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The Genus *Dioscorea* L. in South Africa

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SUMMARY

The distribution and habitat of the 17 southern African *Dioscorea* species are presented briefly, while the seven species occurring in the Transvaal are dealt with in more detail. The persistence of aerial shoots, the occurrence of a solitary perennial tuber, and of bi- or triennial tubers are discussed.

RÉSUMÉ

La répartition géographique et l'habitat des 17 espèces sud-africaines de *Dioscorea* sont présentés brièvement, tandis que les 7 espèces du Transvaal sont traitées d'une façon plus détaillée.

La persistance des pousses aériennes l'existence d'un tubercule solitaire vivace ou de plusieurs tubercules bis- ou triannuels sont discutées.

Distribution and habitat

The *Dioscoreaceae* presumably originated in tropical Indo-China and according to Burkitt (1960) they were already "well diversified in the part of the southern World where the Atlantic rifted in the end of the Cretaceous".

The genus *Dioscorea* is mainly tropical, with Africa very rich in species. In southern Africa alone 17 species are indigenous. In South West Africa *D. asteriscus* and *D. hirtiflora* are confined to the Okavango River area, *D. asteriscus* in riparian forests and islands in the Okavango River and *D. hirtiflora* on sandy soil in dense forests including those of the islands.

Of the eight *Dioscorea* species in the Cape Province west of East London five species are endemic. Of these species *D. mundtii* is found in coastal bush or along forest margins behind the dunes, *D. burchellii* and *D. stipulosa* on south facing slopes in Macchia communities, and *D. elephantipes* and *D. hemicyrpta* mainly on drier, rocky slopes in Karroid communities with an eastern aspect (Archibald, 1967).

Dioscorea brownii, *D. crinita* and *D. diversifolia* occur in Natal and in the eastern Cape Province. *Dioscorea brownii* is found mainly in the forest margins of Coastal Tropical Forests, while *D. crinita* and *D. diversifolia* usually occur in coastal bush or forest margins of the Coastal Forest and Thornveld (Acocks, 1953).

Dioscorea cotinifolia, *D. dregeana*, *D. quartiniana*, *D. retusa*, *D. rupicola*, *D. sylvatica* and *D. undatiloba* are the only *Dioscorea* species occurring in the Transvaal. In addition to the Transvaal, *D. undatiloba* occurs in Natal, while *D. quartiniana* is found in northern Natal and northern South-West Africa. The other five Transvaal species are also found in Swaziland, Natal and the eastern Cape Province, while *D. sylvatica* and *D. cotinifolia* occur in the Harrismith and Bethlehem districts of the Orange Free State as well.

A distribution map of the genus *Dioscorea* in the Transvaal (Fig. 1) was compiled from records in the National Herbarium in Pretoria, the Moss Herbarium at the University of the Witwatersrand, Johannesburg, the Herbarium of the University of Pretoria and from personal records.

Most of the Transvaal *Dioscorea* species occur in the east and north-eastern parts at an altitude between 900 and 1800 m. The average annual rainfall of these regions varies from 706.5 mm to 916.6 mm (Weather Bureau, 1960). Minimum tem-

