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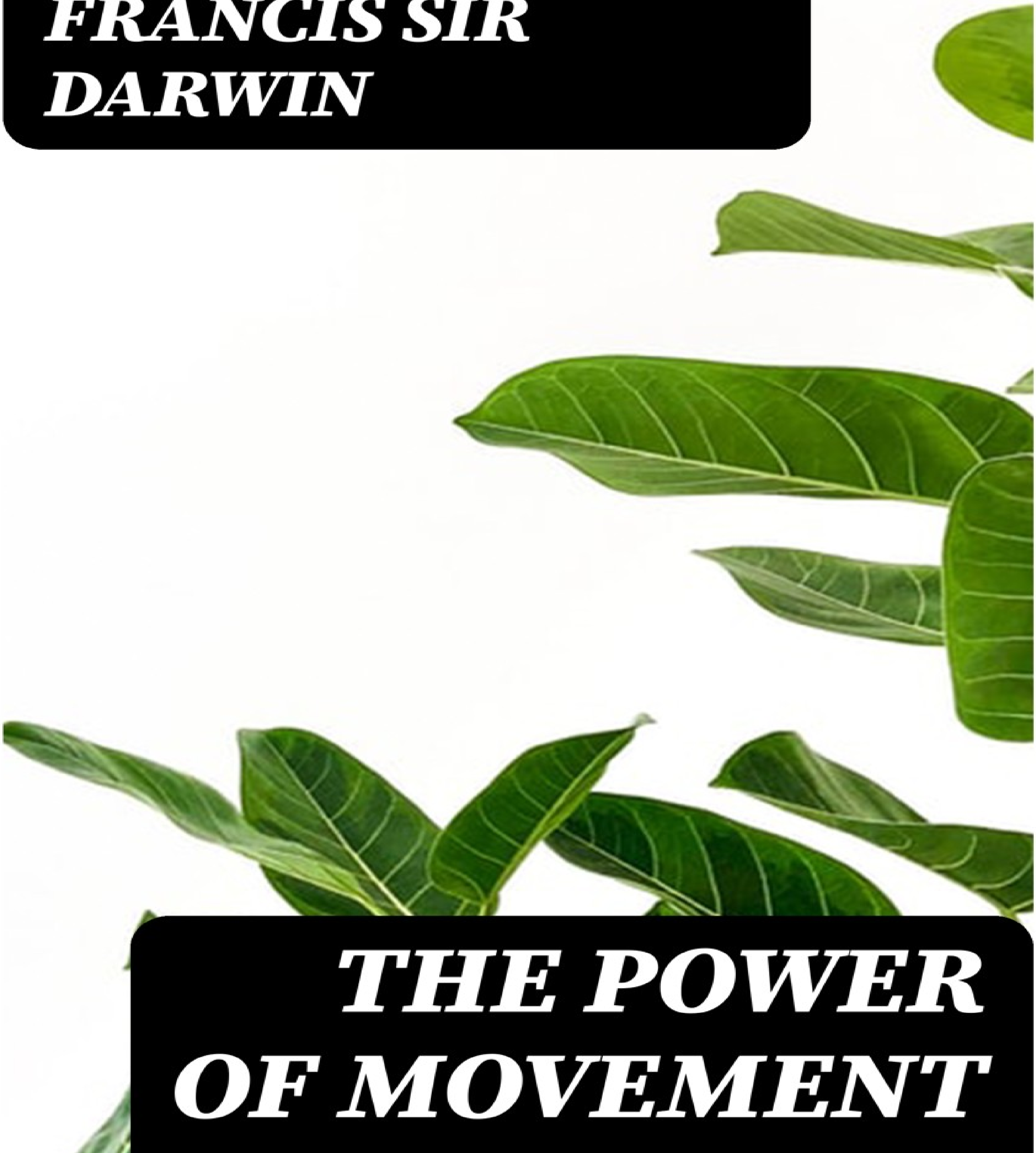

THE POWER OF MOVEMENT IN PLANTS

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The Power of Movement in Plants

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INTRODUCTION.

