 1.5-2 x 1.5-1.8 mm, partially open at anthesis, somewhat flattened at base; bract very widely ovate, acute, 0.7-1 x 0.7-1 mm, decurrent on axis and repressed against it by the flower; bracteole as bract, 0.6-1 x 0.6-1.2 mm; torus enlarged, columnar, 0.6-1.1 x 0.6-0.9 mm; tepals glabrous, coriaceous, the outer ones ovate to very widely ovate, basally broadened and fused to form a broad flat base of flower, apically acute, incurved, 1.2-2.1 x 1.2-1.8 mm, the inner ones obovate or spatulate, 1 x 1.8 x 0.9-1.2 mm, the lower 1/3 fused with torus; stamens free, the filament 0.1-0.4 mm long, the anther 0.4-0.5 mm long, the connective almost as wide as filament; pistillode 0.2-0.3 mm, conical, 3-lobed, the lobe irregularly parted into 2-3 arms. Pistillate inflorescence axillary, solitary, spicate, up to 8-flowered, the rachis 5-14 cm long, angular to round, glabrous. Flowers lax, sessile at anthesis; bract ovate to widely ovate, acute, 2-2.2 x 1.5-1.7 mm; bracteole as bract, ca. 1.6 x 1.2 mm; tepals glabrous, coriaceous; the outer ones widely depressed ovate, ca. 1.2 x 1.3 mm, the inner ones widely obovate, 0.9-1 x 0.8-0.9 mm; staminodes oblong to clavate, ca. 0.5 mm long; ovary ca 5x2 mm, glabrous, with a ca. 1 mm long neck; styles free to base, 0.6-0.7 mm long, stigmas 2-parted into recurved or sickle-shaped arms. Capsules up to 8 per spike, basally truncate to rounded, apically emarginate to obcordate,

2.7-3.5 x 4.2-5.5 cm, pale brown; wings broader than semicircular; stipe obdeltate, 5-6 mm long. Seeds 23-30 mm in diam (6-8 mm exclusive of wing); wing 12-15 mm broad.

Distribution. Northeastern India; occurs in moist regions up to altitudes of ca. 1250 m.

Representative specimens. INDIA. Assam State, Nowgong Dist. : Dimapur, King's collection 101 (E); Sibsagar Dist. : Rajhabari, Watt 11264 (E); Meghalaya State, Cherrapunji, Griffith 5537 (K), Hooker & Thomson s.n. (GH, K); Nagaland State, Naga Hills, Griffith 5557 in part (K);

BANGLADESH. s. loc. Griffith 5537 (NY).

Common names. India: Phan-skong, Palam bok.

The leaf shape and floral structure of this species closely resemble those of D. oppositifolia. However, D. wattii is easily recognized by its prominently elevated reticulation and large capsules.

13. *Dioscorea oppositifolia* Linnaeus, Sp. pl. 1033. 1753,
 excluding reference to Petiver, Gazophyl. nat. 50, pl. 31.
 fig. 6. 1702; Kunth, Enum. pl. 5: 390. 1850; Hooker f. in
 Trimen, Handb. Fl. Ceylon 4: 276. 1898; Knuth in Engler,
 Pflanzenr. 87 (IV, 43): 286. 1924; Prain & Burkill, Ann.
 Roy. Bot. Gard. Calcutta 14: 392, pl. 139. 1939. Type:
 Linnaean specimen 1184/7 (LINN, Lectotype)

Tuber usually solitary, cylindrical, up to 25 cm long and 2 cm in diam., with a long stalk, deeply penetrating vertically into the soil. Stem up to 5 mm in diam., glabrous to pubescent, + unarmed. Bulbils absent. Leaves opposite to subopposite or alternate, the phyllotaxy often varying within a individual; blade elliptic to ovate or obovate, sometimes very variable within a individual, basally acute to rounded, often minutely cordate, apically acuminate or cuspidate, glabrous or rarely pubescent above, \pm pubescent or glabrous below; primary veins 3, acrodromous, basal, perfect, prominent, distinctly reaching apex, with one (2 in broader leaves) less prominent outer pair becoming obscure toward apex; reticulation obscure on both surfaces; margin thick, cartilaginous, yellowish; petiole 0.5-3(4) cm long, glabrous to pubescent stipules absent. Staminate inflorescence axillary, paniculate or less commonly spicate or both; panicles one or rarely two per axil, the rachis 1-30 cm long, usually ascending. glabrous or pubescent, the branches 1-2(3) per axil,

subtended by alternate or opposite to subopposite inflorescence bracts, 10-30(40)-flowered, 0.6-4(5) cm long, ascending to descending. Flowers lax or densely aggregated, partially open at anthesis, flattened at base, 1-2.2 x 1.2-2.4 mm; bract ovate, acuminate, 0.6-1.4 x 0.5-1 mm, glabrous; bracteole ovate, acuminate, 0.5-0.9 x 0.4-0.8 mm, glabrous; tepals basally connate to form, with expanded torus, a flat base of flower, the outer ones widely ovate, apically acute or rounded, 1.1-2.1 x 0.8-1.4 mm, often with thin translucent margins, the inner ones elliptic to obovate, distinctly smaller and fleshier than outer tepals, 0.7-1.5(1.7) x 0.6-1.3 mm; stamens free, the filament 0.2-0.3 mm long, somewhat broader at base, the anther 0.3-0.5 mm long, connective not expanded; pistillode completely 3-parted, 0.1-0.2 mm long. Pistillate inflorescence axillary, solitary, spicate, usually ascending, glabrous pubescent, 2-22 cm long, 2-15-flowered, very rarely paniculate. Flowers lax, almost sessile at anthesis; bract ovate, acuminate, 1-2(2.2) x 0.7-1.4(1.6) mm, glabrous; bracteole ovate, acute, 0.7-1.2(1.5) x 0.4-0.8 mm, glabrous, tepals as in staminate flower, the outer ones 0.8-1.2(1.6) x 0.6-1(1.2) mm, the inner ones 0.5-0.8(-1.2) x 0.4-0.7 (1.3) mm; staminodes 6, 0.1-0.3 mm long; ovary 2-5 x 1-2.8 mm, glabrous or pubescent styles free to base, 0.3-0.5 mm long; stigmas 2-parted. Capsules up to 15 per spike, \pm twice as broad as long, basally truncate, apically truncate to obcordate, straw-colored or pale brown, glossy, glabrous; wings rounded;

stipe obtriangular to obdeltate, 3-5 x 2-3 mm. Seed 6.5-20 mm in diam (3-5.5 mm exclusive of wing); wing 2-9 mm broad.

Distribution. Lower Peninsular India and Sri Lanka; occurs in dry, moist and intermediate regions from low altitudes up to ca. 1300 m.

Common names and uses. India: Tunga, Tunga alu, Pani alu, Nan Mati, Kras mati, Kiras kanda, Kircha; Sri Lanka: Hiritala. Tubers are edible and popular in regions where it grows.

Although Prain & Burkill proposed 4 varieties to accommodate variations in pubescence of the plant and nature of the staminate inflorescence, i.e. whether the flowers are arranged in spikes or panicles, only 2 varieties, based on the presence and absence of pubescence, are retained in this treatment (see key to the species of section Enantiophyllum). Spikes and panicles are often present within the same individual and this character cannot be used to distinguish varieties. Prain & Burkill (1936) observed that the type of D. oppositifolia belonged to var. linnaei which they defined by glabrous, broadly lanceolate or ovate leaves and staminate inflorescences with a brownish pubescence. This variety and others with any degree of pubescence on the leaves or inflorescence axes are placed in var. oppositifolia in this treatment. It is further proposed that D. trinervia is conspecific with the latter variety. The

complete glabrous nature of the plant characterizes the var. dukhunensis and it is very clear that D. intermedia and D. obcuneata are taxonomically identical conspecific with this variety, because they cannot be distinguished on any of the vegetative or floral characteristics.

The pattern of distribution indicates that populations of two varieties occur in same geographical area and inter-varietal hybridization is most probable as suggested by varying degrees of pubescence in var. oppositifolia.

13a. Dioscorea oppositifolia Linnaeus var. oppositifolia. Fig. 30A, B.

Dioscorea oppositifolia Linnaeus var. thwaitesii Prain & Burkill, J. & Proc. Asiat. Soc. Bengal 10: 30. 1914.

Type: Sri Lanka: Walker 147 (lectotype chosen here, K).

Dioscorea oppositifolia Linnaeus var. linnaei Prain & Burkill, Ibid. 10: 30. 1914. Type: Sri Lanka, Walker 46 (lectotype chosen here, K; isoelectotype, E, 3 sheets).

Dioscorea trinervia Roxburgh [ms., nomen nudum] ex Prain & Burkill, Ibid. 10: 32. 1914. Type: India, s. loc., Roxburgh s.n. (lectotype chosen here, K).

Dioscorea oppositifolia Linnaeus var. meeboldtii Prain & Burkill, Ann. Roy. Bot. Gard. Calcutta 14: 393. 1939. Type: India, Kerala State, Cochin Dist.: Perambikolam, Meebold 12374 (n.v.).

Stem, leaf blade, and petiole glabrous to pubescent.

Inflorescence axes in both sexes and ovary pubescent.

Representative specimens. INDIA. Assam State, Cachar Dist.: N. Cachar Hills, Craib s.n. (K); W. Bengal State, Khana, Hooker & Thomson s.n. (K); Meghalaya State, Khasia, Hooker & Thomson s.n. (K); Mysore State, Hassan Dist.: Byra State Forest, Ramamoorthy 1590 (E, MO, US); Bisle, Saldanha 16885 (E, US); Bangalore Dist.:

Bangalore, Cleghorn s.n. (E); Kerala State, Kottayam Dist.: Kottayam, Wight 941 (E); Tamil Nadu State, Nilgiri Dist.: Nilgiri Hills, Watt 22 (E); Salem Dist.: Hosur Taluk, Yeshoda 41(NY); Thanjavur Dist.: Nagappattinam, Wight s.n. (E); Maharashtra State, Kolaba Dist.: Khandala, Santapau 13949 (MO); 13340 (MO); Andhra Pradesh, Chittoor Dist.: Palkonda, Cambell s.n. (E).

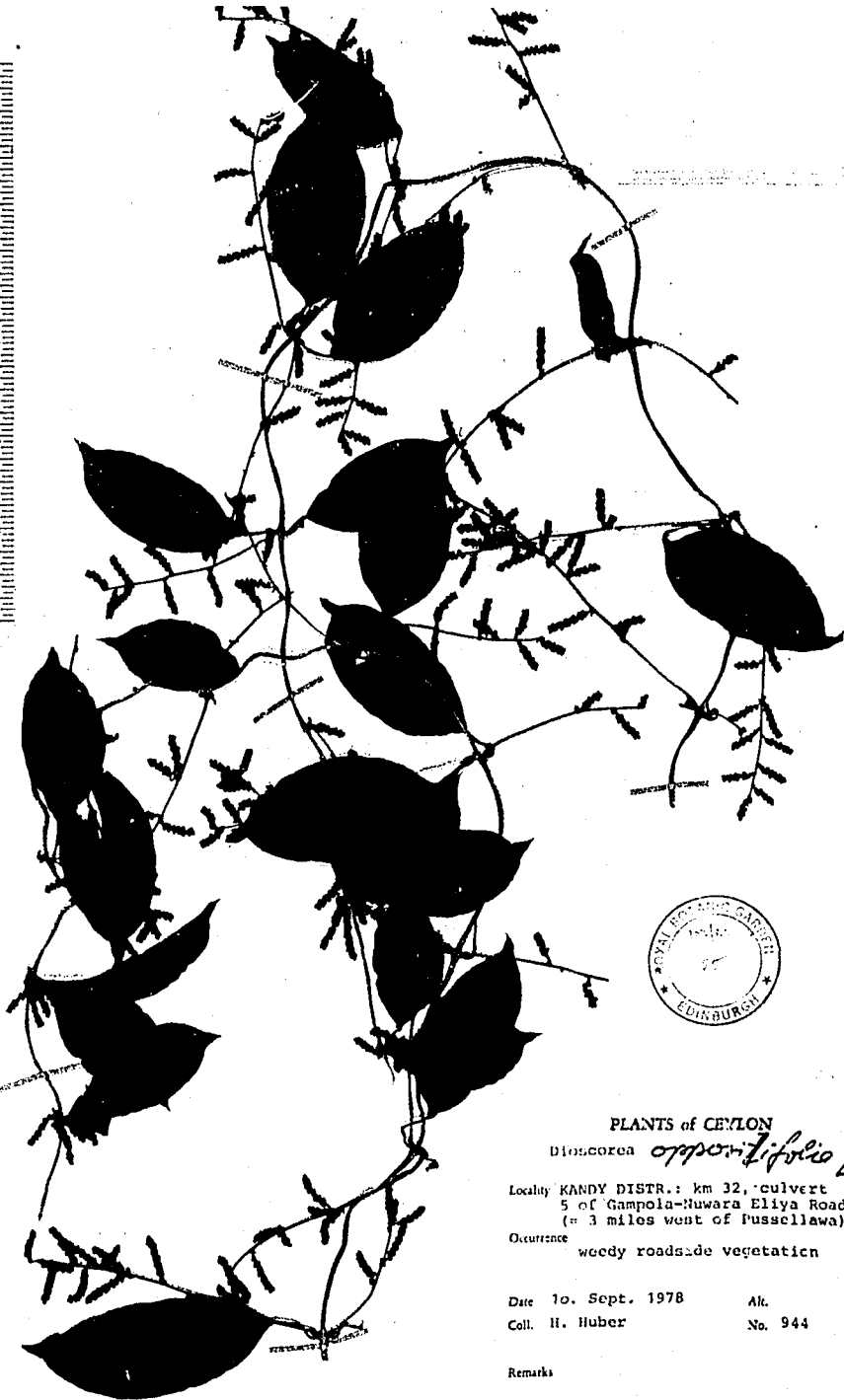
BANGLADESH. Syhet Dist.: Sylhet Wallich 5105 (K); s.loc. Masters in Griffith herb. 5549

SRI LANKA. Vavuniya Dist. : between Medawachchiya and Mannar, Jayasuriya et al. 585 (JEPS, MO, NY, US), 585 1/2 (MO, PDA); Anuradhapura Dist., Issanbassawa, between Medawachchiya and Manner, Rudd 3258 (PDA, US); Ritigala, Bernardi 14308 (PDA, US); Kandy Dist. : 3 miles N.E. of Madugoda, Jayasuriya et al. 486 (PDA, US), 487 (PDA; US); between Gampola and Nawalapitiya, Comanor 524 (JEPS, MO, NY, PDA); W. of Pussellawa, Huber 944 (E, PDA, US); Monaragala Dist. : Monaragala, Alston 16 (PDA); Amparai Dist. Pottuvil Alston s.n. (PDA).