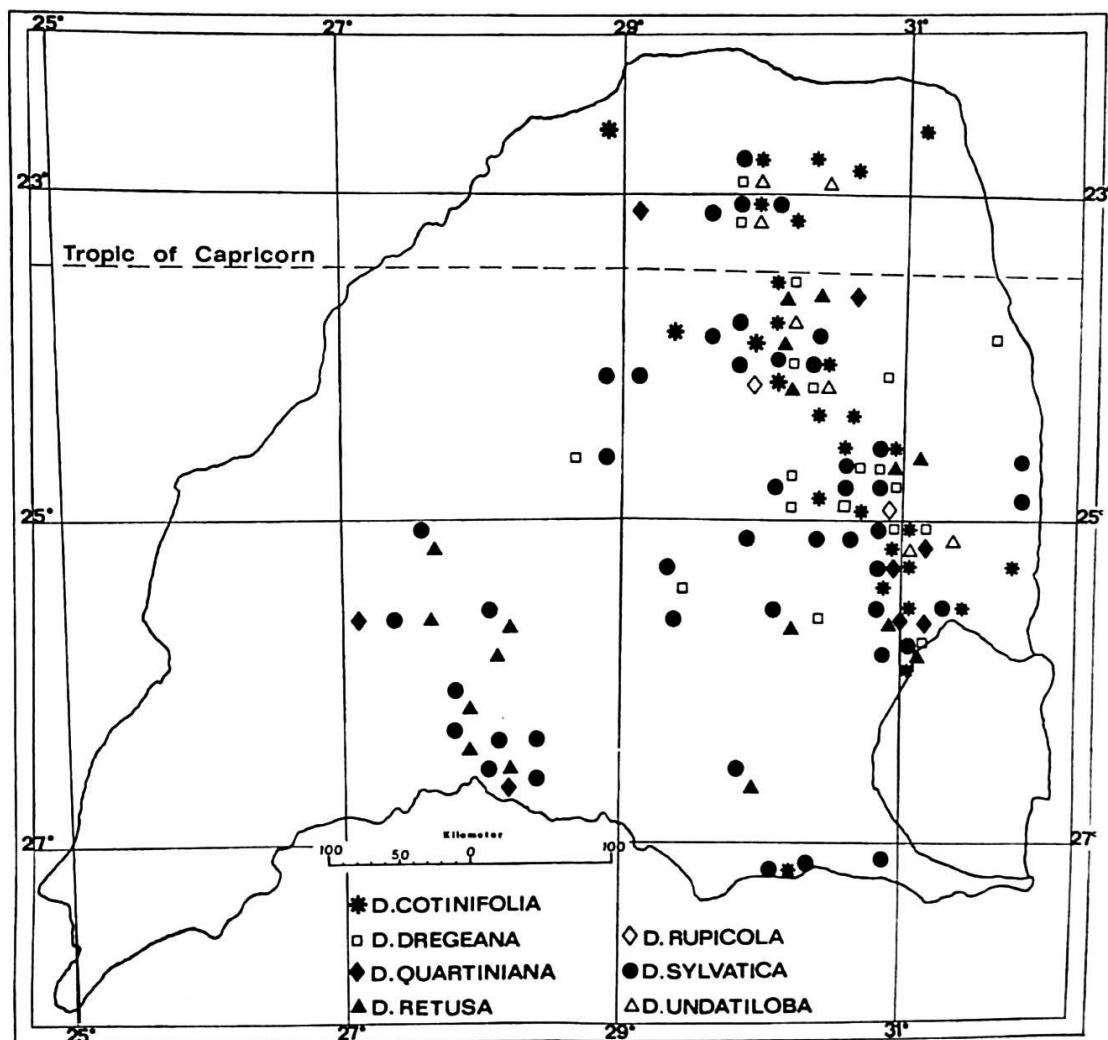


Fig. 1. — The distribution of the genus *Dioscorea* L. in the Transvaal.

peratures below 0°C and maximum temperatures above 35°C occur in these parts on an average of five to ten days per year (Weather Bureau, 1965).

The plants usually occur in mountainous areas in kloofs where north, north-east or north-west facing slopes with shallow, stony to talus soils rich in humus are preferred. Where plants occur along streams and water courses, the soil is as well-drained as in the other habitats. Although all species are shade tolerant, plants are more likely to be found in semi-shade habitats, like forest margins, than in dense shade.

Dioscorea rupicola in particular, but also *D. undatiloba*, *D. dregeana*, *D. retusa* and *D. cotinifolia* are associated with the Inland Tropical Forests (Acocks, 1953). *Dioscorea sylvatica* is found mainly in densely wooded kloofs, or steep, rocky wooded slopes in the North-Eastern Mountain Sourveld and Sourish Mixed Bushveld (Acocks, 1953). It also occurs in deciduous forests. Where *D. sylvatica* and *D. retusa* occur in Bankenveld, they are found in the wooded areas of rocky outcrops.

Dioscorea quartiniana in particular, but also *D. cotinifolia* and *D. retusa* are found in dense bushveld like that of the Lowveld (Acocks, 1953), in kloofs, and along water courses.

Dioscorea dregeana which is a vigorous climber seems to prefer talus-like soils where it grows between boulders. It is also found in the Sourish Mixed Bushveld (Acocks, 1953).

In general the plants prefer a warm, moist and sheltered habitat.

Preliminary morphological taxonomical information

The habit of the South African *Dioscorea* species with their small, green to yellow flowers, shows some interesting features.