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THE chief object of the present work is to describe and connect together several large classes of movement, common to almost all plants. The most widely prevalent movement is essentially of the same nature as that of the stem of a climbing plant, which bends successively to all points of the compass, so that the tip revolves. This movement has been called by Sachs "revolving nutation;" but we have found it much more convenient to use the terms circumnutation and circumnutate. As we shall have to say much about this movement, it will be useful here briefly to describe its nature. If we observe a circumnutating stem, which happens at the time to be bent, we will say towards the north, it will be found gradually to bend more and more easterly, until it faces the east; and so onwards to the south, then to the west, and back again to the north. If the movement had been quite regular, the apex would have described a circle, or rather, as the stem is always growing upwards, a circular spiral. But it generally describes irregular elliptical or oval figures; for the apex, after pointing in any one direction, commonly moves back to the opposite side, not, however, returning along the same line. Afterwards other irregular ellipses or ovals are successively described, with their longer [page 2] axes directed to different points of the compass. Whilst describing such figures, the apex often travels in a zigzag line, or makes small subordinate loops or triangles. In the case of leaves the ellipses are generally narrow.

Until recently the cause of all such bending movements was believed to be due to the increased growth of the side which becomes for a time convex; that this side does temporarily grow more quickly than the concave side has been well established; but De Vries has lately shown that such increased growth follows a previously increased state of turgescence on the convex side.* In the case of parts provided with a so-called joint, cushion or pulvinus, which consists of an aggregate of small cells that have ceased to increase in size from a very early age, we meet with similar movements; and here, as Pfeffer has shown** and as we shall see in the course of this work, the increased turgescence of the cells on opposite sides is not followed by increased growth. Wiesner denies in certain cases the accuracy of De Vries' conclusion about turgescence, and maintains*** that the increased extensibility of the cell-walls is the more important element. That such extensibility must accompany increased turgescence in order that the part may bend is manifest, and this has been insisted on by several botanists; but in the case of unicellular plants it can hardly fail to be the more important element. On the whole we may at present conclude that in-

* Sachs first showed ('Lehrbuch,' etc., 4th edit. p. 452) the intimate connection between turgescence and growth. For De Vries' interesting essay, 'Wachsthumskrümmungen mehrzelliger Organe,' see 'Bot. Zeitung,' Dec. 19, 1879, p. 830.

** 'Die Periodischen Bewegungen der Blattorgane,' 1875.

*** 'Untersuchungen über den Heliotropismus,' Sitzb. der K. Akad. der Wissenschaft. (Vienna), Jan. 1880.

[page 3] creased growth, first on one side and then on another, is a secondary effect, and that the increased turgescence of the cells, together with the extensibility of their walls, is the primary cause of the movement of circumnutation.*

In the course of the present volume it will be shown that apparently every growing part of every plant is continually circumnutating, though often on a small scale. Even the stems of seedlings before they have broken through the ground, as well as their buried radicles, circumnutate, as far as the pressure of the surrounding earth permits. In this universally present movement we have the basis or groundwork for the acquirement, according to the requirements of the plant, of the most diversified movements. Thus, the great sweeps made by the stems of twining plants, and by the tendrils of other climbers, result from a mere increase in the amplitude of the ordinary movement of circumnutation. The position which young leaves and other organs ultimately assume is acquired by the circumnutating movement being increased in some one direction. the leaves of various plants are said to sleep at night, and it will be seen that their blades then assume a vertical position through modified circumnutation, in order to protect their upper surfaces from being chilled through radiation. The movements of various organs to the light, which are so general throughout the vegetable kingdom, and occasionally from the light, or transversely with respect to it, are all modified

* See Mr. Vines' excellent discussion ('Arbeiten des Bot. Instituts in Würzburg,' B. II. pp. 142, 143, 1878) on this

intricate subject. Hofmeister's observations ('Jahreschrifte des Vereins für Vaterl. Naturkunde in Würtemberg,' 1874, p. 211) on the curious movements of Spirogyra, a plant consisting of a single row of cells, are valuable in relation to this subject.