Fig. 30. Dioscorea oppositifolia var. oppositifolia

A. Staminate plant (Huber 944, E).

B. Pistillate plant (Rudd 3258, US).



PLANTS of CEYLON

Dioscorea oppositifolia L.

Locality KANDY DISTR.: km 32, culvert
5 of Gampola-Huwara Eliya Road
(= 3 miles west of Pussellawa)

Occurrence weedy roadside vegetation

Date 10. Sept. 1978

Alt.

Coll. H. Huber

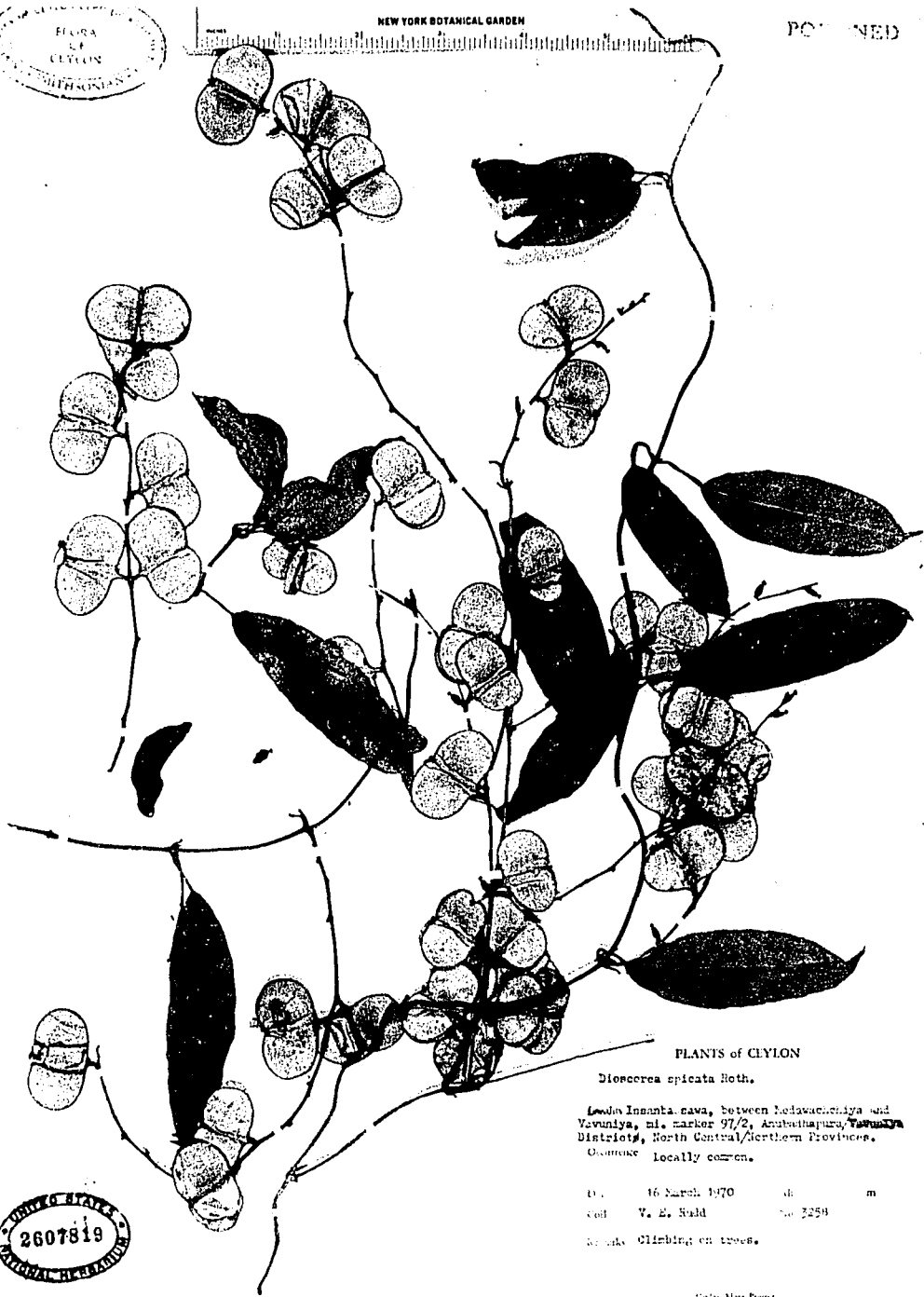
No. 944

Remarks



NEW YORK BOTANICAL GARDEN

POUNDED



PLANTS of CEYLON

Dioscorea spicata Roth.

Lewia Insanta Gawa, between Nedawachchiya and
Yavuniya, mi. marker 97/2, Anubathapura, ~~Yavuniya~~
Districts, North Central/Northern Provinces.

Common. Locally common.

1970 16 March 1970 alt. m
col. V. E. Wald No. 2259

Habit. Climbing on trees.



Gift: Her. Proct.

13b. Dioscorea oppositifolia Linnaeus var. dukhunensis Prain & Burkill, J. & Proc. Asiat. Soc. Bengal 10: 30. 1914; Knuth in Engler, Pflanzenr. 87 (IV. 43): 286. 1924; Prain & Burkill, Ann. Roy. Bot. Gard. Calcutta 14: 393. 1939. Type: India, Tamil Nadu Dist.: Nilgiri Hills, Wight 2825 (lectotype chosen here, K).

Dioscorea intermedia Thwaites, Enum. pl. zeyl. 326. 1864. Type: Sri Lanka, Thwaites C.P. 2870 (lectotype chosen here, BM; isolectotype, K, n.v.).

Dioscorea obcuneata Hooker f., Fl. Brit. India 6: 293. 1892. Type: Sri Lanka: Macrae 111 in Hooker herb. (holotype, K; isotype BM).

Plants glabrous.

Representative specimens. INDIA. Orissa State, Dhenkanal Dist.: Angul, Lace 2542 (E); Mysore State, Hassan Dist.: Byrapura, Nicolson et al. 235 (E, MO, US); Bellary Dist.: Kotturu, Barnes 1002 (GH); Tamil Nadu State, Salem Dist.: Hosur Taluk, Yeshoda 41(A), 237 (NY); Madura Dist.: Kodaikanal, Pulney Hills, Anglade s.n. (A); Kerala State, Trivandrum Dist.: Travancore, Erlanson 5349 (A, NY).

SRI LANKA. Vavuniya Dist.: 2 miles S. of Alampil, Wambeck et al. 2676 (US); Anuradhapura Dist.: Ritigala, Balakrishnan & Jayasuriya 1098 (K, MO, PDA, US); Kurunegala Dist.: Kurunegala

Rock, Huber 382 (PDA, US); Amparai Dist. : Kokgala Hill, Bernardi 15705 (PDA, MO, US); Kandy Dist. : Gannoruwa Hill, Peradeniya, Wirawan 622 (GH, JEPS, NY, PDA, US); Udawatte, Kundu 130 (PDA, US); Galle Dist. : Buona Vista, Cramer 3522 (PDA, US).

14. *Dioscorea pubera* Blume, Enum. pl. Javae 21. 1827; Knuth in Engler, Pflanzenr. 87 (IV. 43): 282. 1924, in part; Prain & Burkill, Ann. Roy. Bot. Gard. Calcutta 14: 402, pl. 143, 1939. Type: from Malaya, no specimen cited. Fig. 31A, B.

Dioscorea anguina Roxburgh [Hort. Bengal. 72. 1814, nomen nudum] ex Roxburgh, Fl. Ind. 3: 803. 1832, excluding reference to Rumphius, Herb. amboin. 5: pl. 122. 1747. Type: from India, W. Bengal State, Howrah Dist.: near Calcutta, no specimen cited.

Dioscorea cornifolia Kunth, Enum. pl. 5: 385. 1850. Type: Indonesia, Java, Zollinger 875 (n.v.).

Tubers 1-2, penetrating vertically into the soil, cylindrical, up to 2 m long and 8 cm diam, the surface tawny-orange, with numerous rootlets, the tissue lemon-yellow, tender, but proximally fibrous. Stem up to 8 mm diam., covered with white hairs turning brownish with maturity, unarmed, usually with brownish warts at base. Bulbils up to 4 cm across. Leaves alternate, or subopposite to opposite especially toward apex; blade ovate to very widely ovate, basally cordate, abruptly acuminate apically, 8-15(24) x 7-15(20) cm, chartaceous, glabrescent above, pubescent below; primary veins campylodromous, usually 7, the inner 5 reaching apex; secondary veins \pm straight, somewhat distant; reticulation obscure; margin firm, prominent, yellowish; petiole \pm half as long as blade, 4-10 cm long,

grey-pubescent; stipules absent. Staminate inflorescence terminal or often axillary, 1-3 per axil, paniculate, the rachis erect to horizontal 4-37 cm long, densely pubescent, the branches opposite to subopposite, 1-4 per axil, subtended by up to 5 mm-long inflorescence bract, 10-14-flowered. Flowers densely aggregated, partially open at anthesis, 1-1.6 mm across; bract ovate, acuminate, ca. 1.2 x 0.8 mm, densely pubescent without; bracteole ovate, acute to rounded apically, the outer ones incurved, 1-1.7 x 0.7-1.1 mm, pubescent without, the inner ones 0.7-1 x 0.5-1 mm, glabrous; stamens free or adnate to base of tepals, the filament 0.2-0.3 mm long. Pistillate inflorescence axillary, solitary, paniculate, erect to horizontal, with densely pubescent axes, the rachis 4-34 cm long, the branches 4-19 cm long, sometimes longer than rachis, usually solitary, opposite to subopposite, subtended by 3-4 mm-long bracts, up to 20-flowered. Flowers lax, nearly sessile at anthesis; bract ovate to widely ovate, acuminate, 1.3-2 x 1-1.3 mm, densely pubescent toward base; bracteole widely oblong-ovate, acute, 0.7-0.8 x 0.6 mm, densely pubescent toward apex; tepals somewhat fleshy, very widely ovate, the outer tepals obtuse, ca 1 x 1 mm, sparsely pubescent without toward base; the inner tepals apically rounded, 0.7-0.9 x 0.8-0.9 mm, glabrous; staminodes 6, ca. 0.2 mm long; ovary 4.5 x 2.5-3.5 mm, densely pubescent, straw-colored; styles free to base, 0.4-0.5 mm long; stigmas terminally parted into two upper, lateral, recurved lobes and one lower, median, short, lobe.

Capsule up to 15 per spike, retuse to cordate basally and apically, more than twice as broad as long, 1.3-1.6 x 3.3-3.6 cm, straw-colored, glabrous to pubescent; stipe obdeltate, 2-3 x 2-3 mm; wing rounded. Seed 16-17 mm diam.(3-4 mm exclusive of wing); wing 4-8 mm broad.

Distribution. Central and eastern Peninsular India, extending to Nepal and Upper Burma; disjunct distribution in southwestern India and in Java; occurs in moist regions from low altitudes to ca. 1100 m.

Representative specimens. INDIA. Sikkim State: Lama Hills, Hooker s.n. (K); s.loc., Hooker s.n. (GH, K); Bihar State: Monghyr, Buchanan-Hamilton in Wallich no. 5103-B (E); s.loc., Watt 9808(E); W. Bengal State, Howrah Dist.: Calcutta, Voigt 379 (GH); Assam State: s.loc., Jenkin s.n. (E, NY); s.coll. 88 (E); Meghalaya State: Khasia Hills, Hooker & Thomson s.n. (GH, K); Shillong, Khasia Hills, Chand 8272 (JEPS); Manipur State: Karong, Koelz 26845 (JEPS); Orissa State, Dhenkanal Dist.: Angul, Antulia Forest, Lace 2585 (E).

