THE DEVELOPMENT OF THE TUBER OF DIOSCOREA SANSIBARENSIS PAX

by

I. H. BURKILL

(Leatherhead, England).

Dioscorea sansibarensis is a rather large liane of wide distribution in tropical Africa whence it extends to Madagascar. It has received various names; for it is *D. macroura* HARMS, *D. Welwitschii* RENDLE and *D. macabiha* JUMELLE and PERRIER: also the nomen nudum *D. toxicaria* BOJER, undoubtedly belongs to it.

It has been placed in the section *Opsophyton* of its genus, but by mistake; as it has altogether dissimilar male inflorescences and a perennial tuber. This tuber, PERRIER tells us (1), attains 30 kilos in weight, lies in the surface of the soil and is secured against the destructiveness of wild pigs and other animals of similar feeding habits by that poisonousness, which caused BOJER on hearing of it in the bulbils to employ the specific name "*toxicaria*" (2).

The author has not been able as yet to obtain seeds for a study of germination, but has been able to follow the growth of the tuber from bulbils supplied to him by Mr R. E. HOLTTUM, Director of Gardens, Singapore; and he has been favoured by Major M. Y. ORR with notes made in the Royal Botanic Garden, Edinburgh. He desires to express his endebtedness to these two botanists, and as well to the Director of the Royal Botanic Gardens, Kew, for facilities for work.

D. sansibarensis produces bulbils in great abundance. They are ellipsoid bodies 2—4 cm long, with a corky lenticellate coat 10—15 cells deep. Under the cork the parenchyma holds a little chlorophyll and deeper a large store of starch. At maturity these bulbils fall to the ground where they may be rolled along the surface for short distances by storm-water; or, as the plant is partial to the neighbourhood of streams, they may fall into water, and if so are floated to new positions (1). While floating they absorb water, grow denser and in time sink.

The absorption of water induces germination; but it should take place on land.

A bulbil which has come to rest on dry soil, lies dormant until wetted. Atmospheric humidity, however intense, does not start germination. In the writer's experiments bulbils were suspended in satured air at temperatures of 20—25° C., which are appropriate, but could not be got to germinate until threads of cotton were suspended from them to the water immediately below which acting as wicks brought the water to them. And it is evident that dormant bulbils lie through the Dry season, in Africa, until at the inception of the Rainy season contact with the wet soil below them provides the stimulus for growth. The shoot is extruded where the stimulus is strongest, i.e. the soil. It happens sometimes that two or even more shoots are extruded: but it seems that when one shoot gets a good start, it arrests the growth of others through the operation of a hormone: but if this leading bud receives injury so that the power of its hormone wanes, another bud immediately grows.

The bud bursts through the cork as a dome-shaped body and bears two scale-leaves at 180° from each other, each sheathing the apex (*figure 1*). The first of the scale-leaves is somewhat ephemeral and becomes torn by the growing tissues within it: the second persists as a wrapping over the apex of the stem and becomes the shield of a lateral bud. Meanwhile the axis, possessing a very marked negative geotropism, curves (*figure 2*), and the lower side of its first internode grows in bulk as well as in length (*figure 3*). This growth in bulk produces the tuber which in due time assumes increments in annual periods and gives rise to annual rings of new roots (*figure 5*). The growth slackens in the centre so that the young tuber flattens below (*figure 3*) and then becomes slightly impressed (*figure 6*). That the position of this growth in bulk is as definitely controlled by gravity as is the directing of the curvature of the internode has been demonstrated by experiments in which, after its inception, the bulbil was suspended with another face downwards, whereby the greater rate of growth was transferred to the other side of the internode. The power of such adaptation probably in time wanes; but it is hoped later to turn a fully formed tuber on its back and to ascertain what then happens. In Nature the destruction of the tuber would seem probable because more delicate tissues become exposed; and moreover PERRIER suggests that these are less poisonous than those above (**1**).

