G.—On the Movements of Plants.

CHAPTER XXIX.

A.—*Introduction.*

THIS is the latest and perhaps the most interesting of the contributions to Botanical science of Charles Darwin. The book is more interesting than any other from a personal point of view. On its title-page is inscribed "By Charles Darwin assisted by Francis Darwin," so that in this his last work, for the present, upon biological subjects we find the great naturalist aided by one of those sons who have given promise that the name of Darwin will lose nothing of its scientific fame as far as they are concerned.

Further, the subject matter of the book is of deepest interest. It will be remembered that one of the old distinctions between plants and animals was the presence of movement in the latter, and its absence in the former. That this distinction does not hold has been already demonstrated, but this book is devoted to the complete destruction of all arguments that attempt to dissever plants from animals on the ground of movement. It shows that movement is universal in plants—nay more, that in connexion with that movement there is at least nervous action if not nervous structure. It demonstrates the line along which the evolution of the more complex movements of plants has passed in the development of these last from the rudimentary and exceedingly simple form of movement presented by all parts of all plants. In the study of the Movements of plants we shall consider (A) the introduction, (B) circumnutation or the universal movement at which hint has been made, (C) its modifications, (D) nervous action, and (E) conclusion.

A. Introduction. In the opening pages of the book there is dealing with the following topics. The object of the book; certain technical terms necessary to be understood by its reader; the general nature of plant movement; its causes; its universality; and the methods of observation.

(1) The *object of the book* is to describe and connect together several large classes of movement common to almost all plants. It is needless to say that in this description there is constant evidence adduced in favor of the great principle of evolution as opposed to special creation.

(2) *Technical terms.* All the world knows that a plant consists of root, stem, and leaves, these last either the ordinary green leaves, or those modified and colored leaves which constitute the flower. The plant in its rudimentary condition within the seed, when it is known as Embryo, has the same three parts—root, stem and leaf. The rudimentary embryonic root, of small size and of very simple structure, is called the radicle (from *radix*, a root). The rudimentary stem, represented by a small simple structured bud, is called the plumule; whilst the first leaves that are formed, also small and simple, though rapidly becoming larger and more complex when once they are raised into the air, are the cotyledons. If anyone will study a seedling plant that has just emerged from the seed and is growing up into its new life they will find a radicle or young root growing down into the ground, a young stem growing up into the air and bearing in most English plants two young leaves, the cotyledons. The radicle, therefore, will mean to us the root of the young seedling plant. The part of the stem that bears, and is below the cotyledons or firstborn leaves is called the hypocotyl (ὑπο = under). The part of the stem that rises above and beyond and more into the air than the cotyledons is the epicotyl (επι = upon). It is very important that the unscientific reader become thoroughly acquainted with the meaning of these terms, and the relative positions of the parts they denote. From below upwards, once again, we have radicle or root, hypocotyl or stem beneath the first leaves, cotyledons or the first leaves, epicotyl or the stem above the first leaves.

Before Charles Darwin took in hand the subject of the movements of plants, certain movements were known and named—those dependent upon the action of light, and those dependent upon the action of gravitation. Many plants had been observed to have the habit of growing towards the light. Such growth towards the light is heliotropism (ἥλιος = sun,

$\tau\rho o\pi o\varsigma$ = direction). Certain others had been observed to bend from the light, and this movement was called aphelio-tropism ($\dot{\alpha}\pi o$ = from). A third form of movement as affected by the action of light is where the plant does not grow directly towards the light nor directly away from it, but assumes a position more or less transverse to the line of light. This form of movement is called diaheliotropism ($\delta\iota\alpha$ = across). In like manner there are three kinds of movements dependent on gravitation, or the attraction towards the earth. When a part of a plant grows straight down towards the earth, we have geotropism ($\gamma\eta$ = the earth). When a part of a plant tends away from the earth, we have apogeotropism ($\alpha\pi o$ = from). And when it tends to place itself transversely to the radius of the earth, diageotropism ($\delta\iota\alpha$ = across). Without pausing at present to inquire into the causes of these various movements, two other terms must even thus early be explained. They are Epinasty and Hyponasty. Epinasty (from $\epsilon\pi\iota$ and *nasco* = I grow) occurs when the upper face of a leaf or allied organ grows more quickly than the lower, and hence the part curves downwards. Hyponasty ($\dot{\upsilon}\pi o$ = under) is the reverse of this, where the lower face of a leaf or allied organ grows more quickly, and the organ curves upwards.

(3) *Nature of the movement.* It is, again, of vital importance that the manner of that movement, which is common to perhaps all plants, should be thoroughly grasped. It is essentially of the same nature as that of the stem of a climbing plant (see page 77). The particular part of a particular plant that is subject to this widely-diffused movement points successively to the north, the east, the south, the west, and back again to the north. Had the movement been quite regular, the apex of the organ that is moving would have described a circle. What actually occurs is that a series of ellipses are described. If the apex be observed at any given moment, and found to be pointing, we will say, due north, it will be seen next to return towards the south, and then again to move forwards to the north. These backwards and forwards movements are not along the same line. They are lines close together, and tracing out long ellipses. Successions of such backwards and forwards movements and successive formations of such ellipses follow. But the axis of each ellipse points to a different point of the compass from

that pointed to by its successor or its predecessor. That is to say, there are a series of backwards and forwards movements along different lines, with description of a series of long ellipses, and also a general slow swing round from north to east, south, west. A double movement, therefore, of the part takes place. This movement is to be named circumnutation (from *circum*, around ; *nuto*, I nod).

(4) *Cause of the movement.* The parts that cause movement are made of cells. Cells upon one particular side of the stem or leaf or branch that is to move become turgescent, that is swollen. Such turgescence occurring in many cells all placed upon one side of an organ will cause the organ to bend away from that side. With the increased turgescence of the cells the greater extensibility of their walls also occurs, and in many cases, as a sequel, there is increased growth of the part. If circumnutation has to take place it is clear that this increased turgescence and its accompanying phænomena must take place first upon one side, and then upon the opposite side, or perhaps still more accurately that the line of increased turgescence must slowly pass around and around the stalk of the leaf or the stem of the flower. So that it is concluded that increased growth first on one side and then on another in many cases, and increased turgescence of cells along lines first on one side and then on another, accompanied by an extensibility of the cell walls are the primary causes of this movement.