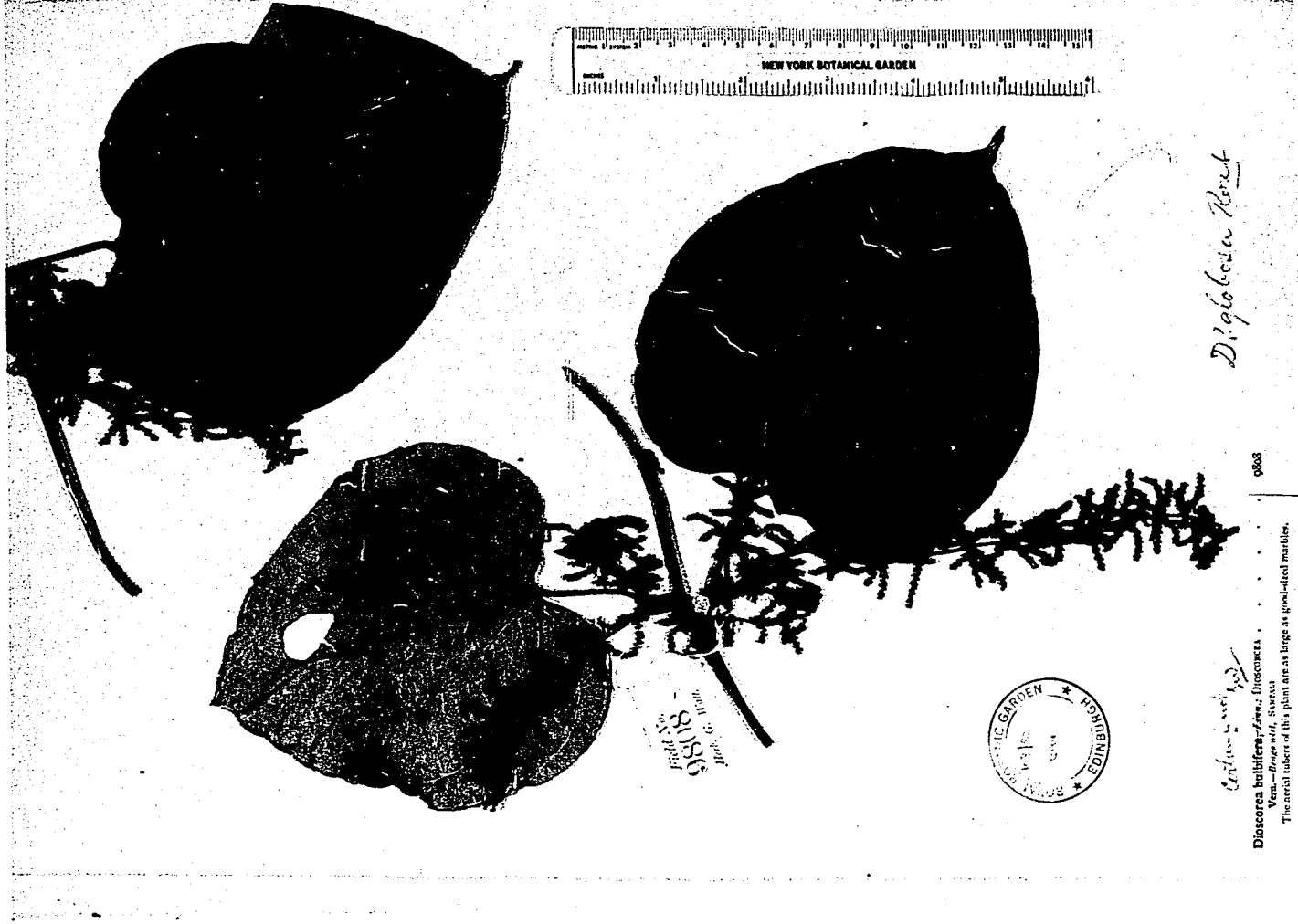
NEPAL. Argam, near Pokhara, Stainton et al. 7191 (E).

Common names and uses. India: Soong bok, Pang lang, Tha ja, Ta shep, Kukare sanga, Toralia. Tubers are edible.

Fig. 31. Dioscorea pubera

A. Staminate plant (Watt 9808, E).

B. Pistillate plant (Lace 2585, E).



Dioscorea bulbifera Hort.

9803

Centrosema

Dioscorea bulbifera *Lam.*; **Dioscorea**.

Vern.—*Binge* *Witt.*, *Saxena*

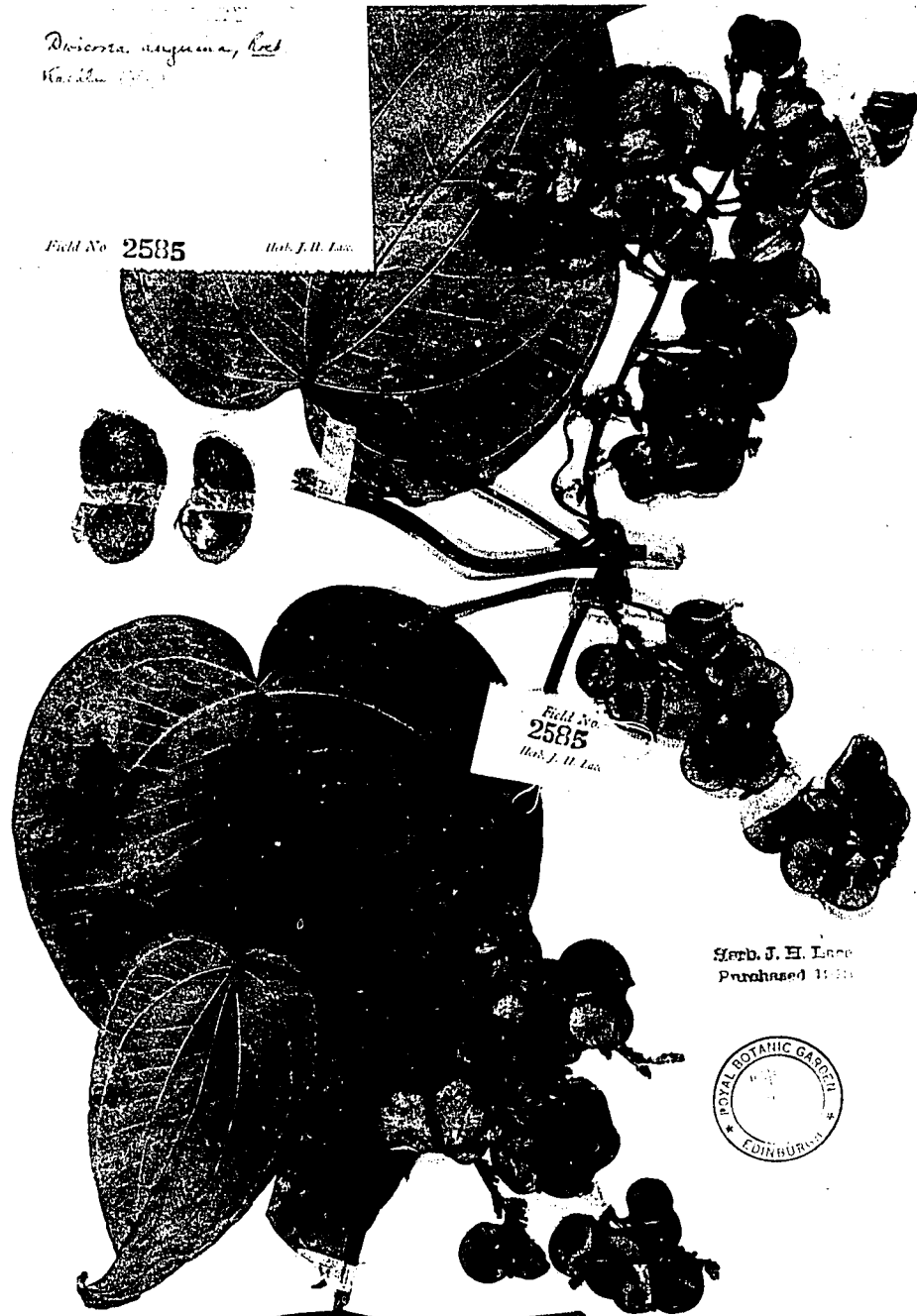
The aerial tubers of this plant are as large as apple-sized nutlets.



Dioscorea argyrea, Root
Kawila 1885

Field No 2585

Herb. J. H. Lane



Herb. J. H. Lane
Purchased 1885



15. *Dioscorea belophylla* J. Voigt [Hort. suburb. Calcut. 653.

1845, nomen nudum] ex Haines, Forest fl. Chota Nagpur 530.
1910; Knuth in Engler, Pflanzenr. 87 (IV. 43): 266. 1924;
Prain & Burkill, Ann. Roy. Bot. Gard. Calcutta 14: 348, pl.
127. 1939. Type: India, Bihar State, Hazaribagh Dist.:
Parasnath, Hooker s.n. (lectotype chosen here, K).

Dioscorea nummularia Lamarck var. *belophylla* Prain, Bengal
pl. 2: 1967. 1903. Type: from India, Bihar State,
Hazaribagh Dist., Chota Nagpur Region: Parasnath, no
specimen cited.

Tubers 1-3, deeply penetrating into the soil, ca. 20 cm long, stalked, the stalk up to 40 cm long, the surface pale brown; the tissue white, tender. Stem terete or often ridged or very narrowly alate, up to 4 mm diam., purplish brown, brown or reddish brown at maturity, unarmed. Bulbils abundant. Leaves commonly alternate or opposite to subopposite; blade ovate or occasionally very widely ovate, basally cordate to sagittate, the sides of sinus in large leaves straight, apically acuminate, 7-16 x 4-12 cm, almost coriaceous, glabrous, green above, paler beneath; primary veins campylodromous, 7-9, the inner 5 reaching apex, prominent above, strongly prominent below, usually straw-colored, the outermost pair usually forked near origin and each outer branch runs parallel to inner margin of the lobe; secondary veins widely acute or approximately perpendicular to

the primary veins, almost straight; reticulation prominent; margin \pm firm, distinct; petiole nearly half as long as blade, 3-11 cm long, \pm angular, deeply grooved above with narrowly alate edges proximally terminating at stipules on either side of the node; stipules narrow, up to 1 mm wide, Staminate inflorescence paniculate or occasionally spicate; panicles terminal or commonly axillary, 1-2 per axil, the rachis 2-54 cm long, glabrous, sharply angled to narrowly alate, the branches alternate to opposite, up to 5 per axil, subtended by 1-3 mm-long bract or small leaf, 10-40-flowered, the axis of branch sharply angular or narrowly alate; spikes when present fascicled in axils of terminal leaves. Flowers lax or densely aggregated, somewhat open at anthesis, 1.3-1.7 x 1.1-1.7 mm; bract decurrent on the axis, widely ovate, acuminate, 0.8-1.3 x 0.9-1 mm; bracteole widely ovate, acute, ca. 0.8 x 0.7 mm; tepals erect to slightly incurved, fleshy, the outer tepal ovate, apically obtuse to rounded, 1.2-1.8 x 0.9-1.4 mm, the inner tepals obovate, apically rounded, 0.8-1.4 x 0.6-1.1 mm; stamens free, the filament 0.2-0.3 mm long, the anther 0.4-0.5 mm long, the connective narrow; pistillode distinguishable into 3 separate, conical lobes, ca. 0.2 mm long. Pistillate inflorescence 1-2 per axil, spicate or rarely paniculate; spikes up to 12-flowered, the axis 4-18 cm long, sharply angular or narrowly alate, glabrous, straw-colored when dried. Flowers lax, sessile at anthesis; bract ovate to widely deltate, acute, 1.1-1.4 x 0.7-0.9 mm; tepals somewhat

fleshy, the outer ones ovate to widely ovate, apically obtuse to rounded, 0.8-1 x 0.7-1 mm, dissimilar in size, with a membranous margin, the inner tepals oblong to spatulate, apically rounded, 0.8-1 x 0.5-0.7 mm, with a scarious margin; staminodes 6; ovary 4-6 x 1.5-2.5 mm, glabrous, the neck distinctly elongated, 0.7-2mm long; styles free to base, 0.4-0.5 mm long; stigmas terminally lobed into two reflexed arms. Capsules 2-11 per spike, basally truncate to rounded or obtuse, apically truncate to emarginate, ca. 1½ as broad as long, 1.8-2.5 x 2.5-3.6 cm, tawny, subglaucous; occasionally 1 or 2 wings abortive; stipe shallowly deltate, ca. 3 x 4 mm. Seed 13-17 mm diam. (4-6 mm exclusive of wing); wing 4-8 mm across.

.Distribution. India; mountain slopes of Himalaya from Kashmir State eastward to Khasia Hills in Assam State, hills in eastern and upper peninsular India; disjunct distribution in the Nilgiri Hills in southeastern India; occurs at altitudes of 300-1600 m.

Representative specimens. JAMMU & KASHMIR STATE. Kotli, Rashid 26986 (BM).