[page 4] forms of circumnutation; as again are the equally prevalent movements of stems, etc., towards the zenith, and of roots towards the centre of the earth. In accordance with these conclusions, a considerable difficulty in the way of evolution is in part removed, for it might have been asked, how did all these diversified movements for the most different purposes first arise? As the case stands, we know that there is always movement in progress, and its amplitude, or direction, or both, have only to be modified for the good of the plant in relation with internal or external stimuli.

Besides describing the several modified forms of circumnutation, some other subjects will be discussed. The two which have interested us most are, firstly, the fact that with some seedling plants the uppermost part alone is sensitive to light, and transmits an influence to the lower part, causing it to bend. If therefore the upper part be wholly protected from light, the lower part may be exposed for hours to it, and yet does not become in the least bent, although this would have occurred quickly if the upper part had been excited by light. Secondly, with the radicles of seedlings, the tip is sensitive to various stimuli, especially to very slight pressure, and when thus excited, transmits an influence to the upper part, causing it to bend from the pressed side. On the other hand, if the tip is subjected to the vapour of water proceeding from one side, the upper part of the radicle bends towards this side. Again it is the tip, as stated by Ciesielski, though denied by others, which is sensitive to the attraction of gravity, and by transmission causes the adjoining parts of the radicle to bend towards the centre of the earth. These several cases of the effects of contact, other irritants, vapour, light, and the [page 5] attraction of gravity being transmitted from the excited part for some little distance along the organ in question, have an important bearing on the theory of all such movements.

[Terminology.—A brief explanation of some terms which will be used, must here be given. With seedlings, the stem which supports the cotyledons (i.e. the organs which represent the first leaves) has been called by many botanists the hypocotyledonous stem, but for brevity sake we will speak of it merely as the hypocotyl: the stem immediately above the cotyledons will be called the epicotyl or plumule. The radicle can be distinguished from the hypocotyl only by the presence of root-hairs and the nature of its covering. The meaning of the word circumnutation has already been explained. Authors speak of positive and negative heliotropism,*—that is, the bending of an organ to or from the light; but it is much more convenient to confine the word heliotropism to bending towards the light, and to designate as apheliotropism bending from the light. There is another reason for this change, for writers, as we have observed, occasionally drop the adjectives positive and negative, and thus introduce confusion into their discussions. Diaheliotropism may express a position more or less transverse to the light and induced by it. In like manner positive geotropism, or bending towards the centre of the earth, will be called by us geotropism; apogeotropism will mean bending in opposition to gravity or from the centre of the earth; and diageotropism, a position more or less transverse to the radius of the earth. The words heliotropism and geotropism properly mean the act of moving in relation to the light or the earth; but in the same manner as gravitation, though defined as "the act of tending to the centre," is often used to express the cause of a body falling, so it will be found convenient occasionally to employ heliotropism and geotropism, etc., as the cause of the movements in question.

The term epinasty is now often used in Germany, and implies that the upper surface of an organ grows more quickly than the

* The highly useful terms of Heliotropism and Geotropism were first used by Dr. A. B. Frank: see his remarkable 'Beiträge zur Pflanzenphysiologie,' 1868. [page 6] lower surface, and thus causes it to bend downwards. Hyponasty is the reverse, and implies increased growth along the lower surface, causing the part to bend upwards.*