(5) *Circumnutation generally.* Apparently every growing part of every plant is continually circumnutating, though of course in many cases on an exceedingly small scale. The root down in the ground, the stem that has climbed up into the air, the leaves that spread forth from that stem, the tiny flower-buds on their minute stalks, and later, when these open, the sepals, petals, stamens, and even the carpels, are all constantly progressing slowly round and round in small circles. And not only is there this general and universal movement, but many parts possess special modification thereof. As these will have to be dealt with in succession let us name and define them.

(*a*) Revolving nutation. The convolvulus as it clambers spirally round and round the wheat stem or the branches of huge shrubs presents this modified form of circumnutation. The great sweeps made by the stems of all climbing plants, and by the tendrils of the vine or the passion flower are due to a mere increase in the extent of the ordinary movement.

(*b*) Leaf movements. This general name is given to those movements by which young leaves assume their normal and most advantageous position. The movements are due to a properly balanced combination of epinasty and hyponasty.

(*c*) Sleep movements. These are the movements by which leaves and flower-leaves also in many cases assume a vertical position at night. The technical name for such movements is Nyctotropic (from νυξ = night, τροπος = direction.)

(*d*) Light movements. The heliotropism and the apheliotropism to which reference has been made above.

(*e*) Gravitation movements. The geotropism and the apogeotropism to which reference has been made above.

(6) *The methods of observation.* It is necessary briefly to describe the plan adopted by the two observers, Charles Darwin and Francis Darwin, in innumerable experiments upon the movements of plants. Stated briefly it was as follows. The plants were grown in pots, either shielded entirely from the light or with arrangement for admitting the light in some particular direction only. A horizontal sheet of glass and a vertical sheet of the same material on one side permitted observation of the plant at the necessary times. A minute glass filament not thicker than a horse-hair and about half-an-inch in length was fixed to the part whose movement was to be observed by shellac dissolved in alcohol. To the thin end of the filament a very small dot of black sealing-wax was fixed, and a card with a black dot was attached to a stick driven into the ground hard by the filament. The observer by shifting his position and careful observation could always at a given moment find a position in which the black dot on the sealing wax and the black dot on the card as viewed through either the horizontal or vertical glass exactly covered each other. Then a spot in indian ink coinciding with their line of position was made on the glass plate. This observation was repeated at short intervals of time and the series of dots of indian ink were joined by straight lines. In this way a tolerably accurate tracing of the movement of the moving part was obtained upon the glass. This tracing was then transferred to paper.

In some cases the sealing-wax tip was discarded and two minute triangles of paper, $^1/_{20}$ of an inch in height, were fixed to the two ends of the glass filament. The indian ink dot was then made on the glass plate at a point corresponding with a line joining the two tips of the paper triangles.

(7) *Nervous action.* The most fascinating part of the book to the ordinary reader and possibly even to the scientific student will be the striking evidence that is adduced as to nervous action in plants. It is difficult as yet to discover any structures that can fairly be called nervous, as far as their histology is concerned, but certain parts of certain organs, however, assuredly have functions not possessed by other parts of the plant, and that it is difficult to call by any other name than nervous functions. For example, it will be shown that with some seedling plants only the upper part is sensitive to light, and that this upper part transmits an influence to the lower causing that to bend. So also the tips of radicles and the tips only are sensitive to stimuli and transmit an influence to the upper part, causing it to bend from or towards the stimulus in different cases. As it is in the possession of a nervous system that animals are popularly supposed to be entirely distinct from plants, all t h evidence in favor of this remarkable nervous action of certain parts of plants will be very welcome to the evolutionist.

CHAPTER XXX.

B.—*Circumnutation.*

B. CIRCUMNUTATION. Turning to the investigation of the general movement known as circumnutation, without at present making any reference to its specialised forms, we have :—

(1) The study of the circumnutation of seedlings or young plants.

(2) The study of the circumnutation of mature plants.

(1) *Circumnutation in seedlings.* This part of the subject will be divided into—(*a*) The plants investigated; (*b*) movements of radicles; (*c*) of hypocotyls; (*d*) of cotyledons; (*e*) of epicotyls; (*f*) the rate at which the movement takes place.

(*a*) The plants investigated. The botanical student of the list given will see that the plants that were selected for observation fairly represent the whole of the vegetable series, with the exception of some of the very lowest Cryptograms. And hence the legitimate inference is that this kind of movement is common to every seedling species.

(*b*) Movement of radicles. Numberless experiments with the primary radicles, or small first roots of plants, demonstrated the fact that all young radicles circumnutate. Consider the value of this constant swing round and round, even on a small scale, of the end of the young root. As soon as ever the tip steals out from the seed it commences to circumnutate, and probably continues to do so, as far as its growing extremity is concerned, as long as growth lasts. This sweeping movement, bringing it into relation to different parts of the soil in which it is, gives it every chance of finding cracks and crevices through which it can make its way. It will be best for it to move in the direction of least resistance, and such direction of least resistance is more likely to be found by a little root persistently changing its position than by one that grows steadily, doggedly downwards. Accompanying the circumnutating movement of the radicle is its own longitudinal and transverse growth. It is not only sweeping round and round. It is elongating and it is expanding. And the force with which young roots elongate and expand is surprising. Thus the longitudinal growth is sufficiently vigorous to cause a downward pressure equal to lifting, in the course of twenty-four hours, a weight of a quarter of a pound, while the force exerted transversely by a growing radicle was experimentally shown to be able, in the course of six days, to make a fissure in a piece of wood, through a hole in which the radicle passed, that required a weight of 8lb. 8oz. for its formation when the radicle was absent. The secondary radicles, that is, those given off from the primary root, were shown by experiment to possess the movement of circumnutation.