INDIA. Punjab State, Gurdaspur Dist.: Pathankot, Stewart 1013 (A, K, NY, PH); Himachal Pradesh State, Chamba Dist.: Dalhousie, Drummond 1465 (K); Kangra Dist.: Kulehr, Hart 501 (E); Mahasu Dist.: Simla, Watt 8039 (E); Uttar Pradesh State, Dehra Dun Dist.: Mussooree, Stewart 11427 (MOAR, NY); Almora

Dist.: Bageswar, Strachy & Winterbottom 3 (K); Sikkim State, s. loc, Hooker s.n. (K); W. Bengal State, s. loc., Biswar s.n. (GH); Bihar State, Palamau Dist.: Palamau, Haines 5112 (K); Hazaribagh Dist.: Parasnath, Clarke 21322-B (BM); Singbaum Dist.: Haines 686-a (K); Madhya Pradesh, Hoshangabad Dist.: Pachmarhi, Hole 855 (US); Raigarh Dist.: Jashpurnagar, Khudia, Dhaupat, Mooney 1897-b (K); Mysore State, Belgaum Dist.: Belgaum, Ritchie 1239 (E).

NEPAL. Balle, Polunin et al. 611 (BM); Jajarkot, Polunin et al. 5721 (BM, E).

Common names and uses. India: Ta rar, Pazok bok, Singul bok, Panu torul, Dura sanga; Nepal: Ban torul.

16. *Dioscorea glabra* Roxburgh [Hort. Bengal. 72. 1814, nomen nudum]; Fl. Ind. 3: 804. 1832; Kunth, Enum. pl. 5: 383. 1850; Hooker f., Fl. Brit. India 6: 294. 1892, in part; Knuth in Engler, Pflanzenr. 87 (IV. 43): 276. 1924; Prain & Burkill, Ann. Roy. Bot. Gard. Calcutta 14: 354, pl. 131. 1939; Burkill, Fl. Males. 4: 331. 1951. Type: Bangladesh, Sylhet Dist.: Sylhet, Wallich 5105-E (lectotype chosen here, K, staminate plant designated as (a); isoelectotypes, BM; E, staminate plant designated as (a). Fig. 32A, B.

Dioscorea glabra Roxburgh var. grisea Prain & Burkill, J. & Proc. Asiat. Soc. Bengal 10: 37. 1914. Type: from Burma, Tenasserim; Malaya; Sumatra; and Java, no specimen cited.

Dioscorea glabra Roxburgh var. salicifolia Prain & Burkill, *ibid.* 10: 37. 1914. Type: from Java, no specimen cited.

Dioscorea glabra Roxburgh var. hastifolia Prain & Burkill, *ibid.* 10: 37. 1914. Type: Andaman Island, Rutland Island, Rogers 278 (holotype, K).

Dioscorea glabra Roxburgh var. vera Prain & Burkill, *ibid.* 10: 38. 1914. Type: no specimen cited.

Dioscorea glabra Roxburgh var. longifolia Prain & Burkill, *ibid.* 10: 38. 1914. Syntype: China, Yun-nan Prov.: Sze-mao, Henry 13540 (NY); Cambodia, Bien-hoa

Prov.: Bien-hoa, Thorel 287 (n.v.); Indo-china: s. loc.,
Balansa 298, 301 (n.v.)

Dioscorea glabra Roxburgh var. tenuifolia Prain & Burkill,
ibid. 10: 38. 1914. Syntype(n.v.): Burma, s. loc., Kurz
2631; Katha Dist.: Katha, Burkill 22656.

Dioscorea glabra Roxburgh var. pahangensis Prain & Burkill,
Ann Roy. Bot. Gard. Calcutta 14: 357. 1939. Type: W.
Malaysia, Malay Peninsula, Pahang State, Sungai Pertang
in Ulu Tembeling, Henderson s.n. (lectotype chosen here,
NY).

Dioscorea glabra Roxburgh var. tincta Prain & Burkill, ibid.
14: 357. 1939. Syntype (n.v.): W. Malaysia, Malay
Peninsula, Perak State: Taiping Hills, Burkill & Haniff
13016, 13020; Pahang State: Raub, Burkill & Haniff
16771-a; Fraser Hill, Burkill & Holttum 8432; Burkill
7860; Semango Pass, Burkill 7889.

Tubers one to several, long-stalked, \pm cylindrical, up to 50
cm long and 4 cm diam., the surface with a few rootlets, the
tissue white, the stalks arising from woody base of stem, nearly
as long as or sometimes longer than tubers. Stems up to 8 m
long, glabrous, smooth, green, those of the first and the second
years unarmed, subsequent ones basally armed with abundant
recurved prickles. Bulbils not seen. Leaves opposite; blade
ovate or oblong-ovate or widely ovate, basally truncate or round

or shallowly cordate, abruptly acuminate apically, 5.5-15 x 3.8-10 cm, chartaceous, the upper surface dark green, often drying light chesnut-brown; primary veins intermediate between acrodromous and campylodromous, 5-7, the inner 3-5 reaching apex, somewhat distinct above, prominent below; secondary veins \pm straight, almost indistinguishable from reticulation; reticulation obscure; margin distinct; petiole nearly half as long as blade, 3-7.5 cm long, deeply grooved above, glabrous; stipules absent. Staminate inflorescence terminal or mostly axillary, 1-2 per axil, paniculate, the rachis 2.5-3.2 cm long, erect to ascending, basally pubescent, terete to angular, the branches opposite to subopposite, 1-3(4) per axil, divaricate, the axis 1-3.5 cm long, angled; inflorescence bracts 1-4 mm long. Flowers usually densely aggregated, partially open at anthesis, 1-1.5 x 0.8-1.5 mm; bract ovate, acuminate, 0.7-1 x 0.6-0.8 mm; bracteole similar to bract, 0.5-0.7 x 0.4-0.5 mm; tepals \pm erect, glabrous, the outer ones slightly connate at base to form flattened base of flower, widely ovate, apically obtuse, 1-1.4 x 0.4-0.5 mm, the inner ones fleshy, obovate, apically obtuse, 0.9-1 x 0.5-0.8 mm; stamens free, the filament broad, flat, roughly triangular, ca. 0.2 mm long, the anther 0.3-0.4 mm long, the connective narrow; pistillode humpy, 3-lobed, 0.2-0.3 mm long. Pistillate inflorescence axillary, solitary or rarely 2, spicate, up to 15-flowered, the axis 3.5-25 mm long, terete to angular, glabrous to pubescent at base. Flowers lax, sessile at

anthesis; bract and bracteole as in staminate flower, the bract 1-1.3 x 1-1.1 mm, the bracteole 0.8-1.2 x 0.8-0.9 mm; tepals fleshy, glabrous, the outer ones very widely ovate, apically obtuse, 0.8-1.1 x 0.6-0.7 mm, with a membranous margin, the inner ones very fleshy, obovate, apically rounded, 0.7-0.8 x 0.6-0.7 mm; staminodes 6, ca. 0.2 mm long; ovary 4-5 x 2.5-3.5 mm, glabrous, the neck indistinct or up to 0.5 mm long; styles connate to apex, ca. 0.6 mm long; stigmas lobed into two lateral, recurved lobes and one median lobe. Capsules 2-7 per spike, basally truncate to obtuse, apically truncate to emarginate, slightly less than twice as broad as long, 1.6-2.4 x 2.8-3.8 cm, glaucous when young, turning yellowish and tawny with maturity; stipe shallowly obdeltoid, 3-5 x 4-7 mm; wing rounded. Seed 5.5-18 mm across (4.8-5.5 mm exclusive of wing); wing 2-9 mm wide.

Distribution. Widely distributed in S. E. Asia with its western limits in the northeastern India; also in Andaman and Nicobar Islands; occurs from low altitudes to ca. 1300 m; cultivated in small scale by some people in Assam State in India.

Representative specimens. INDIA. W. Bengal State, Darjeeling Dist.: Pahar Ghumghumia jhai, Gamble 340-A (K); Jalpaiguri Dist.: Duars, Haines 486 (E, K); Bihar State, Hazaribagh Dist.: Kodarma, Haines 2352 (K); Singbhum Dist.: Haines 435 (K); Dhalbhum Dist.: Gamble 9212 (K); Orissa State,

Dhenkanal Dist.: Angul, Haines 2462 (K); Assam State, Lakhimpur Dist.: Namchik River Valley, Belcher 315 (US); Juan 167 (GH); Meghalaya State: Khasia, Clarke 15234 (BM); Madhya Pradesh State, Bastar Dist.: Dantewara, Jain 5159 (MO); Andhra Pradesh State, Vishakapatnam Dist.: Palkondah, Campbell 1068 (E).

BANGLADESH. Bogra Dist.: Bogra, Clarke 26838-C (BM); Chittagong Dist.: Teknef, Khan 726 (E); Srimati, Cowan 145 (E)

NEPAL. Kailali Dist.: 1 mile S. of Dhangarhi, Nicolson 2810 (BM,US).

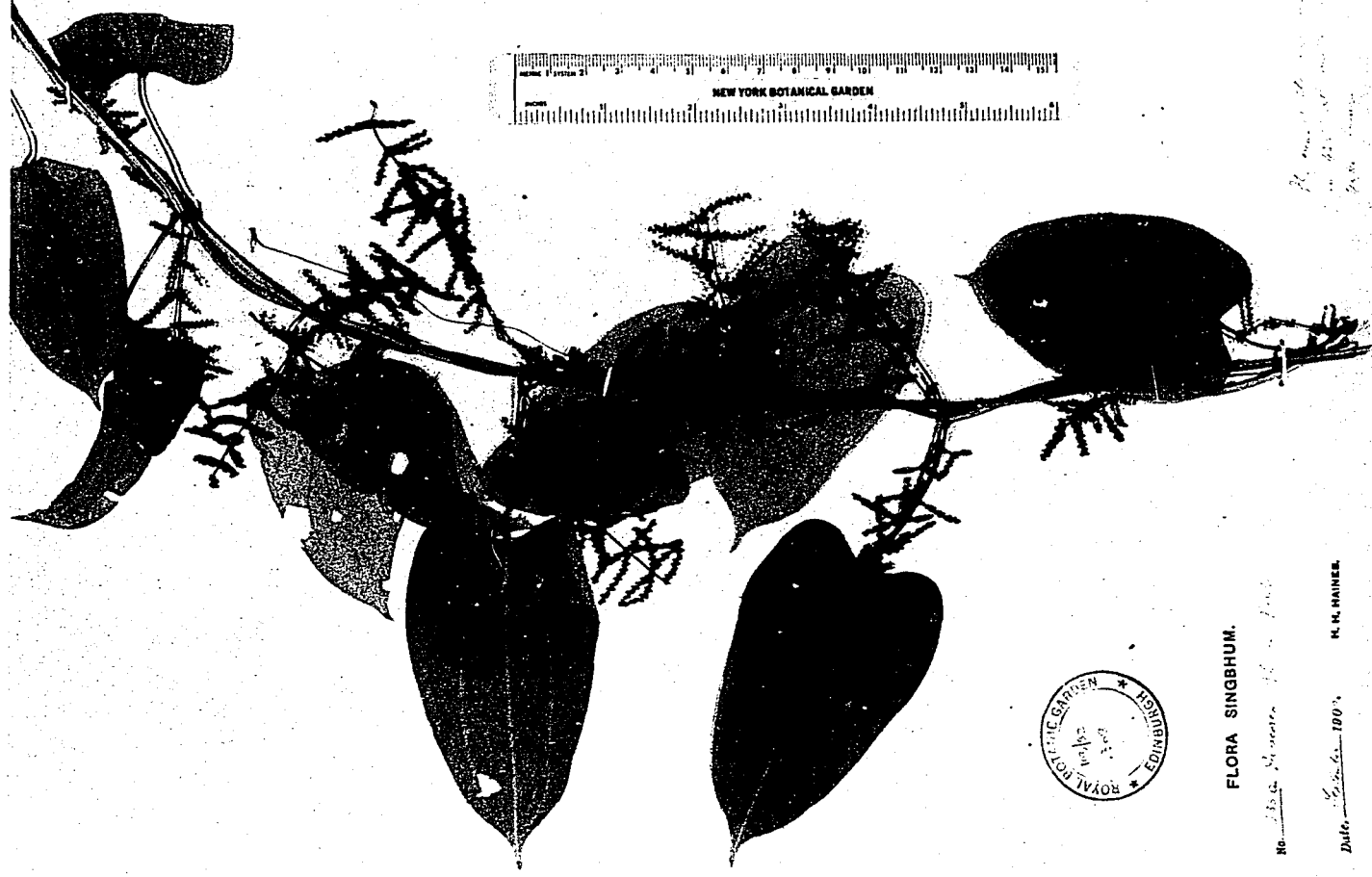
Common names and uses. India: Nai hkai, Chimeo bok, Unur sanga, Bir sanga, Shora alu, Katha alu, Paro gai; Thailand: Man mu; Andaman Island: Gona. Tubers are edible.

D. lepcharum, which is united with D. hamiltonii, shows affinities with D. glabra, and is a probable hybrid between the two species. None of the varieties proposed by Prain & Burkill based on the differences in size, shape, color, and texture of leaves are recognized in view of the wide range of inter-populational and infra-populational variations observed.

Fig. 32. Dioscorea glabra

A. Staminate plant (Haines 435-a, E).

B. Pistillate plant (Thomson s.n., NY).



FLORA SINGBHUM.