The twining stems of the species studied are syntrorse, with the exception of *D. cotinifolia*, where the stem is dextrorse. It was believed that the aerial stem is formed annually from the underground tuber crown and dies back before or during the winter. Archibald (1967), however, reported the persistence of aerial shoots under natural conditions in certain species in the Cape Province. During recent collecting trips in the Transvaal no persistence of aerial shoots was observed. Among the plants which were collected and cultivated in Pretoria, however, a few young plants of *D. cotinifolia*, *D. dregeana* and *D. sylvatica* showed persistence of a small part of the stem. It is possible that the persistence of the stem in the Cape species is associated with the more temperate climatic conditions. According to Archibald (1967), two functional stems are very rarely found on the same tuber in *D. cotinifolia* and *D. sylvatica*. During this study one mature tuber of *D. dregeana* and one of *D. cotinifolia* each formed two stems in cultivation in the Transvaal. Four *D. sylvatica* tubers were collected with two or more crowns, each tuber producing two to four functional shoots. These shoots, however, did not climb as high into neighbouring vegetation as did the single stems. Functional shoots of this kind usually branch 150 to 200 mm above the ground surface, intertwine with one another and with the previous season's shoots and can also extend into short, neighbouring shrubs, over grass and onto surrounding rocks. The habit of these plants is similar

to that of *D. elephantipes*. Only one *D. rupicola* tuber was found with two crowns, each crown with one functional stem.

The scanty knowledge of the tubers of many *Dioscorea* species led to the misconception that solitary perennial tubers are exceptional. Of the thirteen species investigated during this study, nine belonging to the sections *Rhacodophyllum*, *Testudinaria* and *Perennia* (Figs. 2 & 4¹) do have solitary perennial tubers. The tubers of the other four species cannot be called annual either, as will be discussed under sections *Cotinifoliae* and *Lasiophyton*.

The leaves of the Transvaal *Dioscorea* species are exstipulate with the exception of *D. undatiloba* which has simple, inconspicuous stipules. These stipules occur inconsistently, as in the case of the tropical *D. bulbifera* (Burkill, 1960). The variation in leaf form and size, even on a single plant, is remarkable.

The South West African species, *D. hirtiflora*, which was described by Merxmüller and Rössler (1969), is unique in that its seed is entirely surrounded by the wing

SPECIES	SECTION	FLORAL FORMULA	SEED	FIRST LEAF	MATURE LEAF	MATURE TUBER
<i>D. asteriscus</i> Burk.	Opsophyton	$\text{♂} \oplus [P(3+3)A3+3] G\bullet$ $\text{♀} \oplus [P(3+3)A6-6] G(3)$	similar to <i>D. bulbifera</i>			
<i>D. hirtiflora</i> Benth.	Asterotricha	$\text{♂} \oplus [P(3+3)A6-3] G\bullet$ $\text{♀} \oplus [P(3+3)A6-6] G(3)$				
<i>D. rupicola</i> Knuth	Rhacodophyllum	$\text{♂} \oplus [P(3+3)A6-3] G\bullet$ $\text{♀} \oplus [P(3+3)A0-3] G(3)$ disc!				
<i>D. undatiloba</i> Bak.		$\text{♂} \oplus [P(3+3)A3+3] G\bullet$ $\text{♀} \oplus [P(3+3)A6-6] G(3)$		÷		
<i>D. diversifolia</i> Griseb.		$\text{♂} \oplus [P(3+3)A3+3] G\bullet$ $\text{♀} \oplus [P(3+3)A7-6] G(3)$		÷		

Fig. 2. — A schematic representation of some outstanding characteristics of a few South West- and South African *Dioscorea* species.

♂: staminate flower; ♀: pistillate flower; ⊕: actinomorphic; P(3+3) or P(3+3): perigonium --- 2 whorls fused or only basally fused; A 3+3: 2 whorls of stamens; A 6-3: one whorl of stamens reduced to staminodes; A 6-6: 6 staminodes; A 3-3: 3 staminodes only; [P..A..]: stamens inserted on the perigonium, or [P..A..]: partially or probably inserted; G(3): inferior ovary, 3 fused carpels; G•, G* or G*: sterile pistil relatively large, small or absent; ÷: no information available yet.

¹ Data included in Fig. 2 on *D. asteriscus* and *D. hirtiflora* were obtained from Merxmüller & Rössler (1969) and Burkill (1939); data in Fig. 4 on *D. elephantipes* and *D. hemicyrtia* from Burkill (1952) and Archibald (1967) and on the section *Perennia* from Archibald (1967). All other data were based on herbarium material and on material collected in the field.