(*c*) The hypocotyl. The hypocotyl, it will be remembered, is the part of the young stem lying between the radicle, or rudimentary root below, and the cotyledons, or first seed leaves above. The first notable peculiarity of this part of the plant is that it always breaks through the ground in the form of an arch. As many organs of different kinds besides the hypocotyls are also arched when they break through the ground, it is evident that this form must be of much value to the plant. It is of value because the young and more tender parts of the hypocotyl are thus saved from pressure and injury whilst breaking through the ground, and as both legs of the arch, which is shaped like an inverted V, are growing simultaneously, its crown is pushed up through the earth with twice as much force as if they were unarched. Indeed, the force with which a hypocotyl grows upwards is astonishing. Under the study of the epicotyl we shall mention an experiment that determined the force of archgrowth, as seen in the common bean. All the time that the arched part of the stem known as the hypocotyl is growing out of the ground it is circumnutating, and this last movement cannot fail to aid the part in breaking through and struggling out of the ground, especially if the soil be damp and soft.

(*d*) Cotyledons, or first leaves. The movements of these parts of the plants are more easily observable than those of either the radicle or the stem. We will take but one case. One of the Convolvulus order had a cotyledon that in the course of 16 hours 20 minutes moved up and down no less than 13 times. And this movement, it should be observed, was entirely independent of the supporting hypocotyl. The chief seat of the movement is in the lower or basal part of the cotyledon, that is, the part nearest to the stem whence it springs. The movement is constant, and is chiefly in a vertical plane. It was observed in 153 genera. Whilst the movement is constant throughout the day and night, about 4 or 5 in the afternoon there is in all cases a special rise of the cotyledons towards the stem that supports them. This our observers called the "great nocturnal rise." The movement is not governed so much by the actual amount of light that falls upon them as by change in the intensity and degree thereof.

In the movements of the cotyledons of many plants a structure known as the pulvinus (from *pulvinus* = cushion) is concerned. The leaf stalks or petioles of the leaves of *Oxalis sensitiva* and that of the Sensitive plant, *Mimosa pudica*, present this structure. It is an enlargement at the summit of the petiole, just ere that organ expands into the blade or lamina, with convex outline and a structure wholly of colorless, not green cells. It results from the "growth of the cells over a small defined space of the petiole being almost arrested at an early age." The movements of cotyledons gifted with pulvini depends upon the cells on one side of the pulvinus expanding more quickly than those upon the other side of the organ. When cotyledons destitute of pulvini move, the fact of growth being alternately more rapid on one side of the petiole than on the other, is the cause of motion.

(*e*) Epicotyl. The part of the stem above the point of insertion of the cotyledons circumnutates like its companions. After the manner of the hypocotyl or lower portion of the stem, the epicotyl is at first arched and possesses, therefore, from its shape and its power of circumnutation, the advantages in regard to escape from the ground that belong to the hypocotyl. The force wherewith young stems thus struggle from the soil up into the free light and air, may be gathered from an experiment on the epicotyl of the Bean. This in one plant grew upwards with sufficient force to be able to lift a weight of twelve ounces.

(*f*) Rate of movement. The speed with which parts that are circumnutating travel, was in certain cases estimated by observing them under the microscope, as their delicate apices traversed the divisions of a micrometer graduated to five-hundredths of an inch. A radicle thus watched was making way at the rate of 1-50th of an inch in 45 minutes. A cotyledon of a grass accomplished 1-100th of an inch in 22 minutes 5 seconds, and that of a cabbage, whose total oscillation backwards and forwards whilst journeying in any given direction was between 1-500th and 1-250th of an inch, passed over 1-50th of an inch in 6 minutes 40 seconds.

(2) *Circumnutation in mature plants.* The universal movement does not cease as the young plants grow older. It is to be seen in mature plants also. In these also the movement is not confined to one organ or part. It affects all. Circumnutation occurs (*a*) In stems. Here it will be best to mention the plants whose stems are known to swing steadily round, to discuss the amount of stem-circumnutation, to refer to special stem organs which, retaining the morphological character of the stem, retain also the momentous physiological character wherewith we deal.

(i.) Plants observed:—Iberis umbellata, Brassica oleracea, Linum usitatissimum, Pelargonium zonale, Tropæolum majus, Trifolium resupinatum, Rubus idæus, Deutzia gracilis, Fuchsia, Cereus speciocissimus, Hedera helix, Gasania ringens, Azalea Indica, Plumbago Capensis, Aloysia citriodora, Verbena melindres, Ceratophyllum demersum, some Coniferæ, Lilium auratum, Cyperus alternifolius. The number and widely different natures of the orders that have plants whose stems move, and the fact that no plant that has been observed does not move, yield a fair inference that the stem-movement is very general.

(ii.) Amount of movement. Taking but one case, that of Ceratophyllum, the stem was found to move through an angle of more than 200° in six hours and in one instance through 220° in three hours.

(iii.) Modified stems. It is very interesting to observe that when the stem of a plant is modified in position, in structure and to some extent in function, the great function of circumnutation is not lost. (*a*) Stolons. These are long offshoots from the ordinary upright stem that run horizontally along the ground and rooting at some distance from the parent plant send up aerial stems in their turn. The strawberry furnishes an illustration of this kind of stem. Stolons circumnutate. One belonging to a Saxifrage moved as to its apex in twenty-five hours through a distance of $\frac{3}{4}$ of an inch.

β. Flower-stalks. These modifications of stems whilst they are in a growing state perform movements and the movement is not confined to the main flower-stalks. It is seen also in the secondary ones.