No. 1354 Singapore 1890
 Date Oct. 24 1890 N. H. HAINES

Handwritten notes:
 The name of the plant is
 in the list of
 plants in
 the
 Singapore



Herb. Acad. Sci. Stockholm
Quercus fusca Nutt.
 Herb. Acad. Sci. Stockholm
 1811

17. *Dioscorea wallichii* Hooker f., Fl Brit. India 6: 295. 1892; Haines, Bot. Bihar & Orissa, 1120, 1922; Knuth in Engler, Pflanzenr. 87 (IV. 43): 274. 1924; Prain & Burkill, Ann. Roy. Bot. Gard. Calcutta 14: 281, pl.115. 1939. Type: India, Bihar State, Chota Nagpur Region, Ranchi Dist.: Ranchi, Clarke 20369-A (lectotype, K).

Dioscorea aculeata Linnaeus, Sp. pl. 1033. 1753, reference to Rheede, Hort. malab. 7: pl. 37. 1688, in part.

Dioscorea wallichii Hooker f. var. vera Prain & Burkill, J. & Proc. Asiat. Soc. Bengal 10: 31. 1914. Type: from India, no specimen cited.

Dioscorea wallichii Hooker f. var. christiei Prain & Burkill, ibid. 10: 31. 1914. Type: from Burma, no specimen cited.

Tubers deeply penetrating, up to 1 m long, the surface brown, with numerous rootlets, the tissue soft, white, becoming yellowish in proximal parts. Stem terete, glabrous, ± reddish brown when dried, basally somewhat prickly. Bulbils not seen. Leaves alternate; blade widely ovate, basally cordate, apically acuminate, 8-15 x 6.5-15.5 cm, chartaceous, glabrous, dark green above and somewhat glaucous below, becoming reddish brown above and greenish below when dried; primary veins campylodromous, 7-9, the inner 5 ± distinctly reaching apex, prominent below; secondary veins ± perpendicular to primary veins, somewhat bent;

reticulation distinct below; margin distinct, cartilaginous, brownish or yellowish; petiole \pm as long as blade, 5-11.5 cm long, grooved above, glabrous; stipules absent. Staminate inflorescence axillary, 1-3(4) per axil, paniculate, the rachis 2-25 cm long, sharply angled, glabrous, usually reddish brown when dried, the branches alternate, 1-4(6) per axil, 1.5-5 mm long, 5-35-flowered. Flowers lax, solitary or sometimes paired, partially open at anthesis, 1.2-1.5 x 1.3-2 mm, flattened at base, bract decurrent on axis and strongly repressed against it by flower, widely depressed ovate, acute, 0.6-0.7 x 0.7-1 mm; bracteole widely ovate to widely depressed ovate, acute, 0.5-0.7 x 0.5-0.8 mm; tepals glabrous, the outer ones widely ovate, basally broad and connate to form flattened base of flower, apically acute to rounded. 1-1.2 x 0.9-1.1 mm, incurved, the inner ones \pm circular, 0.8-0.9 x 0.9-1.1 mm; stamens free, the filament ca. 0.1 mm long, the connective wide, distinctly separating anther lobes; pistillode ca. 0.2 mm long humpy, 3-lobed. Pistillate inflorescence axillary, 1-2 per axil, paniculate, up to 20-flowered, the axis 2.5-20 cm long, angled to terete, the branches 4-10 per panicle, alternate, 2.5-10.5 cm long, 2-10-flowered. Flowers lax, sessile at anthesis; bract ovate to very widely ovate, acute, 1.1-1.4 x 1-1.1 mm, decurrent on axis; bracteole ovate, acute, ca. 0.9 x 0.6 mm; tepals slightly larger and much fleshier than those in staminate flower, the outer ones ovate to widely ovate, apically acute to rounded,

1.1-1.7 x 1.1.5 mm, the inner ones widely oblong to very widely obovate, apically obtuse to rounded, 0.8-1.4 x 0.8-1.2 mm; staminodes 6, 0.1-0.3 mm long; ovary 4-7 x 2-3.5 mm, glabrous, with a ca. 0.5 mm-long neck; styles connate apex, 0.3-0.6 mm long, stigmas 3-parted into two lateral and one median lobe. Capsules up to 4 per panicle, 2-2.5 x 3.5-3.8 cm, basally truncate to round, apically emarginate to obcordate, pale brown; wing semicircular; stipe 1-1.5 mm long. Seed up to 12 mm across (4.5 mm exclusive of wing); wing 5.5 mm at broadest.

Distribution. India, Burma, and Thailand; discontinuously distributed due to its need for considerable amounts of moisture and, as a result, absent in a greater part of India and the Himalayan region; occurs from low altitudes up to ca. 1000 m.

Representative specimens. INDIA. Bihar State, Singbhum Dist.: s. loc., Haines 695-a (K); Assam State, Cachar Dist.: s. loc., Keenan s.n. (K); Maharashtra State, Kolaba Dist.: Khandala, Santapau 11583 (MO); 13935 (MO); Mysore State, Tumkur Dist.: Chiknayakanhalli, Meebold 10900 (K); Hassan Dist.: Bisle Ghat, Saldanha 12125 (MO, US); Kerala State, Quilon Dist.: Quilon, Wight 1089 (E); Ityanni, Fernandes 128 (A); Tamil Nadu State, Nilgiri Dist.: Wynaad, Beddome 7746 (BM).

Bangladesh. Sylhet Dist.: Sylhet, Wallich 5108-B (BM, GH); Chittagong Dist.: Cox's Bazar, Kelatuli, Sinclair 3860 (E); Hooker & Thomson s.n. (K).

Common names and uses. India: tunga, Tunga alu, Sanga, Bai ili, Tumangai, Jugur kanda; Bangladesh: Gunga; Burma: kadat. Tubers are edible, although supposedly of rather inferior quality compared to several other wild yams.

D. aculeata of Linnaeus (1753) is based on two descriptions and two plates. The first description, "Dioscorea foliis cordatis, caule aculeato bulbifero" (adopted from Linnaeus, Hort. cliff. 459. 1737), is clearly based on Rheede's plate no. 37 (1688). This plate is also cited in Linnaeus' protologue, and the leaves and inflorescences depicted in it resemble those of the species concerned. However, bulbils, so clearly illustrated in this plate, introduce uncertainty to the application of the name (Prain & Burkill 1919, 1939). Furthermore, the prickles, although shown to be present among fertile branches, are not seen among specimens examined. Evidently prickles are located at or near the base of the stem in D. wallichii. The second description, "Dioscorea Indiae orientalis, folio tamni longiore, floribus spicatis, spicis plurimis ex uno puncto exeuntibus, scapo eorum medio geniculato" (from Amman, Mus. imp. petrop. 1: 257. 1745), does not specifically indicate the species concerned. The plate from Francisci (Ost- und West- indische Lust- und Stat- garten, pl. 25. 1668) represents D. alata (Prain & Burkill 1939). This leaves nothing to lectotypify D. aculeata and therefore its rejection is recommended.

Two varieties recognized by Prain & Burkill (1939), based on color of capsules, are not maintained in this treatment to accomodate such variations within the species.

18. *Dioscorea wightii* Hooker f., Fl. Brit. India 6: 291. 1892;
Knuth in Engler, Pflanzenr. 87 (IV. 43): 280. 1924; Prain &
Burkill, Ann. Roy. Bot. Gard. Calcutta 14: 236, pl. 100.
1939. Type: India, Tamil Nadu State, Tirunelveli Dist.:
Kuttalam, Wight 2827 (lectotype chosen here, K;
isolectotype, GH). Fig. 33.

Tubers unknown. Stem terete, straw-colored, unarmed at least in upper parts. Bulbils not seen. Leaves opposite to alternate; blade cordiform, deeply cordate basally, acuminate, 6-7.5 x 3.8-6 cm, chartaceous, glabrous, straw-colored and somewhat glaucous below when dried; primary veins campylodromous, 7-9, the inner 5 reaching apex, prominent below; secondary veins distant, straight or distally branched, only slightly more conspicuous than lesser order veins; reticulation fine, distinct and slightly elevated above, somewhat prominent below; margin distinct; petiole more than half the length of blade, 4-5.5 cm long, slightly channelled above; stipules absent. Staminate inflorescence axillary, 1-3 per axil, spicate, the axis ascending, 3.5-7 cm long, slender, slightly ridged, glabrous, 10-20-flowered. Flowers lax, solitary, sessile, flattened at base, ca. 2 x 1.8 mm; bract and bracteole ovate, acuminate to cuspidate, membranous, the bract ca. 1.5 x 0.8 mm, the bracteole ca. 0.8 x 0.5 mm; outer tepals ovate, obtuse to acute, ca. 2 x 1 mm, the inner tepals distinctly smaller than outer tepals,

oblong-ovate, obtuse to acute, ca. 1.5 x 1 mm; stamens free, the filament ca. 0.4 mm long, the anther ca. 0.3-0.4 mm long, 3-lobed. Pistillate plant unknown.

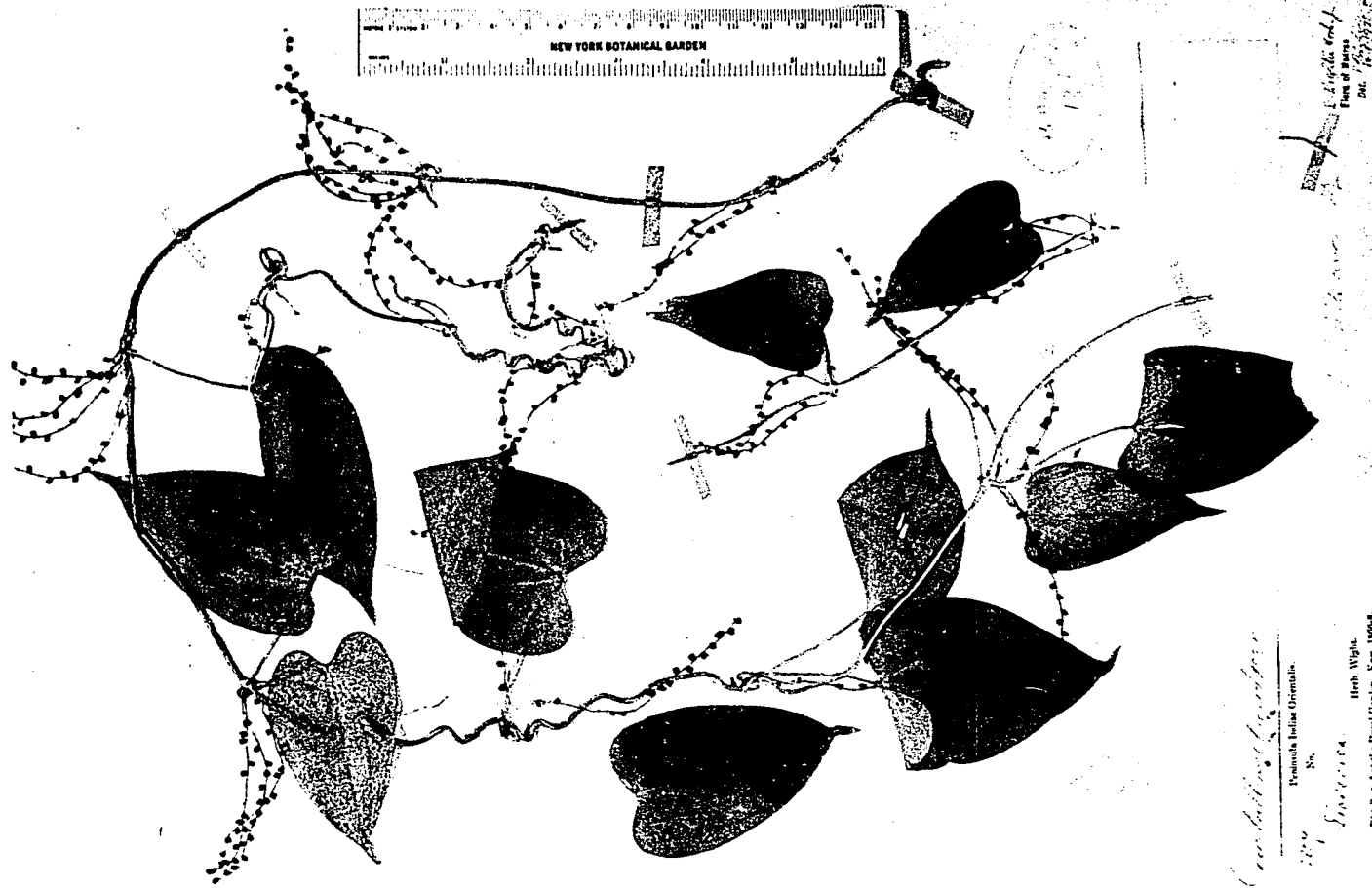
Distribution. S. India; only known from a few collections made during last century.

Specimens examined. INDIA. Tamil Nadu State, Tirunelveli Dist.: Kuttalam, Wight 939 (E), 936-A (A).

Only the staminate plant is known; apparently allied to D. spicata.

Fig. 33. Dioscorea wightii

Staminate plant (Wight 2827, K, lectotype).



Convolvulus
 No. 1000
 Herb. Wight.
 Distributed at the Royal Garden, Kew, India.

