On the Origin, Development, and Morphological Nature of the aërial Tubers in Dioscorea sativa, Linn.

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With Plate XXVI.

THE species *Dioscorea sativa* was founded by Linnaeus in 1753[1], but, according to Bentham[2], nearly all modern authors have transposed the names of this and another Linnaean species, *D. bulbifera*; perhaps because both produce aërial tubers in the leaf-axils. Hooker[3] states that 'the species of *Dioscorea* are in a state of indescribable confusion.' Another source of difficulty in determining the species of *Dioscorea* is the use of the English name 'Yam,' because earlier writers applied it indiscriminately to any edible underground tuber, so that, at first, it included *Batatas* (*Ipomœa*) *edulis* (the sweet potato, one of the Convolvulaceae), *Manihot utilissima* (cassava, one of the Euphorbiaceae) and the aroid *Amorphophallus campanulatus*. Even the potato

[1] Linnaeus, Species Plantarum, vol. ii, p. 1033 (1753).

[2] Bentham, Flora Australiensis, vol. vi, p. 462 ('73). Flora Hongkongensis, p. 368 ('61).

[3] Hooker, Flora of British India, vol. vi, p. 288 ('94).

[Annals of Botany, Vol. XV. No. LIX. September, 1901.]

(Solanaceae) has been confused with them, as its name is a corruption of *Batatas*, and was at first applied to the sweet potato, which was introduced into Europe before the plant we now know as potato.

These difficulties render the history of the Dioscoreas very obscure. The origin of most of the cultivated forms is either unknown or doubtful. According to the writer of the article on *Dioscorea* in the Dictionary of the Economic Products of India ('90), p. 115 et seq., the existing evidence points to a possible independent origin of the cultivated species of *Dioscorea* in Asia, Africa, and America. The same author considers that the reason why these plants were cultivated for food later than other vegetables is because the wild forms produced edible tubers without cultivation.

All attempts to distinguish between the Linnaean species *D. sativa* and *D. bulbifera*, by referring to original authorities, in order to determine the species upon which the observations in this paper were made, have proved unsuccessful. The characters of the species in question agree with Kunth's detailed description of *Helmia bulbifera*[1] which, according to Hooker[2], is a synonym of *D. sativa*, Linn., and *D. bulbifera*, Br. Kunth himself, however, regards his *Helmia bulbifera* as identical with the *D. bulbifera* of Linnaeus and Wight. Bentham[3] regards *Helmia bulbifera*, Kunth, and *D. bulbifera*, Wight[4], non-Linn., as synonyms of *D. sativa*, Linn.

D. sativa, Linn., is a widely distributed plant. It grows wild throughout India, and is the species most generally cultivated, so that it is known as 'the common yam.' It is also known in Malabar, Java, the Philippines, Australia, Queensland, and in the West Indies.

References to the tubers in this species are made by the following authors:—

[1] Kunth, Enumeratio Plantarum, vol. v, p. 435 ('50). In the Index Kewensis this is said to be *Dioscorea sativa*.

[2] Hooker, Flora of British India, vol. vi, p. 295 ('94).

[3] Bentham, Flora Hongkongensis, p. 368 ('61).

[4] Wight, Icones, vol. iii, plate 878.

Hooker[1] says the underground tubers are 'large, and variable in form,' the stem 'bulbiferous.'

Bentham[2] says, 'stems from a tuberous rhizome, elongated and twining, often bearing green globular bulbs in the axils of the leaves.'

Again he says[3], 'Stems glabrous, often bearing green globular bulbs in the axils of the leaves.'

Trimen and Hooker[4] note that the 'root-tubers are very large, globose or elongate, stem ... tuberiferous in the leaf-axils.'

The writer of the article in the Dictionary of the Economic Products of India does not mention the tubers of *D. sativa*, but he notes that in Malabar and Travancore there are two species which bear, on the stems, tubers which are ovate in shape, and which vary in size from about that of a pea, to three inches in diameter. These axillary tubers are eaten, but are chiefly used for 'seed.' These species, however, he identifies with *D. alata*.

In the Stove at the Cambridge Botanic Garden there is a plant of *D. sativa* which produces in the axils of the leaves of its annual shoots, large rounded tubers, six or more inches in diameter and weighing as much as a pound or a pound and a half each. When mature these tubers are greyish or brown in colour, and present depressions in the surface which bear resemblances to those containing the 'eyes' in a potato. In addition to the tuber, the leaf-axil bears several (in some cases as many as eight) long, and very slender, pendulous spikes of flowers. It may be noted that these flowers are structurally hermaphrodite, although those in the wild forms of the plant are unisexual. Wight[5] also notes that when cultivated, the flowers tend to become bisexual.