(Fig. 2). According to Burkill (1960) many of the tropical forest species have this primitive seed form.

The South African species

Section Rhacodophyllum

Knuth (1924) placed *D. rupicola*, *D. undatiloba* and *D. diversifolia* into the section *Rhacodophyllum*. A previous preliminary investigation into their taxonomy, however, indicated that they represent only one taxon (Codd, personal communication ¹). The staminate flower of *D. rupicola* is easily distinguished from staminate flowers of the other two species in that one of the two whorls of stamens is reduced to staminodes (Fig. 2). The pistillate flowers of *D. rupicola* are distinguishable by the presence of a disc and only one whorl of staminodes (Fig. 2). The seeds of *D. undatiloba* and *D. diversifolia* are very similar. They seem to be a transition stage in the evolutionary development from a primitive seed as in *D. hirtiflora* to a seed with equal wings at opposite sides like that of *D. rupicola* (Fig. 2). In *D. rupicola* very deeply lobed, simple leaves, characteristic of many *D. diversifolia* plants from Natal, are not found. *Dioscorea undatiloba*, believed to be virtually confined to the Transvaal, shows a variation in leaf form where distinctly seven-lobed leaves occur at the base of the stem. The number of species in this section in South Africa is still uncertain.

Section Cotinifoliae

Dioscorea cotinifolia is typified by its distally winged seeds (Fig. 3) amongst other features. The size of the mature leaf varies considerably, depending on the habitat. Leaf size of *D. cotinifolia*, however, never exceeds that of *D. rupicola*. The type of seed, the leaf size and the specialization of the tuber habit in *D. cotinifolia* (Fig. 5) could be indicative that this species is more advanced phylogenetically. Germination studies have shown that the hypocotyl gives rise to tubers directly, or indirectly by means of the elongation and branching of a juvenile crown. The juvenile crown and its branches, which Archibald (1967) has described as thick roots, proved to be intermediary organs i.e. anatomically neither typical roots nor typical shoots. The tubers of the mature plants collected and then cultivated for this study, as well as those grown from seedlings, have remained alive for three years and therefore cannot be regarded as annual.

Section Lasiophyton

Knuth (1924) places *D. dregeana* into the section *Lasiophyton* and Burkill & Perrier de la Bâthie (1950) and Burkill (1960) include *D. quartiniana*, *D. retusa* and *D. crinita* also in this section. Most herbarium specimens of *D. dregeana* are named by Burkill as being the variety *hutchinsonii* but this has never been validly published. The most noticeable differences between the flowers of *D. dregeana* and those of *D. quartiniana* and *D. retusa* are shown in the floral formulas in Fig. 3. Information

¹ Dr. L. E. D. Codd, Botanical Research Institute, Pretoria.

SPECIES	SECTION	FLORAL FORMULA	SEED	FIRST LEAF	MATURE LEAF	MATURE TUBER
<i>D. cotinifolia</i> Knuth	Cotinifoliae	$\delta\oplus[P(3+3)A3+3]G\bullet$ $Q\oplus[P(3+3)A6-6]G(3)$				
<i>D. dregeana</i> (Knuth) Dur. & Schinz.	Lasiophyton	$\delta\oplus[P(3+3)A3+3]G\bullet$ $Q\oplus[P(3+3)A6-6]G(3)$				
<i>D. quartiniana</i> A.Rich.		$\delta\oplus[P(3+3)A6-3]G\bullet$ $Q\oplus[P(3+3)A6-6]G(3)$				
<i>D. retusa</i> Mast.		ditto		probably also tripartite		

Fig. 3. — A schematic representation of some outstanding characteristics of a few South African *Dioscorea* species.

δ : staminate flower; Q : pistillate flowers; \oplus : actinomorphic; $P(3+3)$ or $P(3+3)$: perigonium---2 whorls fused or only basally fused; $A 3+3$: 2 whorls of stamens; $A 6-3$: one whorl of stamens reduced to staminodes; $A 6-6$: 6 staminodes; $A 3-3$: 3 staminodes only; $[P..A..]$: stamens inserted on the perigonium, of $[P..A..]$: partially or probably inserted; $G(3)$: inferior ovary, 3 fused carpels; $G\bullet$, $G\circ$ or $G*$: sterile pistil relatively large, small or absent; \div : no information available yet.

on *D. crinita*, which does not occur in the Transvaal, is still very sketchy. According to Baker (1896-1897) the main differences between *D. retusa* and *D. crinita* are found in the male inflorescence and flowers, namely in the length of the raceme, the length of the bract and the length and hairyness of the pedicel.