1841
 Herb. Wight.
 No. 1000
 Oct. 1841

19. *Dioscorea trimenii* Prain & Burkill, J. & Proc. Asiat. Soc. Bengal 10: 29. 1914; Knuth in Engler, Pflanzenr. 87 (IV. 43): 287. 1924; Alston in Trimen, Handb. Fl. Ceylon 6: 287. 1931; Prain & Burkill, Ann. Roy. Bot. Gard. Calcutta 14: 237. pl. 101. 1939. Basionym. *Dioscorea spicata* Roth var. b Thwaites. Fig. 34A, B.

Dioscorea spicata Roth var. b, Thwaites, Enum. pl. zeyl.

326. 1864. Type: Sri Lanka, Kandy Dist.: Ambagamuwa, Feb. 1854, Thwaites C. P. 3119 (lectotype chosen here, PDA; isolectotype, K).

Tubers unknown. Stem terete, glabrous. Bulbils not seen. Leaves opposite, occasionally alternate; blade ovate to lanceolate-ovate, shallowly cordate to sagittate basally, long-acuminate, 5-12 x 2.5-4 cm, glabrous, membranous, drying brown; primary veins subcampylodromous, 5(7), reaching apex, obscure above, somewhat distinct below; secondary veins oblique; reticulation obscure above, somewhat distinct below; margin almost indistinct; petiole 1/3-1/2 the length of blade, 2-5 cm long, slender; stipules absent. Staminate inflorescence axillary, 1-2 per axil, spicate, the axis usually ascending, 4-12 cm long, slender, angled, 18-45-flowered. Flowers lax, flattened at base due to expansion of torus and basal fusion of outer tepals, 1.1-1.8 x 1-1.8 mm; bract decurrent on axis at base, ovate, acuminate, 0.7-1 x 0.7 mm; bracteole widely ovate to

deltate, acute, 0.5-0.6 x 0.5-0.6 mm; outer tepals ovate to widely depressed ovate, basally broadened and slightly connate, apically acute to obtuse, 1.4-1.7 x 1-1.8 mm, the inner tepals distinctly smaller than outer ones, ovate, acute, 0.7-1.2 x 0.5-0.9 mm; stamens free, the filament ca. 0.2 mm long, the anther 0.3-0.4 mm long, the connective narrow; pistillode indistinct or up to 0.2 mm long, lobes indistinguishable. Pistillate inflorescence axillary, solitary, spicate, the axis 3.5-10 cm long. terete, angular. Flowers not seen. Capsules up to 3 per spike, basally truncate to rounded, apically acute to acuminate with truncate to rounded shoulders, ca. 3/4 as long as wide, 1.8-2.5 x 2.4-3.2 cm; wings nearly truncate or rounded on sides; stipe 3.5-5 mm long, obtriangular. Seed \pm squarish with rounded corners, 10-15 mm across (4-5 mm exclusive of wing); wing 2-5 mm at broadest.

Distribution. Sri Lanka; moist and intermediate regions from low altitudes to ca. 1000 m.

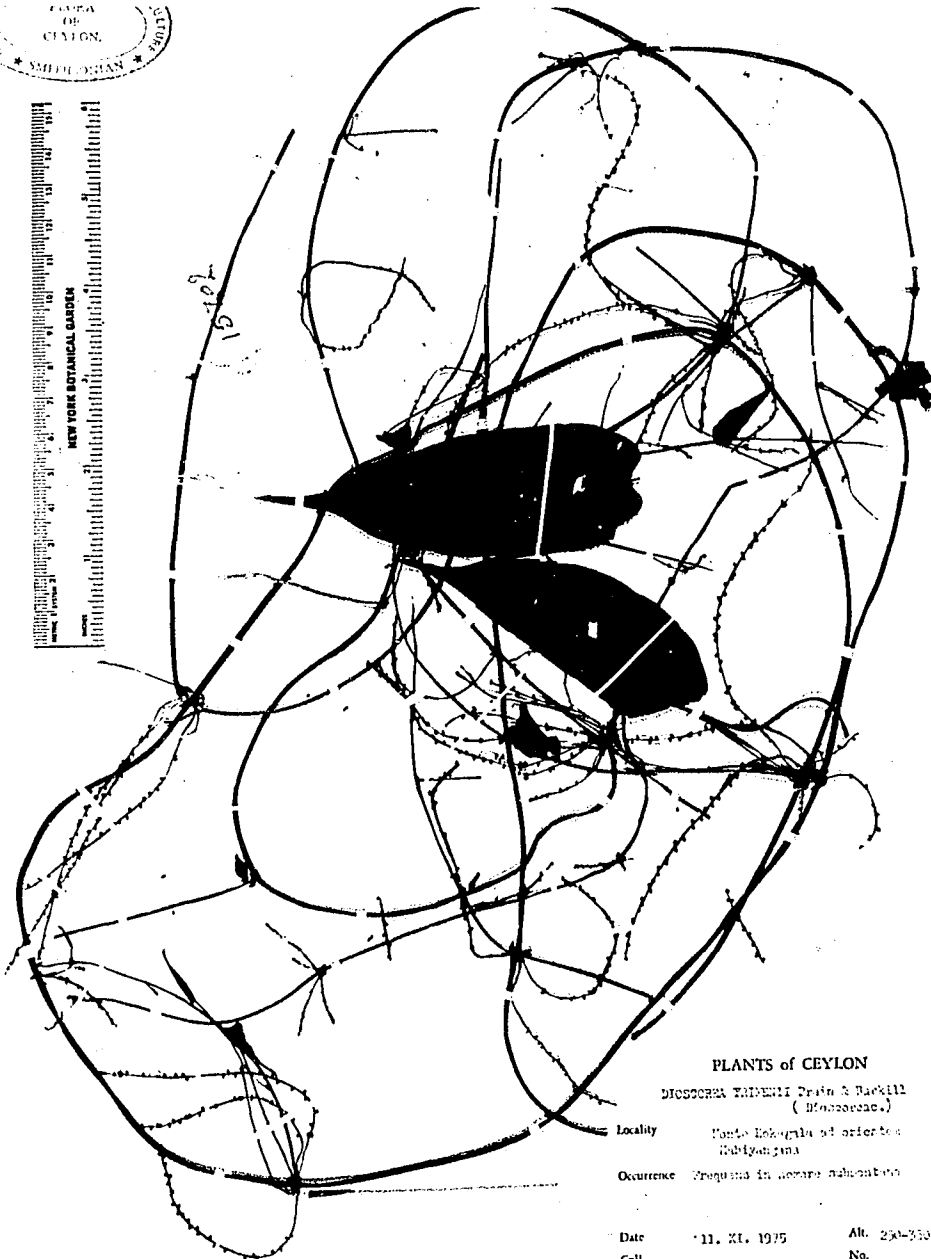
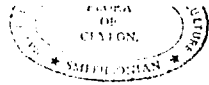
Representative specimens. Sri Lanka. Matale Dist.: Pallegama, Silva 170 (PDA); Amparai Dist.: Kokagala, Bernardi 15702 (PDA, US); Monaragala Dist.: Pitakumbura, Sohmer et al. 8306 (GH, MO, PDA, US).

Apparently related to D. spicata, but shallowly cordate leaves with longer petioles, relatively obscure reticulation, and flowers with dissimilar cycles of tepals distinguish it from D. spicata.

Fig. 34. Dioscorea trimenii

A. Staminate plant (Bernardi 15702, US).

B. Pistillate plant (Thwaites C.P. 3119, PDA).



PLANTS of CEYLON

DIOSCOREA THIBETICA Deane & Backell
(Dioscoreaceae.)

Locality Monte Kokogala ad orientem
Ceylonensis

Occurrence Frequens in nemore admontato

Date 11. XI. 1925 Alt. 250-300 m
Coll. L. Bernierii No. 15707

Remarks Spiculum et septena foliis ovatis
tenuibus equalibus teracibus viridis-fuscis; fo-
lia angustata. Spicis gracilibus & productis floris
in alabastris atro-fuscis.

Ceylon Herbarium

UNITED STATES
28087-11
NATIONAL HERBARIUM

PROPERTY OF
THE NATIONAL HERBARIUM
DEPARTMENT OF AGRICULTURE
PERADENYA - SRI LANKA



Peradenya Herbarium, Ceylon.

Name: *Dioecra Trimenii* Ram+Burkitt

Native Name:

Locality: *Ambagamuwa* Altitude:

Habit: *Common, 1500, etc.*

Collector: *Stk. Swaine* No. *82317* Date: *21. 1954*

Dioecra spicata, Pollett.
var. *β.* *Emm*

20. *Dioscorea spicata* Roth, Nov. pl. sp. 371. 1821; Kunth, Enum. pl. 5: 399. 1850; Hooker f., Fl. Brit. India 6: 291. 1892, in Trimen, Handb. Fl. Ceylon 4: 277. 1898; Knuth in Engler, Pflanzendr. 87 (IV. 43): 279. 1924; Prain & Burkill, Ann. Roy. Bot. Gard. Calcutta 14: 238, pl. 102. 1939. Type: India, s. loc., Heyne s.n.(n.v.). Fig. 35A, B.

Dioscorea spicata Roth var. *parvifolia* Prain & Burkill, J. & Proc. Asiat. Soc. Bengal 10: 29. 1914. Type: Sri Lanka, Galle Dist.: s. loc., Oct. 1861, Thwaites C. P. 2871, in part (lectotype chosen here, K; isolectotypes, BM, NY, PDA-2 sheets).

Dioscorea spicata Roth var. *anamallayana* Prain & Burkill, Ibid. 10: 29. 1914. Type: Sri Lanka, Kandy Dist.: Ambagamuwa, Dec. 1852, Thwaites C. P. 2871, in part (lectotype chosen here, PDA; isolectotype, K, n.v.).

Tubers up to 1 m long and 7 cm diam, the surface pale brown. Stem up to 20 cm long, slender, dull green with purplish to brownish mottlings, sparingly prickly at base. Bulbils not seen. Leaves alternate, occasionally opposite, variable within a individual; blade ovate or obovate or elliptic or lanceolate, basally acute or rounded or shallowly cordate, apically acuminate or cuspidate, 5-22 x 2-9 cm, chartaceous, glabrous; primary veins acrodromous to subcampylodromous, 3-5(7), \pm distinctly reaching apex, prominent; secondary veins oblique, often with elbows,

only slightly more conspicuous than lesser order veins; reticulation distinct above, strongly prominent and elevated below, with fine quadrangular to hexagonal areoles; margin almost indistinct; petiole 0.8-3.5 (5) cm long, often geniculate; stipules absent. Staminate inflorescence axillary, solitary, rarely more than one, spicate (rarely with a few alternate, lateral branches), the axis usually ascending, 5-23 cm long, slender, angled, glabrous, up to 85-flowered. Flowers lax, solitary or in 2 (3 or 4)-flowered cymes, sessile or rarely very shortly pedicelled, 1.3-2 x 1.4-2 mm; bract and bracteole widely ovate, long-acuminate or cuspidate, 0.5-1.2 x 0.5-1 mm (latter slightly smaller); outer and inner tepals similar, ovate to widely ovate, 1.1-1.6 x 0.7-1.5 mm, membranous or slightly fleshy; stamens free, the filament 0.4-0.6 mm long, narrowly oblong, the anther 0.3-0.5 mm long, the connective narrow; pistillode humpy or conical, 0.2-0.4 mm long, obscurely 3-lobed. Pistillate inflorescence axillary, solitary, spicate, 7-30 cm long, 5-26-flowered. Flowers lax, almost sessile at anthesis; bract and bracteole as in staminate flower, the bract 0.8-1.5 x 0.8 mm, the bracteole 0.7-0.9 x 0.5-0.6 mm; tepals as in staminate flower, 1-1.3 x 0.6-1 mm, staminodes 6, ca. 0.3 mm long; ovary 1.5-7.5 x 1-2.8 mm, with a distinct neck; styles coonate, 0.7-1.1 mm long; stigmas lobed into two upper, lateral, recurved lobes and a lower, median, short lobe. Capsules up to 8 per spike, \pm truncate basally and apically, nearly twice as broad

as long, 1.8-3.2 x 3.3-6 cm; stipe 2-8 mm long; wing rounded. Seed 15-30 mm diam. (5-7 mm exclusive of wing); wing 5-15 mm broad at broadest.

Distribution. S. India and Sri Lanka; moist lowlands and up to altitudes of ca. 1250 m.

Representative specimens. INDIA. Kerala State, Trivandrum Dist.: Santhanpara, Meebold 13256 (K); Tamil Nadu State, Coimbatore Dist.: Anamallai, Wight 2825 (GH); Tirunelveli Dist.: between Natenkal to Sengalteri, Hooper & Ramaswamy 38644 (K); Madura Dist.: Palni Hills, Beddome 7740 (PM).

SRI LANKA. Kandy Dist.: Wattegodde, Thwaites C. P. 2871, in part (PDA); Ratnapura Dist.: Kurulugala, Bulutota Pass, Huber 568 (PDA, US); Gilimale Forest Reserve, Meijer 933 (PDA, US); Galle Dist.: Neluwa, Balakrishnan 223 (PDA, US); Galle, Kundu & Balakrishnan 532 (PDA, US); Kegalle Dist.: Dikhena, Wass 1670 (PDA, US); Kitulgala, Kostermans 28314 (K, PDA).