In order to observe the mode of origin and structure of the axillary tubers, successive series of sections were cut with a microtome. The plane of the sections is that which is

[1] Hooker, Flora of British India, vol. vi, p. 295 ('94).
[2] Bentham, Flora Australiensis, vol. vi, p. 461 ('78).
[3] Bentham, Flora Hongkong., p. 368 ('61).
[4] Trimen and Hooker, Flora of Ceylon, vol. iv, p. 278 ('98).
[5] Wight, Icones, vol. iii; Description of Plate 878.

common to the stem and petiole, as far as this is possible on account of the difficulties which occur owing to torsion. Hence the sections are chiefly longitudinal. It will be convenient to trace the growth of the tubers by describing these sections from the apex of the stem downwards.

A median longitudinal section through the apex of a shoot, shows at each node a young leaf arching over the buds in its axil. Most of these buds, which generally number as many as six or eight, are the young spikes of flowers. At the young nodes the buds are undifferentiated and placed on a more or less conical mass of tissue in the leaf-axil.

Four or five nodes from the apex the differentiation of the buds has proceeded so rapidly that the two or three nearest to the stem have attained to the condition of elongated peduncles bearing lateral flower-buds. The youngest buds, nearest to the subtending leaf, are still rudimentary. The peduncles are arranged in pairs in the leaf-axils, the older anterior and the younger posterior. The youngest buds, posterior to the peduncles, are solitary. At this stage there is no trace of a tuber in the leaf-axil.

Somewhat lower down the stem the first beginning of the tuber is seen as a slight swelling below the youngest bud (Pl. XXVI, Fig. 1).

Sections through a node in which the young tuber is visible to the naked eye show that it is at this stage already distinctly separated from the surrounding tissues. Between the youngest of the peduncles and the tuber, in the series of sections examined, there was a single median vegetative bud, much less developed than those which form the peduncles. The tuber itself had two rudimentary buds lying in the median plane, one near the point of attachment of the tuber and the other more remote, and posterior. These buds caused angular projections on the tuber. The tissue lying a little below the cortex, between the buds, and especially between the posterior bud and the attachment of the tuber, was meristematic, and the most rapidly growing part of the structure.

In a young stem in another plant, grown under peculiar

circumstances to be described later [1], the arrangement of the structures in the leaf-axils was as follows. Between the main stem and the subtending leaf, and nearest to the stem, was one median axillary branch, immediately below and in front of this was the tuber on which were three buds. One, which was most developed, was just at the point of attachment of the tuber. The other two were also close to the point of attachment, one on the anterior side and the other on the posterior.

Two well-developed roots were formed on some tubers, one on each side of the biggest bud of the tuber (Fig. 5).

These buds, and the axillary branch, appear to be homologous with the impaired median buds in those leaf-axils which bear peduncles as well as tubers, but when flowering branches are produced the median vegetative branch remains undeveloped.

In a quite small tuber, about two mm. in diameter, the tissues are becoming differentiated. Within the epidermis is a cortex of parenchymatous cells containing chlorophyll. Many of these cells are enlarged and contain raphides. Beneath the cortex is a meristematic zone, which is most marked on the posterior side of the tuber. The central part consists of parenchymatous cells which already contain a considerable quantity of starch. Some enlarged cells are filled with raphides.

The two smaller buds are still, and remain for an indefinite time, quite rudimentary. They are in some cases entirely, in other cases partially, enclosed by the scale-like covering (Fig. 2).

A tuber about the size of a pea is covered with a single layer of epidermal cells beneath which is a thick layer, about twelve or fifteen cells deep, of cortical parenchyma which is brown in colour and beginning to lose its cell-contents. Then follows a zone of meristematic cells, separating the cortex from the central part which is made up of parenchymatous

[1] See p. 497.

cells, containing no starch. Cells with raphides occur in both cortex and medulla. At this stage there is no cork.

A tuber about three inches in diameter shows in addition to the buds large numbers of circular areas indicating the position of adventitious roots. The roots are produced most abundantly on the side of the tuber nearest to the point of attachment, although this is the side which also produces buds, and which, moreover, is turned towards the light as the tuber hangs on the stem. It should be stated that in the greenhouse the stem is trained horizontally on wires immediately under the glass roof. The question arises, does the stem grow vertically when wild, so that the roots will then be formed on the shaded side?