(*b*) In leaves. (i.) Plants observed:—Sarracenia purpurea, Glaucium luteum, Crambe maritima, Brassica oleracea, Dianthus caryophyllus, Camellia Japonica, Pelargonium zonale, Cissus discolor, Vicia faba, Acacia retipoides, Lupinus speciosus, Echeveria stolonifera, Bryophyllum calycinum, Drosera rotundifolia, Dionæa muscipula, Eucalyptus resinifera, Dahlia, Mutisia clematis, Cyclamen Persicum, Allamanda Schottii, Wigandia, Petunia violacea, Acanthus mollis, Cannabis sativa, Pinus pinaster, Pinus austriaca, Cycas pectinata. Thirty-three genera belonging to twenty-five widely different orders present to us circumnutating leaves. Once more, as the leaves observed circumnutate, as none of them did not possess this property, the inference is fair that all leaves of all plants move.

(ii.) Rate of movement. A cabbage-leaf was observed. Its apex moved through an angle of 10° in twenty-four hours, the actual distance traversed in the time being, up and down, $^4/_5$ of an inch.

(*c*) Other parts. (i.) Stamens. In Cereus, one of the Cactus order, Morren has noticed a movement apparently circumnutatory. (ii.) The column formed by the one stamen and the gynœcium of a certain Orchid, the Stylidium, circumnutates. (iii.) Even the Cryptogamia, that cannot be truly said to have actual leaves, show the movement. The fresh-water Alga, Oscillatoria describes a circle in every forty seconds. Spirogyra moves in two and a-half hours four times in one direction, thrice in the opposite. The fungi called Moulds apparently circumnutate. In the highest therefore and in the lowest of plants this strange movement, so full of potentialities of development in many useful ways, is exhibited.

CHAPTER XXXI.

C.—*Modifications of Circumnutation.*

C. MODIFICATIONS OF CIRCUMNUTATION. Whilst all parts of all growing plants are circumnutating, certain parts of certain plants have certain special movements known by special names. Each and all of these diverse movements would appear, however, to be derived from the primordial, simple, universal form already dealt with.

(1) *Revolving nutation.* This is the form of specialised circumnutation encountered in climbing plants. The main difference between it and the more general form of motion is the greater extent of the sweep of stem or branch in the climbing plant. No need is there of micrometers and microscopes to watch it, nor even of glass plates and glass filaments, and sealing wax, and indian ink dots. So greatly is the amplitude of the movement increased, that the most casual observer notices the great alteration in position of the Clematis or the Passion-flower. In my analysis of the Climbing-plants I have presented the results of Charles Darwin's observations on revolving nutation, and therefore no more need here be said than that to our two experimentalists all the movements of climbing plants are modified circumnutation.

(2) *Epinasty and hyponasty.* These processes especially affect leaves. The upper or the under surface of these organs at times grows more rapidly than the under or the upper surface. Hence curving downwards or curving upwards of the leaf. An opening leaf-bud is an instance or is a multitude of instances of epinasty. At first all the tiny, green things are closely crowded together and nearly erect. Then one by one, as their upper surfaces grow more rapidly than their under, they curve slowly outwards and away from each other, seeking the sunshine. Instances of these

growth methods in leaves and in other organs are innumerable, but in all cases the movements resulting are from their nature and their effects evidently but modifications of circumnutation.

(3) *Nyctotropism.* The sleep of leaves. Our authors do not employ the term "sleep" or the more technical word "nyctotropism" unless the movement of the leaves is sufficiently marked to be distinguishable from the constant day movement already described. Unless the leaves at eventide move upwards towards the vertical position or downwards from the horizontal through an angle of at least 60°, they are not called nyctotropic. We shall deal with the position assumed, and the advantages accruing therefrom, the experiments that were made, the plants investigated.

(*a*) Position and its advantages. The blade of sleeping leaves is nearly or quite vertical at night and in many cases the upper faces of contiguous leaves are opposed. As the constant fact is only that the blade stands approximately vertical, the apex or the base or either edge of the leaf may look zenithwards. This position is assumed as the result either of alternation of turgescence on opposite sides of pulvini or of growth alternately preponderating on one side and then on the other of the petiole or midrib. The great advantage to the plant of this assumption of an erect position by the leaves at night is the protection of the upper surface from evaporation and radiation at a time when the sun being below the horizon, no compensation in the way of heat-return is possible. That this protection from radiation is of great moment, the experiments demonstrate.

(*b*) Experiments. Certain leaves of certain plants were compelled by the aid of pins and the like human contrivances to remain in a horizontal or day position during the nighttime. Whilst other leaves were allowed to assume their normal nocturnal position, the former were exposed to a temperature of 4° on a March night. And in the morning all the leaves which were pinned opened were killed, whilst only one-third of those that had not been interfered with were injured.