Common names and uses. Sri Lanka: Gon-ala. Tubers edible.

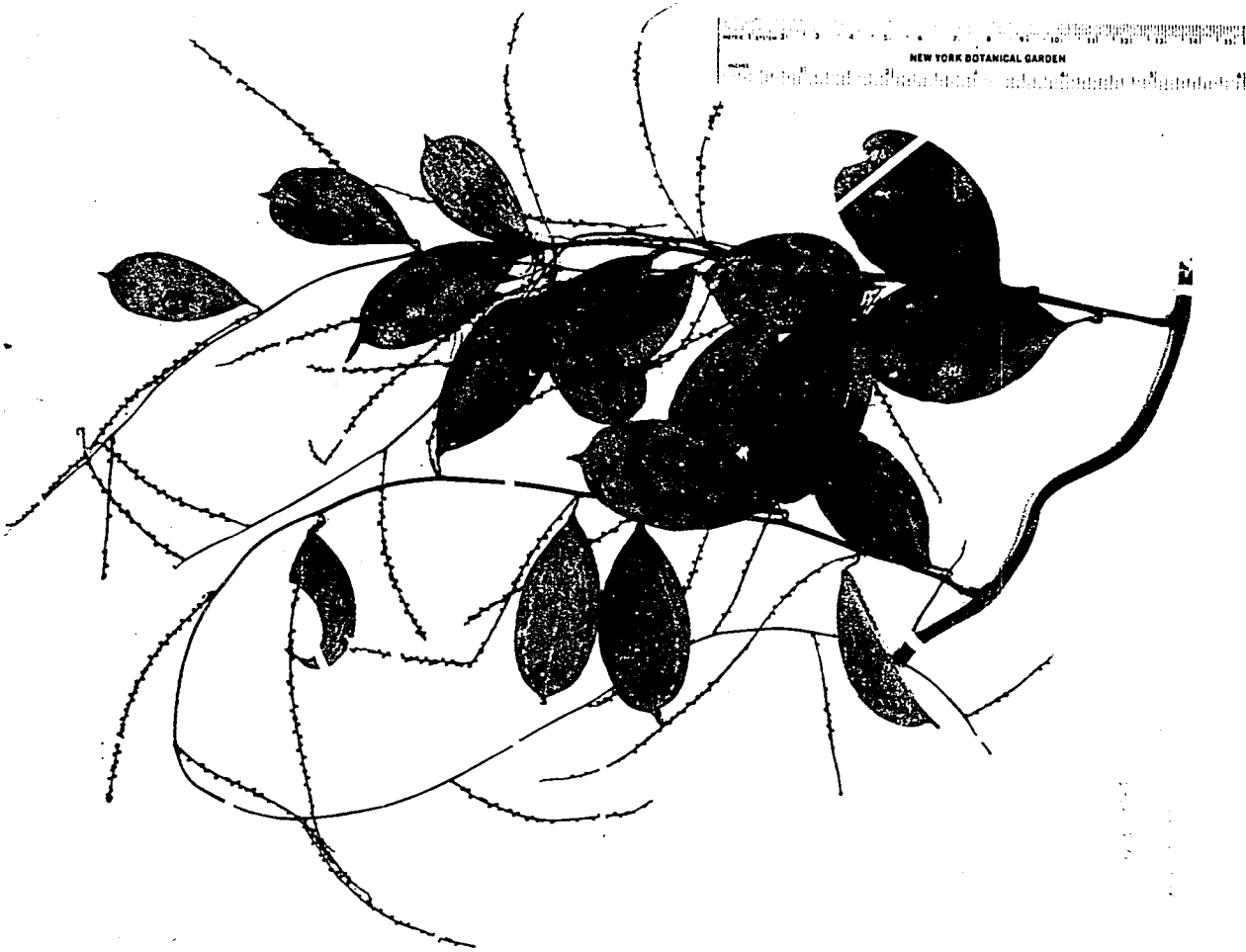
Prain & Burkill (1914) distinguished 2 varieties based on differences in leaf-size. However, it is observed that there is a continuous range of leaf-lengths from 4.8 to 21 cm and furthermore, in the specimens with larger leaves, inflorescence leaves tend to be small. Leaf-size also vary greatly within a individual. Therefore any subdivision of the species on such a variable character is unwarranted.

Fig. 35. Dioscorea spicata

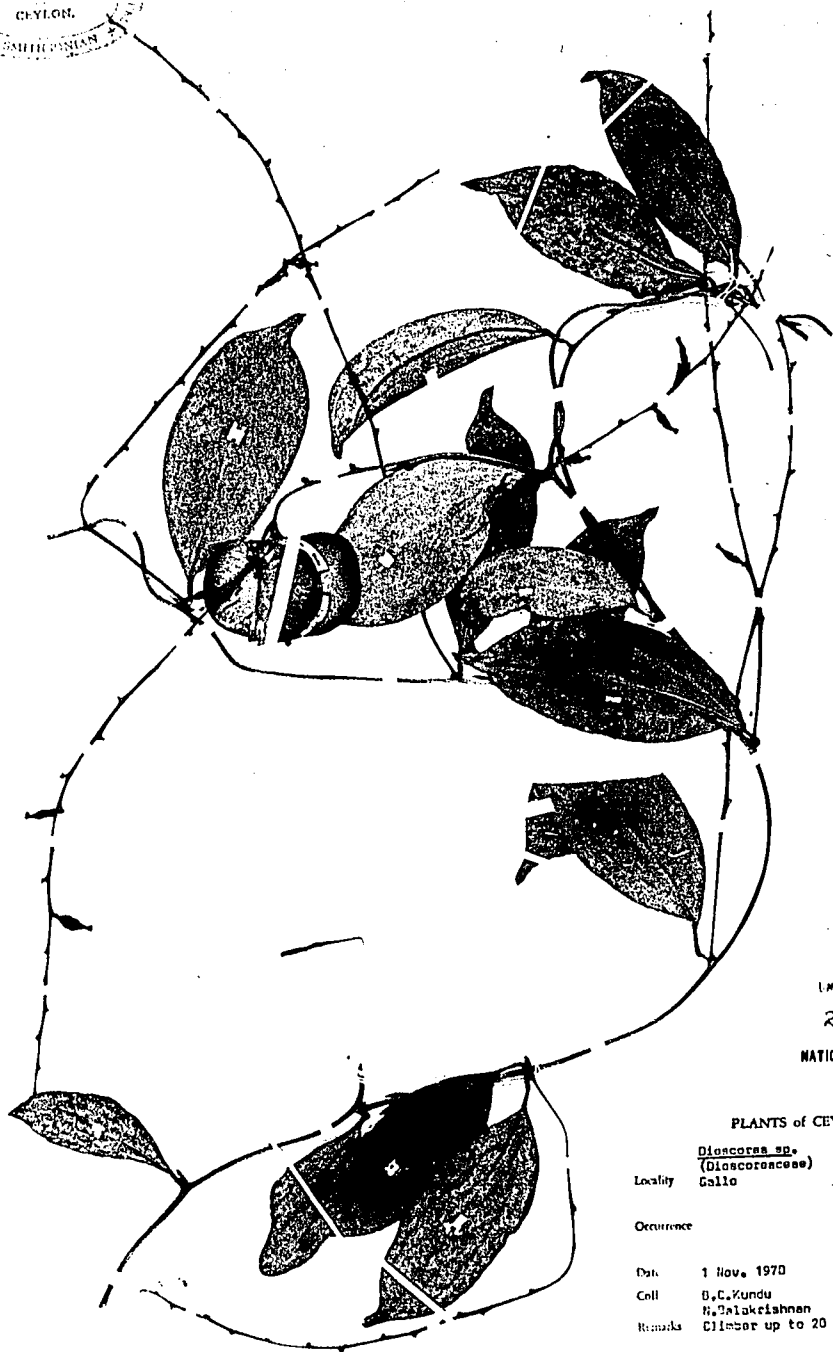
A. Staminate plant (Thwaites C.P. 2871, BM).

B. Pistillate plant (Kundu & Balakrishnan 532, US).

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CEYLON
SMITHSONIAN



537

NEW YORK BOTANICAL GARDEN
 ARTHUR S. GENT
 1970

UNITED STATES
 2609093
 NATIONAL HERBARIUM

PLANTS of CEYLON

Dioscorea sp.
 (Dioscoreaceae)
 Gallo

Locality

Occurrence

Date: 1 Nov. 1970 Alt: m
 Coll: D.C. Zunder No. 532
 H. Palakrishnan
 Remarks: Climber up to 20 m. Fruit green.

21. *Dioscorea koyamae* Jayasuriya, sp. nov. Type: Sri Lanka, Ratnapura Dist.: Karawita Kanda, 30 Sept. 1973, Waas 25 (holotype, PDA; isotype, US). Fig. 36.

Tubers unknown. Stem terete, glabrous, rough, sparingly armed with stout, blunt prickles. Bulbils not seen. Leaves alternate; blade lanceolate to ovate or elliptic, basally acute to obtuse or rounded, apically acuminate, 7-16 x 2.5-8 cm, glabrous, coriaceous, drying green to brownish above and green to glaucous below; primary veins 3, acrodromous, prominent, stout, ridged below, often with one (two in broader leaves) additional submarginal pair becoming gently scalloped and obscure toward apex, the innermost pair of veins for the most part located closer to margin than to midrib, sometimes becoming submarginal especially in smaller leaves; secondary veins straight or sometimes bent or branched, slightly distinct above, distinct from lesser order veins below; reticulation mostly obscure on both surfaces; margin ca. 0.2 mm wide, very prominent, firm, slightly undulated and inrolled, yellowish; petiole less than 1/4 the length of blade, 1-3.5 cm long, stout, geniculate, deeply channelled above with two edges narrowly winged or thickened; stipules absent. Staminate inflorescence spicate, fascicled up to 10 in axils or arranged on a up to 1 cm-long rachis, the axis 2-8.5 cm long, up to 50-flowered, angled, glabrous. Flowers lax, 1.2-1.5 x 1.2-1.5 mm, shortly pedicelled; pedicel 0.2-0.5 mm

long, thick; bract and bracteole widely ovate, acute, membranous, blotched with red, the bract 0.6-0.8 x 0.6-0.8 mm, the bracteole 0.5-0.7 x 0.4-0.5 mm; tepals similar in size, 1-1.2 x 0.6-1 mm, erect, leathery, blotched with red, the outer ones ovate to widely ovate, acute, the inner ones ovate, apically acute to obtuse; stamens free, the filaments columnar, nearly thrice the length of anther, 0.5-0.6 mm long, often blotched with red, the anther ca. 0.2 mm long, the connective narrow; pistillode 0.5-0.8 mm long, fleshy, conical, 3-lobed. Pistillate inflorescence axillary, solitary, spicate (rarely fascicled on a short rachis), the axis 4-20 cm long, erect, angled, glabrous, up to 12-flowered. Flowers lax, nearly sessile at anthesis; bract and bracteole as in staminate flower, but larger and somewhat fleshy, the bract ca. 1.4 x 1.3 mm, the bracteole 1-1.2 x 0.8-1 mm; tepals as in staminate flower, but somewhat fleshy, 1.1-1.4 x 1-1.2 mm, the inner ones slightly narrower than outer tepals; ovary 3.5-5 x 1.5 mm, glabrous, with a short neck; staminodes 0.2-0.3 mm long; styles connate, .8-1 mm long; stigmas free, each lobed into 3 short arms. Capsules up to 12 per spike, 3-3.2 x 4-4.2 cm; wing slightly rounded to straight on sides. Seed not seen.

A latin diagnosis is deliberately omitted, so that distribution of copies of this dissertation cannot be considered to constitute publication of the name.

Distribution. Sri Lanka; lowland rain forests of southwestern region.

Specimens examined. SRI LANKA. Ratnapura Dist.: Kukulawa Vihara kanda, Waas 271 (PDA, US); Siharaja, Yakinadola, Waas 2051 (PDA, NY, US); Palabeddala, Sumithraarachchi et al 1024 (PDA, US); between Opanaika and Wewelwatte, Nooteboom 3291 (PDA, US); Kukul korale, Thwaites C.P. 3022 (BM, K).