The seeds of *D. dregeana*, *D. quartiniana* and *D. retusa* are proximally winged (Fig. 3).

The compound leaves of *D. crinita* are very similar to the tri- or quinquepartite leaves of *D. retusa*. Germination studies of *D. dregeana* and *D. quartiniana* showed that the first leaf is tripartite. Tripartite leaves are also common on the young shoot of *D. quartiniana* and *D. retusa*, while the lateral leaflets of mature *D. dregeana* leaves are rarely distinctly two-lobed.

Morphologically the tubers of *D. dregeana*, *D. quartiniana* and *D. retusa* occur in groups, each tuber in the group developing successively and apparently independently of any other. The remains of one or more very old tubers, as well as ageing tubers which had already supplied most of their reserves to the growing shoot at the beginning of the new season, were found in many tuber groups. In addition, young developing tubers and/or mature tubers are present in the same group of tubers. From field observations and those made on cultivated plants, it is clear that the

SPECIES	SECTION	FLORAL FORMULA	SEED	FIRST LEAF	MATURE LEAF	MATURE TUBER
<i>D. sylvatica</i> Eckl.	Testudinaria	$\text{♂} \oplus [P(3+3)A3+3]G\bullet$				
<i>D. elephantipes</i> (L'Herit.) Engl.		$\text{♀} \oplus [P(3+3)A6-6]G\bullet$	ditto			
<i>D. hemi-crypta</i> Burk.		ditto		÷		
<i>D. mundtii</i> Bak.	Perennia	$\text{♂} \oplus [P(3+3)A3+3]G\bullet$ $\text{♀} \oplus [P(3+3)A6-6]G\bullet$				
<i>D. burchellii</i> Bak.		ditto		÷		
<i>D. stipulosa</i> Uline ex Knuth		♂ ditto G.		÷		

Fig. 4. — A schematic representation of some outstanding characteristics of a few South African *Dioscorea* species.

♂: staminate flower; ♀: pistillate flower; ⊕: actinomorphic; P(3+3) or P(3+3): perigonium --- 2 whorls fused or only basally fused; A 3+3: 2 whorls of stamens; A 6-3: one whorl of stamens reduced to staminodes; A 6-6: 6 staminodes; A 3-3: 3 staminodes only; [P..A..]: stamens inserted on the perigonium, or [P..A..]: partially or probably inserted; G(3): inferior ovary, 3 fused carpels; G•, G* or G*: sterile pistil relatively large, small or absent; ÷: no information available yet.

tubers are usually triennial or at least biennial. The group of tubers is therefore never annual. In *D. retusa* subterranean stems join two or more groups of tubers and up to four groups of tubers per plant were seen in the field. This habit of the tuber groups in *D. retusa* is also found in very young plants in the field and must be regarded as a diagnostic characteristic (Fig. 3).

Dioscorea brownii

Dioscorea brownii, occurring mainly in Natal, is not well known at all. Knuth (1924) placed it in the subsection *Isocantha* which has proximally winged seeds. He did not examine any tuber material. The lanceolate leaves seem to be characteristic of this species.

Section Testudinaria

Of the section *Testudinaria* only *D. sylvatica* occurs in the Transvaal, while *D. elephantipes* and *D. hemicyrpta* are endemic to the Cape Province west of East London. Burkhill who described this section (Burkhill, 1952), mentions that *D. hemicyrpta* is considered to be a subspecies of *D. elephantipes* by other workers. Archibald (1967), however, treated *D. hemicyrpta* as a separate species. There is still some doubt about the validity of the varieties which Burkhill recognized in *D. sylvatica* and which he based chiefly on the size, form and texture of the lamina and the size of the capsules. The subspecies *lydenburgensis* described by Blunden & al. (1971) also needs further careful investigation. The size and form of the leaf in *D. sylvatica* in the seedling differ from the size and form in the adult plant, but differences also occur within a single plant. Leaf morphology is affected by the habitat as are tuber form and the depth at which tubers are buried. *Dioscorea sylvatica* in the Transvaal shows no correlation between the occurrence of certain types of tubers, which vary from flat to conical (Fig. 4) and the presence of certain types of leaves. The morphology of the flowers and seeds of the three species in this section are very similar whereas their leaf form and tuber type easily distinguish them from one another (Fig. 4).