(*c*) Examples. (i.) Of cotyledons that sleep. The cotyledons of the following plants have been observed to rise or sink at night to an angle of at least 60° above or beneath the horizon :—Brassica oleracea, Brassica napus, Raphanus sativus, Githago segetum, Stellaria media, Anoda Wrightii, Gossypium, Oxalis rosea, Oxalis floribunda, Oxalis articulata, Oxalis Valdiviana, Oxalis sensitiva, Geranium rotundifolium, Trifolium subterraneum, Trifolium strictum, Trifolium leucanthemum, Lotus ornithopodioides, Lotus peregrinus, Lotus Jacobæus, Clianthus Dampieri, Smithia sensitiva, Hæmatoxylon Campechianum, Cassia mimosoides, Cassia glauca, Cassia florida, Cassia corymbosa, Cassia pubescens, Cassia tora, Cassia neglecta, Cassia (three other Brazilian unnamed species), Bauhinia, Neptunia oleracea, Mimosa pudica, Mimosa albida, Cucurbita ovifera, Cucurbita aurantia, Lagenaria vulgaris, Cucumis dudaim, Apium petroselinum, Apium graveolens, Lactuca scariola, Helianthus annuus, Ipomœa cærulea, Ipomœa purpurea, Ipomœa bona-nox, Ipomœa coccinea, Solanum lycopersicum, Mimulus, Mirabilis jalapa, Mirabilis longiflora, Beta vulgaris, Amaranthus caudatus, Cannabis sativa. Altogether we have 153 genera observed, and of these 30 genera belonging to 16 families undergo a movement that is of sufficient extent to be called nyctotropic. Out of the 30, 24 presented the rising movement. We must hence opine that the sleep of cotyledons, whilst not universal, is fairly general. ii. Of leaves. In this connexion we may mention (α) the plants whose leaves sleep, (β) the method of their sleep, and (γ) the rate of movement. (α) The plants whose leaves are known to undergo the sleep movement are:—Githago, Stellaria, Portulaca, Sida, Abutilon, Malva, Hibiscus, Anoda, Gossypium, Ayenia, Triumfetta, Linum, Oxalis, Averrhoa, Porlieria, Guaiacum, Impatiens, Tropæolum, Crotolaria, Lupinus, Cytisus, Trigonella, Medicago, Melilotus, Trifolium, Securigera, Lotus, Psoralea, Amorpha, Dælea, Indigofera, Tephrosia, Wistaria, Robinia, Sphærophysa, Colutea, Astragalus, Glycyrrhiza, Coronilla, Hedysarum, Onobrychis, Smithia, Arachis, Desmodium, Urania, Vicia, Centrosema, Amphicarpæa, Glycine, Erythrina, Apios, Phaseolus, Sophora, Cæsalpinia, Hæmatoxylon, Gleditschia, Poinciana, Cassia, Bauhinia, Tamarindus, Adenanthera, Prosopis, Neptunia, Mimosa, Schrankia, Acacia, Albizzia, Melaleuca, Ænothera, Passiflora, Siegesbeckia, Ipomœa, Nicotiana, Mirabilis, Polygonum, Amaranthus, Chenopodium, Pimelia, Euphorbia, Phyllanthus, Abies, Thalia, Maranta, Colocasia, Strephium, Marsilea. (β) Concerning the method of this movement, of course the blades are placed in a position quite or nearly vertical. And this is usually affected by the rotation of the plane of the blade of the leaf. That rotation is effected either through the agency of a pulvinus or aggregate of small colorless cells, the pulvinus becoming alternately more turgescent on nearly opposite sides, or it is effected by the increased turgescence and increased growth on the opposite sides of the petioles destitute of a pulvinus. This nyctotropic movement is strikingly affected by external conditions. Thus the movement is delayed or fails if the ground is too dry. A definite temperature is necessary for it. Thus French plants, according to Rouer, do not sleep if the temperature falls below 5°. The violent agitation that follows from a strong wind prevents sleep, and, above all, unless the leaves are well illuminated during the day, they are not likely to sleep at night. This last fact shows us again that the important consideration is the change of intensity in the light. It is not so much the amount of light as the relative amount at different times that determines the movement. (γ) Rate of movement of *Oxalis acetosella.* The ordinary wood sorrel completed two ellipses at the rate of 1·25 per hour ; *Marsilea quadrifoliata*, at the rate of one in 2 h.; *Trifolium subterraneum*, in 3 h. 30 m.; and *Arachis hypogæa*, in 4 h. 50 m. (δ) The study and history of these nyctotropic or sleep movements compel us to believe that they are but especial modifications of circumnutation that are of distinct advantage to the plant, inasmuch as they prevent radiation from the upper surface of the leaves during the night-time, a time at which no compensating heat supply is derivable from the sun.

(4) *Movements due to light.* (*a*) Kinds of movement. These are heliotropism, movement towards the light ; apheliotropism, movement from the light; diaheliotropism, in which parts of plants place themselves transversely to the direction of the light (the transversal heliotropismus of Frank) ; paraheliotropism, a movement by which leaves exposed to more light than is good place themselves so as to be less intensely illuminated. This is the day sleep of plants. All these four kinds of movement differ essentially from the nyctotropic movements previously studied in that they depend upon the direction of the light, whilst the periodic movements noticed in sleeping plants depend upon the intensity of the light, and have no relation to its direction.

(*b*) Heliotropism. Studying the cases in which a plant bends, and then continues to move towards the light, it is necessary to mention—(i.) The plants that were investigated.— Beta vulgaris, Solanum lycopersicum, Apios graveolens, Brassica oleracea, Phalaris Canariensis, Tropæolum majus, Cassia tora. These only represent a few of the plants on which experiments were made. Heliotropism really obtains most extensively amongst the higher plants. There are extremely few whereof some part, be it stem, or leaf-stalk, or flower-stalk, does not bend towards a stream of light. Two interesting exceptions to the nearly universal heliotropism are worthy of recordal. They are insectivorous plants and tendril-bearing plants. But the insectivorous plants do not live upon carbon dioxide. Now it is known that the agency of light is essential for plants that feed upon carbon dioxide and decompose that gas whilst retaining its carbon. As the insect-eating plant does not feed upon the gas, little good would have resulted were it heliotropic. Again, had tendril-bearing plants been heliotropic, movement towards the light would have frequently resulted in their being drawn away from their supports.

(ii.) Modified circumnutation. Heliotropism and circumnutation graduate the one into the other, and the ordinary view that they are two distinct kinds of movement, will probably have to be abandoned by those that study the book of the two Darwins. For against this ordinary view that heliotropism and circumnutation are essentially distinct we have (α) The fact that a bright lateral light should stop circumnutation. Such a bright lateral light induces the plant to grow straight towards it, and, therefore, if the two movements are distinct from the other, puts a stop to circumnutation. (β) Only a lateral light would have this remarkable power, for plants lighted from above do continue to circumnutate. (γ) In the life of every plant, circumnutation precedes heliotropism, for stems and leaf-stalks are circumnutative in the darkness of the earth before any light falls upon them.

(*c*) Apheliotropism. A rare movement. Only two cases were observed, those of *Bignonia Capriolatus* and *Cyclamen persicum*.

(*d*) Diaheliotropism. The best illustrations of this assumption of position are afforded by young seedlings, whose first plant leaves are generally extended horizontally, and thus place their upper surfaces at right angles to the light. The student who will take the trouble to look at the leaves of all trees will be struck with the pertinacity with which the leaves under very unfavorable circumstances yet attempt to arrange themselves in the like horizontal position.