The reader will have appreciated the fact that the tuber is formed from a single internode. The elongated outline of the young tuber in

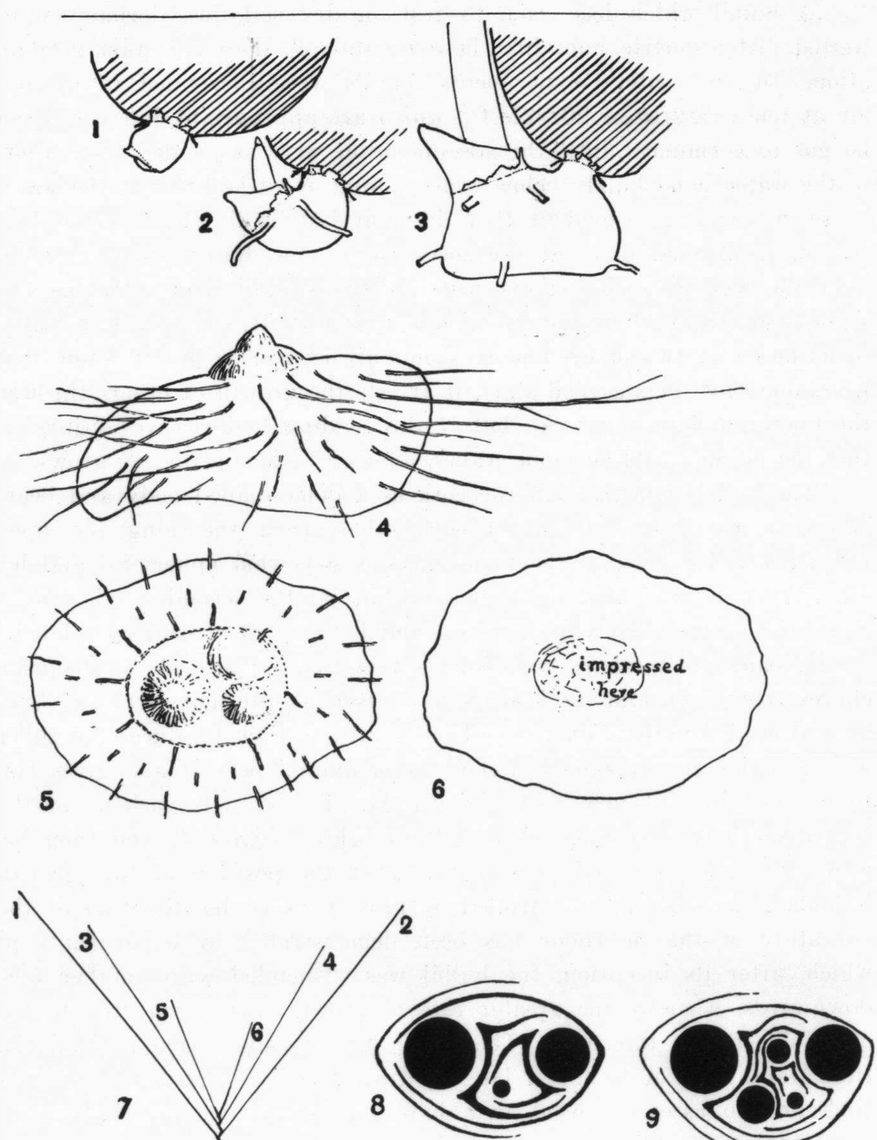

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figure 5 shows that the tendency natural to an internode to elongate is not completely balanced by the tendency to broaden. The tendency of the growth to weaken in the centre leads to it taking the shape of the letter O. Perhaps the rings of roots help to increase the peripheral growth.

A question has arisen which cannot be finally answered until experiments with new bulbils have been made; it is this: is the first internode of the stem equally responsive to gravity in all parts, or does it curve only in the plane of its two scale leaves? At the time of writing the latter of these alternatives seems right.

The first scale-leaf of the new stem — that which perishes soon and is represented tattered in *figures 2* and *3*, rarely shields anything of the nature of a bud, and apparently never an effective bud: but in the axil of the second scale-leaf a well developed bud arises. The internode between these two scale-leaves is completely suppressed. The third internode of the stem normally elongates much; the fourth is unlikely to elongate more than a little: the fifth probably elongates considerably, the sixth little. In this way there is a marked tendency to bring the leaf-scales and leaves together in pairs, and the internodes which elongate most are those of odd number — nos. 1, 3, 5, etc. (3).

The bud in the axil of the second scale-leaf is that of the axis in reserve for the next year: but if the axis in growth is cut off in the internode above it, it develops, i.e. it is no longer under the influence

Explanation of the figures.

Figure 1. A bud thrust downwards brought the ruptured corky coat of the bulbil, its apex with two sheathing scale-leaves.

Figure 2, the same, curved in response to gravity, with adventitious roots, with the first scale-leaf tattered, and the stem thrust out from the second scale-leaf.

Figure 3, the same after the tuber has taken shape.