In a tuber of this size the structure is the same as in younger stages except that a layer of cork has been developed externally to the cortex, and replacing the epidermis. It arises in the cells immediately below the epidermis. Young vascular bundles, and also the adventitious roots, are formed from the meristematic zone.

When a large tuber is planted, one of the buds begins to grow rapidly and forms a strong shoot, from the base of which a large number of adventitious roots are produced (Figs. 3 and 6). No use is made of the numerous well-developed roots already formed in the tuber. Should the first formed shoot meet with an accident, as happened in the case of one of the tubers planted in the Botanic Garden, another bud develops. The formation of axillary tubers on these shoots begins very early.

The shoot arising from one of the tubers planted at the Botanic Garden was kept comparatively short, about a dozen or more nodes only being preserved. It was pegged down to the earth at intervals in order to see if it would form underground tubers at these points, as this is said to be a method of cultivation used by the Chinese to produce large crops of small tubers resembling potatoes[1]. At these

[1] Economic Products of India, p. 123 ('90).

nodes tubers were not formed, though they were developed at all the free nodes.

When the plant died down in the autumn a new underground tuber had been formed at the base of the annual stem, of smaller size than the original axillary one, which had been emptied of its contents but still remained attached to the stem (Fig. 6). The new tuber was covered with roots, which were arranged in more or less definite rings on its surface, as is the case also in the undeveloped roots of the axillary tubers (cf. Figs. 3 and 6).

The axillary tubers of another species of *Dioscorea*, perhaps *D. divaricata*, behaved differently when planted. This species grows out of doors at the Botanic Garden, and in the autumn it produces numerous small tubers which are about the size of peas, either rather smaller or a little larger. Usually there is only one in the axil of each leaf, but there may be two or even three. As in *D. sativa*, they possess both buds and roots. In both species the structure is similar. When one of these little tubers is planted it sends up one shoot, and begins itself (Fig. 7) to grow downwards as an elongated mass, while at the same time it forms, like *D. sativa*, a comparatively large new tuber, often of irregular shape.

Some interesting points were noted in tubers which formed shoots in the laboratory, without water, but in the presence of light. In two cases a single stem, six or eight feet long, was produced by each tuber, while from two other points smaller shoots were formed. It is noteworthy that at the bases of these stems buds were formed, which must be adventitious. Although the stems were so long and were also comparatively thick, the leaves were scarcely developed at all, and the axillary branches remained small (Figs. 3 and 4). Nevertheless, small tubers about half an inch in diameter were formed in the axils of most of these arrested leaves. The number and arrangement of the buds on these tubers and in the leaf-axils which bore them have been described above (p. 495). Round the bases of all the shoots numerous adventitious roots were formed, some of which became about

half an inch long and about an eighth wide. They were covered by a rough, almost scaly epidermis.

It is evident from the foregoing observations that the axillary tubers of *Dioscorea sativa* are of the morphological nature of stems bearing buds which are both axillary and adventitious, and roots which are adventitious. Apparently the underground tubers in this species are of the same morphological value. When developed below the ground, the roots in the tuber grow out and become functional, whereas in the aërial tuber, even if this be planted, they never appear outside the epidermis or periderm. This may be due to the fact that in large tubers the external tissues are thick and corky, so that the root may not be able to penetrate them.

Concerning the morphological value of the different kinds of tubers in various species of *Dioscorea* there is diversity of opinion.

De Bary[1] places the underground tubers in three categories:—

(1) Tuberous swollen roots, e. g. *Dioscorea Batatas.*

(2) Rhizomes with scaly leaves and composed of many internodes, e. g. *Dioscorea villosa.*

(3) Leafless tubers, resulting from the swelling of the first epicotyledonary internode of the seedling, e. g. *Tamus communis*, *T. polycarpus*, *Testudinaria*, and many species of *Dioscorea.*

There seems to be a general consensus of opinion that the underground tubers of *D. Batatas* are true roots[2]. According to Royer[3] the perennial part of *D. Batatas* is a small almost globular body about the size of a hazel nut, situated at the top of, but distinct from, the tuberous root. Each year this perennial organ, which is morphologically a stem, produces a twining stem and a tuberous root, and it is itself marked

[1] De Bary, Comp. Anat. of the Phanerogams and Ferns, Eng. edit., p. 622 ('84).

[2] De Bary, l. c. Engel and Prantl, vol. ii, 5, p. 131 ('88).