(*e*) Paraheliotropism. This occurs in certain plants when the sun shines too brightly upon them. The leaves change their position and present their edges to the light. Apparently, this is dependent upon the fact that the green color matter or chlorophyll of leaves is apt to be injured by too intense a light. The experiments of Weissner on the young leaflets of Robinia, our ordinary Acacia, show the importance of paraheliotropism. He fixed certain leaflets in such a position that they were intensely illuminated and unable to get away from the sun. In the course of two days they suffered exceedingly, whilst other leaflets that had not been interfered with, were in very good health.

(5) *Movements due to gravitation.* (*a*) Divisions. These are geotropism, when the plant bends towards the earth; apogeotropism, when it bends from the earth; diageotropism, when it assumes a position horizontal in respect to the earth.

(*b*) Geotropism. This movement is almost confined to roots. The ordinary root of an ordinary plant is largely affected by geotropism, and is thus directed steadily down into the ground. Aerial roots, that is, roots given off from the stems outside the ground, are in many cases under the like influence, but not in all, the Ivy to wit. With the exception of the roots, however, but few organs can be found showing movement due to geotropism. The seed capsules of one or two members of the order Leguminosæ are buried in the ground as the result of geotropism of their flower stalks. The *Trifolium subterraneum*, a species of clover, and the *Arachishypogœa* or ground nut, both present this remarkable phænomenon. In the latter case the pod has been observed to be buried in the ground to the depth of an inch, and this is effected by the curving over and growth downwards towards the earth of the stalk supporting the gynœcium. This is a movement of geotropism.

(*c*) Apogeotropism. A far more frequent movement than the former, and far more extensive. The hypocotyl of the Beet in 3 hours 8 minutes passed through an angle of 109° in a direction away from the earth.

(*d*) Diageotropism. No experiments were made upon this by our observers, and the statement that this movement actually exists, is based upon the researches of Frank.

Finally, we may conclude that the three kinds of movement dependent upon the action of gravitation, consist once again of modified circumnutation.

CHAPTER XXXII.

D.—*Nervous Action.*

D. NERVOUS ACTION IN PLANTS. Despite the fact that multitudes of the lower animals showed no trace of a nervous structure, and many of them no trace of nervous function, one of the distinctions between vegetables and animals most insisted upon aforetime was the absence of nervous energy in the former, and its presence in the latter. The experiments of Charles and Francis Darwin establish the fact that plants have nerve-energy.

Reducing nervous function to its simplest form, leaving out of consideration all complex and specialised structures, such as spinal cords and brains, and considering only nerve-fibres and nerve-cells in their simplicity, we find nervous structures are responsive to stimuli: we find they are sensitive: we find they have to do with movement: we find they have the power of transmitting energy. The nerve ends in the skin of an animal, are responsive to stimuli, *e.g.* of the prick of the pin. Certain of the nerve-fibres transmit to nerve-centres more internally placed, and consciousness of the external stimulus results. Energy may then flow down other nerve-fibres ending in certain muscles and thus these last be stimulated to contraction. Now, in plants all these phænomena are encountered. It will be shown that parts of plants are sensitive to stimuli, that from them transmission of influence to a distance takes place, that sensitiveness and movement occur.

In the treatment of this subject the following divisions of it will be studied: Facts; Effect of Pressure on the tips of radicles; of Caustic; of Cutting; of Moisture; of Geotropism; Secondary Radicles; Pressure above the apex of the radicle; Effect of Heliotropism; Coordination.

(1) Facts. Radicles growing in the ground encounter stones, roots, a score of obstacles. Radicles are sure to meet

with opposition, and this opposition they have to surmount. Experiments were made on the growing roots of plants. As result it was found that the delicate cap of the root when first it touched any opposition surface underwent a slight transverse flattening. This transverse flattening soon became oblique, and in a few hours was seen no more. By that time the apex was pointing at right angles to its original direction, and the radicle gliding along over the opposing surface in a new direction. Further, it was not the touched apex of the radicle that curved. A length of 8 to 10 millimetres ($^8/_{25}$ to $^2/_5$ of an inch) became curved. These facts (verified times and again) have to be explained. Three explanations offer.

(*a*) That the curvature is due to mechanical resistance to the growth of the radicle in its original direction. The objections to this are: (i.) The radicles have not the aspect of organs that have been subjected to pressure enough to account for the curvature. (ii.) The growing part just within the apex of the radicle is more rigid than the non-growing part above. Hence the latter ought to have yielded and curved, not the former. (iii.) An object yielding with the greatest ease serves to deflect the radicle.

(*b*.) That pressure checks the growth of the apex, and growth only continuing on one side, the radicle becomes rectangularly bent. But this does not explain the curvature affecting parts so far from the apex as 10 millimetres.

(*c*.) That the apex is sensitive to contact, and thence is transmitted influence to the upper part of the radicle. This upper part is thus stimulated to bend *away from* the touching object.

The plants upon the radicles of which experiments were made were *Vicia faba* (Common bean), *Pisum sativum* (Pea), *Phaseolus multiflorus* (Scarlet Runner), *Tropæolum majus* (Indian Cress), *Gossypium herbaceum* (Cotton), *Cucurbita ovifera* (Cucumber), *Raphanus sativus* (Radish), *Æsculus hippocastanum* (Horse-chestnut), *Quercus robur* (Oak), *Zea mays* (Maize).

(2) Effect of pressure on the radicles. When one side of the apex of a young radicle is pressed by any object, the growing part bends away from that object. This would seem to be an excellent adaptation for avoiding obstacles in the soil, and moving along a line of least resistance. We

must carefully notice that the apex only is touched, for if the pressure be applied a little above the apex, the bending is like that of a tendril towards the touching object. Studying this bending away from pressure when that pressure is applied to the apex we shall speak of the experiments, the effect of temperature, the discriminative power of the radicle, and the struggle with geotropism.