Figures 4, 5 and *6,* a tuber a few years old, drawn by Major M. Y. ORR, from the side, from above and from below. In figure *4* the bud of a new stem is seen above and the rings of roots are evident. In figure *5* the bud of the incoming year's stem is seen on the left, the scar of an old stem and the bud which should lie dormant for a whole year on the right: the rings of roots are indicated. In figure *6* the impression under the tuber is indicated.

Figure 7. Axes 1—6 of a rhipidium.

Figure 8. Successive axes and sheathing scale leaves from a plant whereof two axes had been cut turn.

Figure 9, from a plant in which four axes had been cut. The first scale-leaf in each and the main axis is on the left. The relative size of the axes indicates their succession.

of a hormone from the actively growing parent axis. Many experiments have been done by cutting the parent axis in its third internode, thereby provoking the bud into growth; then when it had extended, cutting it in its turn; whereon a third axis was called out, and so on. By doing this the plant is made to reveal the succession of axes which would otherwise be unfolded only over as many years. It is learned from such experiments that the plan of branching is a *rhipidium* (*figure 7*); for, as the scale-leaves arise at 180° from each other, the branching is in one plane. Such a way of setting axes together is confined to the Monotyledons (**4**). In this *Dioscorea* the second scale-leaf of the first axis protects the bud of the second axis, whose first scale-leaf, arising at 180° from the parent scale-leaf, protects the bud of the third, and so forward. The internodes between these scale-leaves are entirely suppressed, so that all are sessile on the tuber (**5**). Theoretically, as the scale-leaves are all in one plane, the bases of the successive axes should lie in a straight line; and theoretically, if, as appears to be the case, the geotropic curvature of the first internode of the first axis occurs only in the plane of its two scale-leaves, that straight line should lie along the top of the tuber in its long axis. It does not, for pressure crumples up the line: *figures 8* and *9*, drawn from young tubers with axes successively cut back, show in what way. The damage to the plant which gave *figure 9* had been carried further than that to the plant which gave *figure 8*.

The experimental treatment of these plants exaggerated the displacement, because the plants were called on to renew their growth before the tuber had had time to make room for it. But the top of the undisturbed tuber (*figure 5*) shows displacement of the same nature. Pressure which drives the successive axes out of the straight line, may be invoked also to account for the double keel off the scale leaves.

One last remark is called for — in typical members of the section *Opsophyton*, the tuber acts as a bulbil by sending out a bud which forms a tuber at the end of its life of a year. And it must be claimed that the section of *D. sansibarensis* is more specialized than the section *Opsophyton*, because in it the differentiation of bulbil and tuber is carried further than, say, in *D. bulbifera*, which is typical of the section *Opsophyton* and indeed the plant around which ULINE built the section (**6**).

Summary.

The bulbils of *Dioscorea sansibarensis* fall at maturity and are carried away from the parent plant, if at all, by water: they rest

through the Dry season; and germinate when the soil under them is able to supply moisture. The new plant, is thrust into the surface of the soil and there shaped by its geotropic responsiveness. Its tuber is the result of a more or less one-sided enlargement of the first internode of the axis: it is perennial and its greatest growth becomes annular. The annual stems, which rise from the tuber are produced cymosely, each from the lowest axil of its parent axis; and, by arrest of internodes between them, all are sessile on the tuber. Thus crowded they are unable to grow in positions which are theirs theoretically and are accommodated by a certain amount of fluidity in the growth of the top of the tuber.

D. sansibarensis must be excluded from the section *Opsophyton* because its tubers are more specialized organs than its bulbils, as well as on differences in the male inflorescences.

References.

1. PERRIER DE LA BATHIE, Les Dioscoréacées de Madagascar in Mém. Soc. Linn. de Normandie, N. S., sect. Bot. I fasc. 2, p. 13; 1928.
2. BOJER, Hortus Mauritianus, p. 352; 1837.
3. For the association of elongated internodes with leaves in certain positions see BURKILL, The phyllotaxy of Dioscorea glauca Muhl. in Journ. Bot. 1936 p. 87; and The phyllotaxy of Tamus communis L. p. 153.
4. EICHLER, Blüthendiagramme, p. 41; 1875.
5. cf. Miss SPARSHOTT, Observations on the tuber of Testudinaria elephantipes, in Journ. Linn. Soc. Lond., Bot. xlix, p. 607; 1935.
6. ULINE in ENGLER, Pflanzenfamilien, Nachträge zu ii—iv, p. 84, 1897; and compare R. KNUTH, Dioscoreaceae, in ENGLER, Pflanzenreich iv—43; 1924.