[3] Royer, Le tubercle de l'Igname est une racine, mais non pas un rhizome. Bull. de la Soc. Bot. de France, vol. xxx, p. 225 ('83).

with two series of cicatrices which result from the annual detachment of the stem and root respectively.

Bucherer[1] points out that the tuber of *D. Batatas* has the structure of a root.

Only one author, Morot[2], appears to hold that these underground tubers are stems. He regards each of them as consisting of a single reduced internode. In this way he explains the absence of scales.

The majority of tubers in the Dioscoreaceae are, however, undoubtedly stem-structures. They are considered to be rhizomes in *D. bulbifera* and *D. pentaphylla*[3] and, as already mentioned, in *D. villosa*. In *D. aculeata*[3] short stolons bear, at their distal ends, rounded tubers about the size of the fist. One plant bears as many as seven or eight[4].

The tuber is in some species the first internode of the stem, and is therefore leafless, e.g. *Tamus*, *Testudinaria*, and some species of *Dioscorea*. According to von Mohl[5], the tuber of *Tamus* (*Testudinaria*) *Elephantipes* is to be regarded as an adventitious bud, which each year is formed anew between the wood and the cortex of the tuber-like stem. Consequently the annual shoots are developed from adventitious buds.

The axillary tubers are, in all cases, stem-structures, the only question being as to the number and nature of the buds which occur upon them. Such aërial tubers are formed on many species; their development has been described in *D. Batatas*, Decsne, and *Helmia bulbifera*, Kunth, by Queva[6]. In *D. Batatas* the tuber arises as a single axillary bud. There are in each axil also one or two other buds which are branches. The surface of the tuber is covered with slight

[1] Bucherer, Beiträge zur Morphologie und Anatomie der Dioscoreaceen. Bot. Centr., vol. xliii, p. 121 ('90).

[2] Morot; see Royer, l. c., p. 227.

[3] Vieillard, Plantes utiles de la Nouvelle Calédonie. Ann. des Sci. Nat., 4e sér., vol. xvi, pp. 39–40 ('62).

[4] Sagot, Des Ignames. Bull. de la Soc. Bot. de France, vol. xviii, p. 309 ('71).

[5] Von Mohl, Untersuchungen über den Mittelstock von *Tamus Elephantipes*, L. Verm. Schrift. Bot. Inhalts, p. 193 ('36).

[6] Queva, Les Bulbilles des Dioscorées. Comptes Rendus des Séances de l'Acad. des Sciences, vol. cxvii, pp. 316–318 ('93).

elevations which mark the position of adventitious roots. The plant described by Queva as *Helmia bulbifera*, Kunth, appears to be the one which was considered above to be identical with *Dioscorea sativa*, Linn., i. e. the species under consideration in this paper. This opinion is confirmed by a comparison of the development of the tubers as described by Quéva and by the present writer. The descriptions may be briefly compared in some points. Queva observes that the growing points of the original buds (usually three) remain in the plane of symmetry of the organ, which corresponds with that of the leaf. On the mature tuber the growing point of the posterior bud is placed on the lower surface, that of the middle bud on the upper side, while the anterior bud remains near the point of attachment of the tuber. The observations made on the tubers grown at Cambridge show that in large tubers the three buds lose their original positions and all come to lie close to the point of attachment. They are therefore all on one side of the tuber in an advantageous position when they begin to grow. Adventitious buds are also formed, close to the original buds.

The abundant formation of axillary tubers in many species of *Dioscorea* seems as if it were connected with the fact that these plants do not appear to form seed readily. The experiments with the plants grown without water in the laboratory show that the tubers, and the shoots which they produce, have a great power of resisting drought, which would often kill the more delicate tissues of a seedling. Vegetative reproduction by means of axillary tubers appears to a large extent to have superseded sexual reproduction in this genus.

In conclusion I wish to thank Professor Marshall Ward for allowing me to work in the University Botanical Laboratory, and for the help which he always so willingly gives.

EXPLANATION OF FIGURES IN PLATE XXVI.

Illustrating Miss Dale's paper on *Dioscorea sativa*.

Fig. 1. Longitudinal section through a node of *Dioscorea sativa*, showing young tuber and young inflorescences. *s*. main stem; *a*. petiole; *b*. young inflorescences; *c*. bud on young tuber.

Fig. 2. Longitudinal section through older tuber about 2 mm. in diameter. *s*. main stem; *b*. young inflorescence; *c*. buds on tuber.

Fig. 3. Old axillary tuber which has produced long shoots without being planted or watered. *s*. stems; $r.^1$ undeveloped adventitious roots on the tuber; $r.^2$ young adventitious roots on the young shoots; *sc*. scales; *l*. arrested leaves with branches in their axils.