Section Perennia

It has been suggested that *D. mundtii*, *D. burchellii* and *D. stipulosa* be placed together in the section *Perennia* (Archibald, 1967). The section is characterized by proximally winged seeds. The flowers of these species show some similarities in general morphology while the leaves of the three species are readily distinguishable on the basis of form and size (Fig. 4).

Differences in adult tubers of the different species are noticeable in the type of crown, the form and number of tuber branches, the texture and colour of the outer skin and the inner flesh (Archibald, 1967).

CONCLUSION

The genus *Dioscorea* is widely distributed in southern Africa over a wide range of habitats which include dry Karroid communities and moist tropical forests.

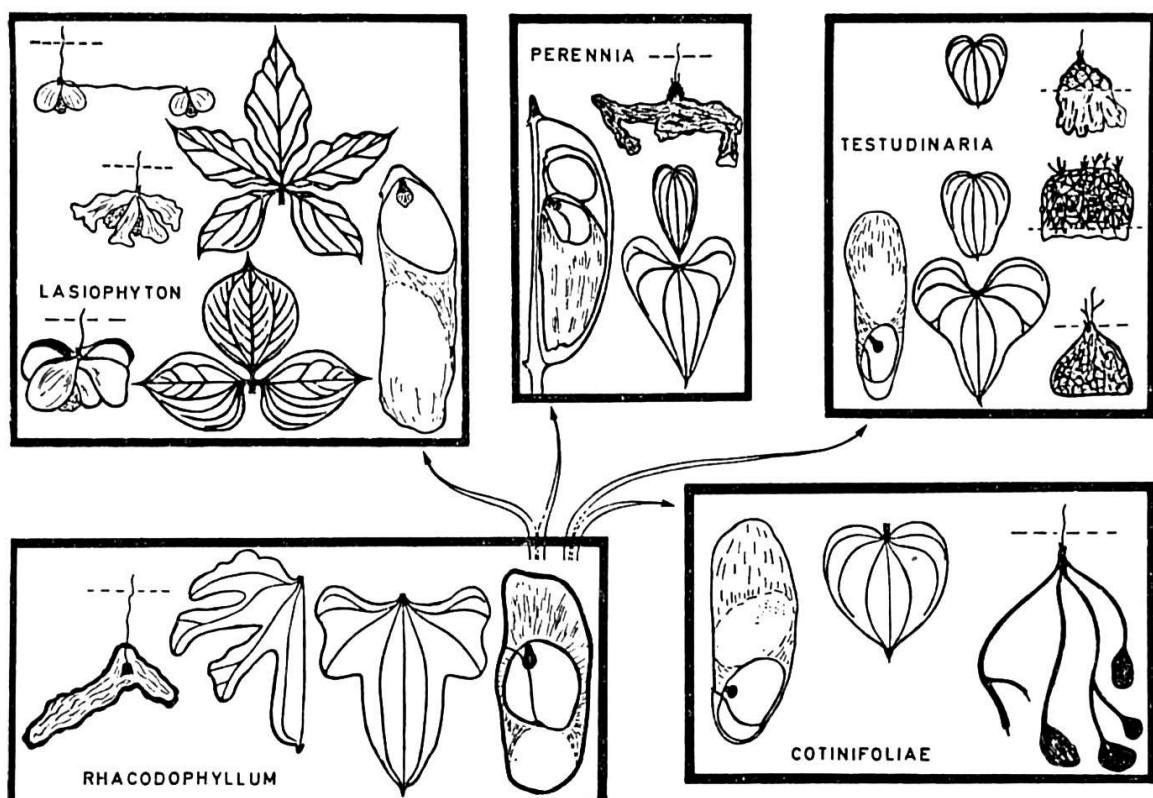


Fig. 5. — A schematic representation of five sections of the genus *Dioscorea* in South Africa and their possible phylogeny.

There is enough evidence that the genus *Dioscorea* in South Africa is represented by at least five distinct sections (Fig. 5), which include at least five endemic species, namely *D. elephantipes*, *D. hemicrypta*, *D. burchellii*, *D. stipulosa* and *D. mundtii*. The sections are easily identified by the seed wing, leaf form which may be simple, simple but lobed, or compound, and the type of tuber. The tuber is distinctly solitary and perennial in three sections and bi- or triennial in the other two (Fig. 5). All 17 *Dioscorea* species in southern Africa are not well defined and, for this reason, further detailed morphological taxonomical studies are necessary.

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