Methods of Observation.—The movements, sometimes very small and sometimes considerable in extent, of the various organs observed by us, were traced in the manner which after many trials we found to be best, and which must be described. Plants growing in pots were protected wholly from the light, or had light admitted from above, or on one side as the case might require, and were covered above by a large horizontal sheet of glass, and with another vertical sheet on one side. A glass filament, not thicker than a horsehair, and from a quarter to three-quarters of an inch in length, was affixed to the part to be observed by means of shellac dissolved in alcohol. The solution was allowed to evaporate, until it became so thick that it set hard in two or three seconds, and it never injured the tissues, even the tips of tender radicles, to which it was applied. To the end of the glass filament an excessively minute bead of black sealing-wax was cemented, below or behind which a bit of card with a black dot was fixed to a stick driven into the ground. The weight of the filament was so slight that even small leaves were not perceptibly pressed down. another method of observation, when much magnification of the movement was not required, will presently be described. The bead and the dot on the card were viewed through the horizontal or vertical glass-plate (according to the position of the object), and when one exactly covered the other, a dot was made on the glass-plate with a sharply pointed stick dipped in thick Indian-ink. Other dots were made at short intervals of time and these were afterwards joined by straight lines. The figures thus traced were therefore angular; but if dots had been made every 1 or 2 minutes, the lines would have been more curvilinear, as occurred when radicles were allowed to trace their own courses on smoked glass-plates. To make the dots accurately was the sole difficulty, and required some practice. Nor could this be done quite accurately, when the movement was much magnified, such as 30 times and upwards; yet even in this case the general course may be trusted. To test the accuracy of the above method of observation, a filament was fixed to an

* These terms are used in the sense given them by De Vries, 'Würzburg Arbeiten,' Heft ii 1872, p. 252.

[page 7] inanimate object which was made to slide along a straight edge and dots were repeatedly made on a glass-plate; when these were joined, the result ought to have been a perfectly straight line, and the line was very nearly straight. It may be added that when the dot on the card was placed half-an-inch below or behind the bead of sealing-wax, and when the glass-plate (supposing it to have been properly curved) stood at a distance of 7 inches in front (a common distance), then the tracing represented the movement of the bead magnified 15 times.

Whenever a great increase of the movement was not required, another, and in some respects better, method of observation was followed. This consisted in fixing two minute triangles of thin paper, about 1/20 inch in height, to the two ends of the attached glass filament; and when their tips were brought into a line so that they covered one another, dots were made as before on the glass-plate. If we suppose the glass-plate to stand at a distance of seven inches from the end of the shoot bearing the filament, the dots when joined, will give nearly the same figure as if a filament seven inches long, dipped in ink, had been fixed to the moving shoot, and had inscribed its own course on the plate. The movement is thus considerably magnified; for instance, if a shoot one inch in length were bending, and the glass-plate stood at the distance of seven inches, the movement would be magnified eight times. It would, however, have been very difficult to have ascertained in each case how great a length of the shoot was bending; and this is indispensable for ascertaining the degree to which the movement is magnified.

After dots had been made on the glass-plates by either of the above methods, they were copied on tracing paper and joined by ruled lines, with arrows showing the direction of the movement. The nocturnal courses are represented by straight broken lines. the first dot is always made larger than the others, so as to catch the eye, as may be seen in the diagrams. The figures on the glass-plates were often drawn on too large a scale to be reproduced on the pages of this volume, and the proportion in which they have been reduced is always given.* Whenever it could be approximately told how much the movement had been magnified, this is stated. We have perhaps

* We are much indebted to Mr. Cooper for the care with which he has reduced and engraved our diagrams.

[page 8] introduced a superfluous number of diagrams; but they take up less space than a full description of the movements. Almost all the sketches of plants asleep, etc., were carefully drawn for us by Mr. George Darwin.