(*a*) Experiments. 55 radicles were treated in the following way. Little squares or oblongs of card were fixed to their conical tips by shellac. The seeds whence the radicles protruded were pinned inside the cork lids of glass vessels half-filled with water. All light was excluded. Careful observation was then made for the purpose of seeing if the radicles had worked straight down, or had bent in one direction or another. Out of 55 dealt with, 52 were bent often considerably from the perpendicular, and invariably away from the side to which the piece of card was attached. Exceedingly small pressure will determine their movement. A weight of matter less than ·32 milligrammes—about $\frac{1}{2000}$ of a grain, in two cases sufficed to excite movement.

(*b*) Temperature. The sensitiveness of the radicle, like all other functions of living beings, is only possible within certain ranges of temperature. A temperature rather above 21° C. destroys the sensitiveness of the radicles. Pieces of card placed on radicles when the temperature was higher than this, produced no effect whatever. Clearly the natural temperature of the earth in the early spring when radicles are busy, would not be so high as 21° C. The experiments reveal the fact that the most favorable temperature for the sensitiveness of the radicle is between 13° and 15°.

(*c*) Discrimination. Not only does the part above the apex of a radicle undergo movement when the apex is stimulated, but the latter remarkable organ has an extraordinary power of discriminating between two pressures. When a square of sanded paper and a square of paper so thin that it was not adapted for writing purposes, of the same size —about 1-20th of an inch—were fixed on opposite sides of the bases of 12 radicles, in almost all cases the radicle bent from the side with the sanded paper. The relative thicknesses of the two pieces of paper were between ·15 and ·2 millimetres in the case of the one, and ·045 millimetres in the other. Here then is evidence that the apex of the radicle has the capacity to discriminate between thin card and very thin paper, and so transmit influence to one side only of the upper part of the radicle.

(*d*) The struggle with geotropism. Experiments were made in the following manner. Eight beans were so placed that their radicles extended horizontally. Hence geotropism or the growth towards the earth would come into play. Eight other radicles placed in a like position were also treated as the radicles spoken of above; little pieces of card were fixed to the lower sides of their tips. The stimulus due to the cards would cause the radicles to curve upwards, that is, in the opposite direction to the geotropic movement; but in these cases before the expiration of twenty hours, seven out of the eight were bending downwards towards the centre of the earth. The cards seemed to have produced no effect. Geotropism had easily won the battle. In a second experiment three radicles with squares fixed to one side of the apex were suspended vertically. The stimulus of the squares tended to make them move from the vertical line, geotropism tended to keep them in the vertical line. But in this case within nine hours the radicles had bent considerably out of the vertical. Here then geotropism was defeated in the struggle, and the stimulus due to the pressure of the squares had triumphed. But in these two sets of cases it will be observed that whilst the action of the pressing card is constant that of geotropism varies. For in the first case with horizontal radicles geotropism acts on the radicle at right angles, whilst in the second case geotropism acts at a very oblique angle, and therefore at a disadvantage. It is concluded in consequence that the power of an irritant on the apex of a radicle is inferior to that of geotropism when the latter acts at right angles to the radicle, but is superior to that of geotropism when the latter acts obliquely on the radicle.

(3) Effect of caustic. Dry caustic or nitrate of silver was used to irritate one side of the apex upon fifteen radicles. There was evident proof that the radicles bent away from that side of the apex which had been irritated by the caustic.

(4) Effect of cutting. Exceedingly delicate slices were removed from the radicle, the cutting being made parallel to the sloping sides of the apex by aid of a razor.

Out of eighteen radicles thus treated 14 bent away from the cut surface.

(5) Effect of moisture. A few years ago the great German botanist Sachs showed that the radicles of young plants bend towards the side where moisture is. The Darwins arranged certain sieves containing seeds germinating in damp sawdust in such a position that the base of each sieve was at an angle of 45° with the horizon. It is plain that had geotropism alone acted the radicles would have grown perpendicularly down. But it was found that they grew persistently towards the damp sawdust in the sieve. They were deflected as much as 50° in many cases from the perpendicular. The tips of a number of radicles of the bean were covered with grease so that it was impossible for moisture to act upon them. These greased radicles in scarcely any cases curved towards the damp sawdust, and this was to be expected as the effect of the moisture could not possibly be transmitted through the grease covering.

(6) Of geotropism. The effect of geotropism is in nature as a nervous effect. The sensitiveness to gravitation appears localised in the apex of the radicle, and there is undoubted transmission to the upper regions of that organ. Radicles that had been left extended horizontally for some time were placed before they had begun to bend downwards in a vertical position and their bases cut off, and yet very shortly they bent as if still acted upon by geotropism. This would seem to demonstrate that some influence had been already transmitted to the bending region from the apex before the latter was amputated. That the action of geotropism is upon the apex was further shown by the removal of the tips of twenty-nine radicles and the after placing of them in a horizontal position. They did not become geotropic. Unmutilated radicles bent under the action of geotropism in eight or nine hours, but these whose apices had been removed were distinctly not affected by the attraction of the earth.

(7) Secondary radicles. The tips of secondary radicles are also sensitive to contact. Further they are sensitive to geotropism, but geotropism does not make these secondary radicles bend vertically down. The line of direction assumed by secondary radicles is a sub-horizontal one, somewhere

intermediate between a completely horizontal and a completely vertical line. This is the normal position of the secondary radicle, but if the primary be removed accidentally or designedly one of the nearest secondary radicles proceeds to grow perpendicularly down and to take the place of the primary. This is akin to what is frequently observed with the shoots of trees. If the main shoot be destroyed a lateral one will generally take its place, growing in a vertically upright direction instead of a sub-horizontal one.

(8) Pressure above the apex. All the experiments narrated and reasoning worked out thus far have had to do with stimulus applied to the actual apex. Whether the stimulus be that of contact, or of caustic, or of cutting, the influence transmitted to the upper part of the radicle has always been of such a nature as to make the apex bend *from* the source of irritation. But if any pressure be applied at the distance of a few millimetres *above* the apex the action is as that of a tendril and the radicle bends *towards* the touching object.