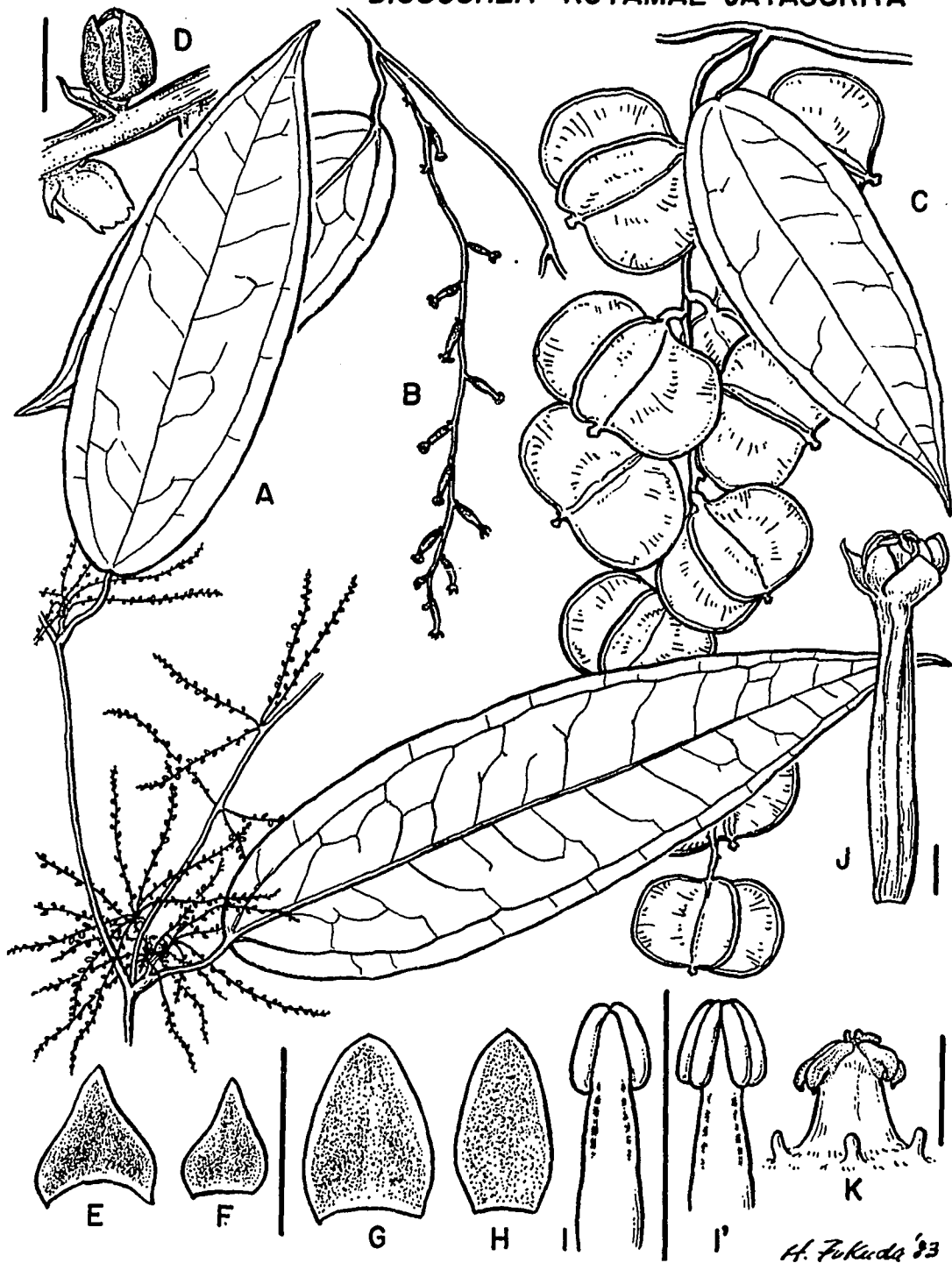
Allied to D. spicata, but readily recognized by its coriaceous leaves and absence of close, well-developed areolation on both surfaces of the leaves.

Fig. 36. Dioscorea koyamae

- A. Staminate plant with upper leaf and lower leaf showing upper and lower surfaces respectively (x 2/3, from Waas 25, US).
- B. Pistillate plant showing a spike (x 2/3, from Sumithra-arachchi et al. 1024, PDA).
- C. Pistillate plant with capsules (x 2/3, from Waas 271, US).
- D. Side view of staminate flower.
- E. Outer surface of bract.
- F. Outer surface of bracteole.
- G. Outer surface of outer tepal.
- H. Outer surface of inner tepal.
- I, I'. Outer and inner view respectively of stamen.
- J. Pistillate flower
- K. Upper part of pistil showing connate styles, stigmas, and staminodes.

(scales = 1 mm)

DIOSCOREA KOYAMAE JAYASURIYA



SYNOPSIS OF MAJOR CLASSIFICATIONS OF DIOSCOREA
IN THE INDIAN SUBCONTINENT

Knuth (1924)	Prain & Burkill (1936, 1939)	Proposed scheme
Subg. Eudioscorea		
Sect. Macropoda	Sect. Stenophora	Sect. Stenophora
D. deltoidea	D. deltoidea	D. deltoidea
D. prazeri	D. prazeri	D. prazeri
D. sikkimensis		
D. clarkei		
Sect. Conbiliun	Sect. Conbiliun	Sect. Dioscorea
D. esculenta	D. esculenta	D. sativa
var. spinosa	var. spinosa	
fulvido-tomentosa		
fasciculata	fasciculata	
Subg. Helmia		
Sect. Opsophyton	Sect. Opsophyton	Sect. Opsophyton
Subsect. Euopsophyton		
D. bulbifera	D. bulbifera	D. bulbifera
var. vera	var. vera	
simbha	simbha	
kacheo	kacheo	
suavior	suavior	
bimanica	bimanica	
sativa	sativa	
elongata	elongata	
deltoidea	deltoidea	
	heterophylla	

Knuth (1924)	Prain & Burkill (1936, 1939)	Proposed scheme
Sect. <i>Triumphorstemon</i>	Sect. <i>Lasiophyton</i>	Sect. <i>Triumphorstemon</i>
<i>D. tomentosa</i>	<i>D. tomentosa</i>	<i>D. tomentosa</i>
<i>D. pentaphylla</i>	<i>D. pentaphylla</i>	<i>D. pentaphylla</i>
var. <i>unifoliolata</i>		
<i>linnaei</i>	var. <i>linnaei</i>	
<i>thwaitesii</i>	<i>thwaitesii</i>	
<i>suli</i>	<i>suli</i>	
<i>jacquemontii</i>	<i>jacquemontii</i>	
<i>cardonii</i>	<i>cardonii</i>	
<i>simplicifolia</i>	<i>simplicifolia</i>	
<i>rheedei</i>	<i>rheedei</i>	
<i>malaica</i>	<i>malaica</i>	
<i>hortorum</i>	<i>hortorum</i>	
<i>communis</i>	<i>communis</i>	
<i>kussok</i>	<i>kussok</i>	
	<i>papuana</i>	
	<i>javanica</i>	
	<i>palmata</i>	
	<i>sacerdotalis</i>	
	<i>siamica</i>	
<i>D. arachnida</i>	<i>D. arachnida</i>	
<i>D. jacquemontii</i>		
<i>D. kalkapershadii</i>	<i>D. kalkapershadii</i>	
<i>D. kamoensis</i>	<i>D. kamoensis</i>	<i>D. kamoensis</i>
	var. <i>vera</i>	
	<i>straminea</i>	
	<i>fargesii</i>	
	<i>delavayi</i>	
	<i>henryi</i>	
	<i>engleriana</i>	
	<i>praecox</i>	
	<i>media</i>	
	<i>brevifolia</i>	

Knuth (1924)	Prairie & Burkill (1936, 1939)	Proposed scheme
D. engleriana		
D. fima		
D. rotundifoliolata		
D. mengtzeana		
D. fargesii		
D. subfusca		
D. delavay		
D. burkillii		
D. mairei		
D. dissecta		
D. melanophyma	D. melanophyma	D. melanophyma
Sect. Lasiophyton		Sect. Lasiophyton
D. triphylla		
var. daemona		
reticulata		
mollissima		
	D. hispida	D. hispida
	var. daemona	
	reticulata	
	mollissima	
	scaphoides	
	neo-scaphoides	
Subg. Eudioscorea		
Sect. Enartiophyllum	Sect. Enartiophyllum	Sect. Enartiophyllum
D. hamiltonii	D. hamiltonii	D. hamiltonii
D. lepcharum	D. lepcharum	
vera	vera	
bhamoica	bhamoica	
D. alata	D. alata	D. alata
D. wattii	D. wattii	D. wattii

Knuth (1924)	Prain & Burkill (1936, 1939)	Proposed scheme
<i>D. oppositifolia</i>	<i>D. oppositifolia</i>	<i>D. oppositifolia</i>
var. <i>thwaitesii</i>	var. <i>thwaitesii</i>	
<i>linnaei</i>	<i>linnaei</i>	
<i>dukhunensis</i>	<i>dukhunensis</i>	var. <i>dukhunensis</i>
	<i>meeboldtii</i>	
		<i>oppositifolia</i>
<i>D. trinervia</i>	<i>D. trinervia</i>	
<i>D. intermedia</i>	<i>D. intermedia</i>	
<i>D. obtuneata</i>	<i>D. obtuneata</i>	
<i>D. pubera</i>	<i>D. pubera</i>	<i>D. pubera</i>
<i>D. anguina</i>		
<i>D. belophylla</i>	<i>D. belophylla</i>	<i>D. belophylla</i>
<i>D. glabra</i>	<i>D. glabra</i>	<i>D. glabra</i>
var. <i>grisea</i>	var. <i>grisea</i>	
<i>salicifolia</i>	<i>salicifolia</i>	
<i>hastifolia</i>		
<i>vera</i>	<i>vera</i>	
<i>longifolia</i>	<i>longifolia</i>	
<i>tenuifolia</i>	<i>tenuifolia</i>	
	<i>pahagensis</i>	
	<i>tincta</i>	
<i>D. wallichii</i>	<i>D. wallichii</i>	<i>D. wallichii</i>
var. <i>vera</i>	var. <i>vera</i>	
<i>christiei</i>	<i>christiei</i>	
<i>D. wightii</i>	<i>D. wightii</i>	<i>D. wightii</i>
<i>D. trimenii</i>	<i>D. trimenii</i>	<i>D. trimenii</i>
<i>D. spicata</i>	<i>D. spicata</i>	<i>D. spicata</i>
var. <i>parvifolia</i>	var. <i>parvifolia</i>	
<i>anamallayana</i>	<i>anamallayana</i>	
		<i>D. koyamae</i>

APPENDICES

Appendix 1. Taxa of Dioscoreaceae mentioned in the text (except Systematic Treatment)

<u>Averta</u> Perrier de la Bathie	<u>D. elephantipes</u> Engler
<u>Asterotricha</u> Uline (sect.)	<u>D. elmeri</u> Prain & Burkill
<u>Brachyandra</u> Uline (sect.)	<u>D. flabellifolia</u> Prain & Burkill
<u>Cardiocaspa</u> Uline (sect.)	<u>D. floribunda</u> Mart. & Gal.
<u>Dioscorea anacachensis</u> Knuth	<u>D. heteropoda</u> Baker
<u>D. anomala</u> (Kunth) Griseb.	<u>D. hexagona</u> Baker
<u>D. birmanica</u> Prain & Burkill	<u>D. humilis</u> Bert.
<u>D. Buchananii</u> Benth.	<u>D. inopinata</u> Prain & Burkill
<u>D. bryoniaefolia</u> Poepp.	<u>D. insignis</u> Morton & Schubert
<u>D. caucasica</u> Lipsky	<u>D. japonica</u> Thunb.
<u>D. cayenensis</u> Lam.	<u>D. laurifolia</u> Wall.
<u>D. cirrhosa</u> Lour.	<u>D. macroura</u> Harms
<u>D. cochleari-apiculata</u> de Willd.	<u>D. mangenotiana</u> Miede
<u>D. colocasiaefolia</u> Pax	<u>D. membranacea</u> Pierre
<u>D. cotinifolia</u> Kunth	<u>D. minima</u> Robins. & Seaton
<u>D. cretacea</u> Lesq.	<u>D. multiflora</u> Mart.
<u>D. cumingii</u> Prain & Burkill	<u>D. multinervis</u> Benth.
<u>D. cyphocarpha</u> Robinson	<u>D. mundtii</u> Baker
<u>D. foxworthyi</u> Prain & Burkill	<u>D. nipponica</u> Makino
<u>D. diversifolia</u> Kunth	<u>D. opposita</u> Thunb.

- D. dregeana (Kunth) T. Dur. & Schinz
D. dumetorum (Kunth) Pax
D. piscatorum Prain & Burkill
D. praehensilis Benth.
D. preussii Pax
D. pyrenaica Bub. & Bord.
D. quartiniana A. Rich.
D. rotundata Poir.
D. rupicola Kunth
D. sansibarensis Pax
D. scortechinii Prain & Burkill
D. smilacifolia de Willd. & Dur.
D. spiculiflora Hemsl.
D. sylvatica Ecklon.
D. stenophylla Uline
D. sumatrana Prain & Burkill
D. tacanensis Lundell
D. tamarisciflora Prain & Burkill
D. tenuipes Franch. & Sav.
D. tokoro Makino
D. trifida L.
D. undatiloba Baker
D. villosa L.
- D. orbiculata Hook. f.
D. perdicum Taubert
D. pilosiuscula Bert.
Dioscorides lyelli (Wat.) Fritel
Dioscorites resurgens Sapota
Macrocarpaea Uline (sect.)
Macrourae Knuth (subsect.)
Madagascarienses Knuth (sect.)
Paramecocarpa Prain & Burkill (sect.)
Pygmaephyton Uline (sect.)
Rajania L.
Rhacodophyllum Uline (sect.)
Shannicorea Prain & Burkill (sect.)
Stenocorea Prain & Burkill (sect.)
Stenomeris Planch.
Syntepaleia Uline (sect.)
Tamus L.
T. communis L.
Testudinaria Salisb.
Trichopus Gaertn.

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