As shoots, leaves, etc., in circumnutating bend more and more, first in one direction and then in another, they were necessarily viewed at different times more or less obliquely; and as the dots were made on a flat surface, the apparent amount of movement is exaggerated according to the degree of obliquity of the point of view. It would, therefore, have been a much better plan to have used hemispherical glasses, if we had possessed them of all sizes, and if the bending part of the shoot had been distinctly hinged and could have been placed so as to have formed one of the radii of the sphere. But even in this case it would have been necessary afterwards to have projected the figures on paper; so that complete accuracy could not have been attained. From the distortion of our figures, owing to the above causes, they are of no use to any one who wishes to know the exact amount of movement, or the exact course pursued; but they serve excellently for ascertaining whether or not the part moved at all, as well as the general character of the movement.]

In the following chapters, the movements of a considerable number of plants are described; and the species have been arranged according to the system adopted by Hooker in Le Maout and Decaisne's 'Descriptive Botany.' No one who is not investigating the present subject need read all the details, which, however, we have thought it advisable to give. To save the reader trouble, the conclusions and most of the more important parts have been printed in larger type than the other parts. He may, if he thinks fit, read the last chapter first, as it includes a summary of the whole volume; and he will thus see what points interest him, and on which he requires the full evidence.

Finally, we must have the pleasure of returning our [page 9] sincere thanks to Sir Joseph Hooker and to Mr. W. Thiselton Dyer for their great kindness, in not only sending us plants from Kew, but in procuring others from several sources when they were required for our observations; also, for naming many species, and giving us information on various points. [page 10]

CHAPTER I. THE CIRCUMNUTATING MOVEMENTS OF SEEDLING PLANTS.

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whilst still buried beneath the ground, whilst rising above the ground and
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Githago, Gossypium, Oxalis, Tropaeolum, Citrus, Aesculus, of several
Leguminous and Cucurbitaceous genera, Opuntia, Helianthus, Primula,
Cyclamen, Stapelia, Cerinthe, Nolana, Solanum, Beta, Ricinus, Quercus,
Corylus, Pinus, Cycas, Canna, Allium, Asparagus, Phalaris, Zea, Avena,
Nephrodium, and Selaginella.

THE following chapter is devoted to the circumnutating movements of the radicles, hypocotyls, and cotyledons of seedling plants; and, when the cotyledons do not rise above the ground, to the movements of the epicotyl. But in a future chapter we shall have to recur to the movements of certain cotyledons which sleep at night.

[Brassica oleracea (Cruciferae)'.—Fuller details will be given with respect to the movements in this case than in any other, as space and time will thus ultimately be saved.

Radicle.—A seed with the radicle projecting .05 inch was fastened with shellac to a little plate of zinc, so that the radicle stood up vertically; and a fine glass filament was then fixed near its base, that is, close to the seed-coats. The seed was surrounded by little bits of wet sponge, and the movement of the bead at the end of the filament was traced (Fig. 1) during sixty hours. In this time the radicle increased in length from .05 to .11 inch. Had the filament been attached at first close to the apex of the radicle, and if it could have remained there all the time, the movement exhibited would have [page 11] been much greater, for at the close of our observations the tip, instead of standing vertically upwards, had become bowed downwards through geotropism, so as almost to touch the zinc plate. As far as we could roughly ascertain by measurements made with compasses on other seeds, the tip alone, for a length of only 2/100 to 3/100 of an inch, is acted on by geotropism. But the tracing shows that the basal part of the radicle continued to circumnutate irregularly during the whole time. The actual extreme amount of movement of the bead at the end of the filament was nearly .05 inch, but to what extent the movement of the radicle was magnified by the filament, which was nearly 3/4 inch in length, it was impossible to estimate.

Fig. 1. Brassica oleracea: circumnutation of radicle, traced on horizontal glass, from 9 A.M. Jan. 31st to 9 P.M. Feb. 2nd. Movement of bead at end of filament magnified about 40 times.