Fig. 4. Part of one of the shoots produced by an unplanted tuber. *t*. tuber; *l*. arrested leaf; *b*. bud; *br*. branch.

Fig. 5. A tuber on a similar branch. *t*. tuber; *a*. petiole; *b*. branch; c^1, c^2, c^3, buds; *d*. root.

Fig. 6. Axillary tuber *T*, which has been planted and produced a new tuber, *t*; *s* 1, scar of first developed bud, injured by an accident; *s* 2, second stem replacing the injured one; $r.^1$ undeveloped adventitious roots on old tuber; $r.^2$ adventitious roots on young tuber.

Fig. 7. Behaviour of the axillary tuber *T*, of another species of *Dioscorea*, perhaps *D. divaricata*. T^1, newly developed part of original tuber; *t*. new tuber; *b*. bud on original tuber.

Fig. 1.

Fig. 2.

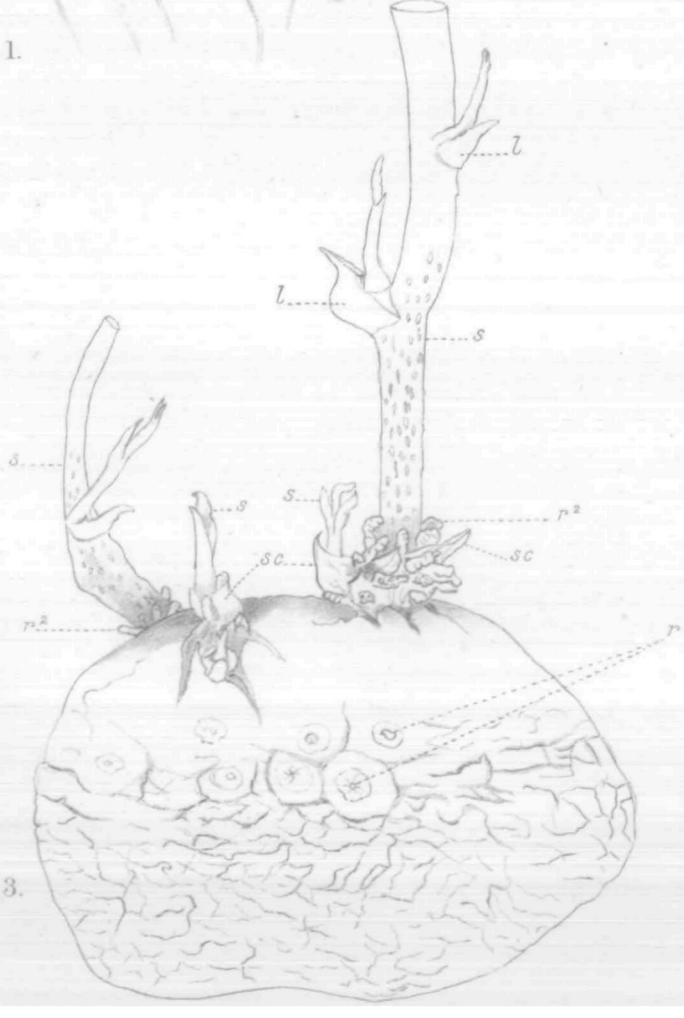

Fig. 3.

Fig 4.

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Fig. 6.

Fig. 5.

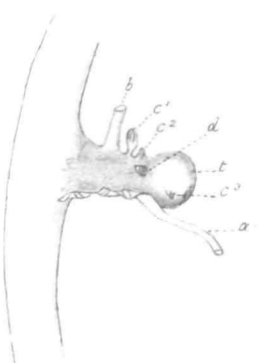
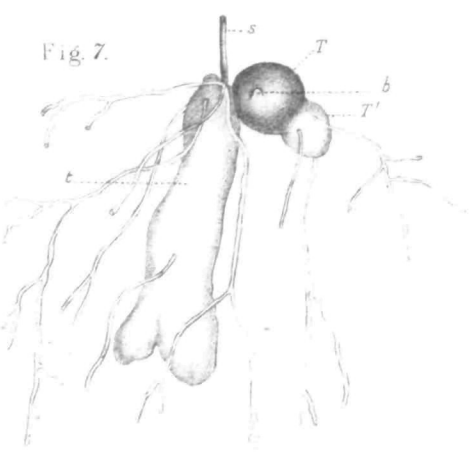


Fig. 7.



University Press, Oxford