Another seed was treated and observed in the same manner, but the radicle in this case protruded .1 inch, and was not Fig. 2. Brassica oleracea: circumnutating and geotropic movement of radicle, traced on horizontal glass during 46 hours.

fastened so as to project quite vertically upwards. The filament was affixed close to its base. The tracing (Fig. 2, reduced by half) shows the movement from 9 A.M. Jan. 31st to 7 A.M. Feb. 2nd; but it continued to move during the whole of the [page 12] 2nd in the same general direction, and in a similar zigzag manner. From the radicle not being quite perpendicular when the filament was affixed geotropism came into play at once; but the irregular zigzag course shows that there was growth (probably preceded by turgescence), sometimes on one and sometimes on another side. Occasionally the bead remained stationary for about an hour, and then probably growth occurred on the side opposite to that which caused the geotropic curvature. In the case previously described the basal part of the very short radicle from being turned vertically upwards, was at first very little affected by geotropism. Filaments were affixed in two other instances to rather longer radicles protruding obliquely from seeds which had been turned upside down; and in these cases the lines traced on the horizontal glasses were only slightly zigzag, and the movement was always in the same general direction, through the action of geotropism. All these observations are liable to several causes of error, but we believe, from what will hereafter be shown with respect to the movements of the radicles of other plants, that they may be largely trusted.

Hypocotyl.—The hypocotyl protrudes through the seed-coats as a rectangular projection, which grows rapidly into an arch like the letter U turned upside down; the cotyledons being still enclosed within the seed. In whatever position the seed may be embedded in the earth or otherwise fixed, both legs of the arch bend upwards through apogeotropism, and thus rise vertically above the ground. As soon as this has taken place, or even earlier, the inner or concave surface of the arch grows more quickly than the upper or convex surface; and this tends to separate the two legs and aids in drawing the cotyledons out of the buried seed-coats. By the growth of the whole arch the cotyledons are ultimately dragged from beneath the ground, even from a considerable depth; and now the hypocotyl quickly straightens itself by the increased growth of the concave side.

Even whilst the arched or doubled hypocotyl is still beneath the ground, it circumnutates as much as the pressure of the surrounding soil will permit; but this was difficult to observe, because as soon as the arch is freed from lateral pressure the two legs begin to separate, even at a very early age, before the arch would naturally have reached the surface. Seeds were allowed to germinate on the surface of damp earth, and after they had fixed themselves by their radicles, and after the, as yet, only [page 13] slightly arched hypocotyl had become nearly vertical, a glass filament was affixed on two occasions near to the base of the basal leg (i.e. the one in connection with the radicle), and its movements were traced in darkness on a horizontal glass. The result was that long lines were formed running in nearly the plane of the vertical arch, due to the early separation of the two legs now freed from pressure; but as the lines were zigzag, showing lateral movement, the arch must have been circumnutating, whilst it was straightening itself by growth along its inner or concave surface.

A somewhat different method of observation was next followed: Fig. 3. Brassica oleracea: circumnutating movement of buried and arched hypocotyl (dimly illuminated from above), traced on horizontal glass during 45 hours. Movement of bead of filament magnified about 25 times, and here reduced to one-half of original scale.

as soon as the earth with seeds in a pot began to crack, the surface was removed in parts to the depth of .2 inch; and a filament was fixed to the basal leg of a buried and arched hypocotyl, just above the summit of the radicle. The cotyledons were still almost completely enclosed within the much-cracked seed-coats; and these were again covered up with damp adhesive soil pressed pretty firmly down. The movement of the filament was traced (Fig. 3) from 11 A.M. Feb. 5th till 8 A.M. Feb. 7th. By this latter period the cotyledons had been dragged from beneath the pressed-down earth, but the upper part of the hypocotyl still formed nearly a right angle with the lower part. The tracing shows that the arched hypocotyl tends at this early [page 14] age to circumnutate irregularly. On the first day the greater movement (from right to left in the figure) was not in the plane of the vertical and arched hypocotyl, but at right angles to it, or in the plane of the two cotyledons, which were still in close contact. The basal leg of the arch at the time when the filament was affixed to it, was already bowed considerably backwards, or from the cotyledons; had the filament been affixed before this bowing occurred, the chief