(9) Heliotropism. We have seen that the apex is sensitive to pressure, that the apex is sensitive to the action of the earth. When we turn to the consideration of the cotyledons, which are affected by light rather than by gravitation, we shall find kindred phænomena. There also the sensitiveness is localised—localised in the upper part of the cotyledons; its effect is transmitted to the lower part, nearer the main axis of the plant, and that part bends. It is beautiful to see the striking evenness in the action of stimuli upon radicles, upon cotyledons, upon leaves. The apex of the cotyledon and the tip of the leaf are the sensitive parts. From these is transmitted influence to parts at a distance from the apex, and these last, under that influence, undergo movement that affects the apex in its turn. It is almost impossible to fail in these instances to see the similarity to reflex action in animals. Reflex action is action resulting from an external stimulus and unattended with sensation, and in these cases there is an external stimulus of light or of contact acting upon a part of an organ. Its effect is transmitted up to another part of that organ. That effect is then—if I may use the phrase—reflected back to certain parts that move.

Here once again it is not the amount of light which determines the degree of movement of any part of a plant. It is the amount of change that affects this, and so is it in many instances in animals. The retina of the eye cannot perceive a dim light after it has been exposed to a bright one, and plants which have been kept in the daylight do not move so rapidly towards a faint lateral light as do others which have been kept in complete darkness.

Yet one final parallelism. The retina of the eye, after being stimulated by a bright light, feels the effect thereof even when the light has ceased, and so plant-leaves which have been moving under the action of light continue to move for some time after the light has ceased.

(10) Co-ordination of movements. Surveying all the different causes that will result in movement of the radicle of a young plant, growing in the ground, it is not difficult to picture to ourselves how they all work together for good. When the primary radicle first comes from the seed, geotropism guides it vertically downwards, and the capacity to be thus acted upon resides in its apex. But the secondary radicles that branch off from that primary one are acted on by geotropism so that they only bend obliquely downwards or in a slanting direction. Had the action of geotropism been identical on the main root and on its branches, we should have a bunch of roots all huddled up together. The tertiary radicles, or those given off by the secondary, are not influenced by geotropism at all. They spread themselves abroad in the structure of the earth in every direction. Meanwhile with all this downward growth there is circumnutation. The ends of the primary and secondary radicles are slowly revolving round and round. It is just possible that such movement may aid them in penetrating the ground, but this help could be but of the slightest. The real value of it is that as the tip is always endeavoring to bend to all sides, it will press on all sides, and as its discriminative power for different pressures is exceedingly marked, it will move constantly in the direction of less resistance by bending from the harder soil towards the more friable. So also where there is difference in amount of moisture, the sensitiveness of the apex of a radicle will come into play. It will bend towards the more moist region of the soil. And finally, as the direction taken by the apex of the root determines the whole course of the root, it is of the utmost

importance that that apex should pursue from the first the direction of most advantage to the plant. This desirable result follows from the fact that the sensitiveness to geotropism, the sensitiveness to contact, and the sensitiveness to moisture all reside in the tip.

CHAPTER XXXIII.

E.—*Conclusion.*

TAKING a retrospective survey of this, the last of Darwin's botanical works, and, indeed, at the present the absolutely last from his pen, we see (1) That all growing parts in all plants are continually circumnutating; (2) That the various movements known as heliotropism, geotropism, nyctotropism, movements of twining plants are but modifications of the universal circumnutation; (3) That the influence which modifies circumnutation may be transmitted after the fashion of nervous influence from one part to another. (1) We may extend the survey of the life-history of the root that was made a page or so further back to the life-history of the plant as a whole. Whilst the radicle is stealing out of the seed, anon circumnutating in the ground, and by its sensitiveness to various stimuli is penetrating the ground, now in one direction and now in another, but always along the line of least resistance, the stem is also breaking through the seedcoats. Generally the hypocotyl struggles out, but if the cotyledons or first seed leaves are to remain under ground, it is the epicotyl which breaks forth. Always are these organs arched at first, and thus twice as great pressure in the upward struggling is possible. These arched stem organs are circumnutating before they break through the ground and after. Upon the arch apogeotropism and heliotropism are both acting, the former directing the seedling blindly upwards, heliotropism guiding the stem through any crack in the soil, or through the interstices of entangled vegetation towards the light. As the stem arch grows upwards the cotyledons are drawn out of the ground. The swelling of these organs casts off the seedcoats, and now the cotyledons, bathed in the air and the sunshine, assume the function of leaves, and feed upon carbon dioxide. The hypocotyl is strengthened and the cotyledons are fully expanded. Both hypocotyl and cotyledons are swinging slowly round above ground, and now the stem grows up and leaves appear upon its sides. The branches outspread from the axils of these leaves, and the stem, leaves, and branches are all circumnutating. So indeed is every shoot, every leaflet, every flower-stalk, and hence from the stem, high climbing towards the sunshine, to the minute rootlets deep down in the darkness, all parts are moving through small ellipses or circles continually.

(2) The modifications of circumnutation are epinasty or hyponasty, wherein the upper or the lower surface of organs has excessive growth, the movements of climbing plants in which the extent of the circumnutation is largely amplified, the nyctotropic movements of leaves, of cotyledons whose result, attained by various means, is that the blade at night time is so placed that but little radiation from its upper surface occurs, the heliotropic movements due to the action of a lateral light, with their division into heliotropism, growth towards the light, apheliotropism, growth from the light, diaheliotropism, where the leaves place themselves transversely to the light, paraheliotropism, where the edges are directed towards the light, and lastly geotropic movements with divisions of similar nature to those just given under the light movements.

(3) Nervous action. Finally the most striking revelation of all those made in the series of experiments on the movements of plants is that of the resemblance between those movements and the reflex actions of animals. In the plant movement and in the animal movement a very small stimulus is sufficient. The habit of movement is transmitted from plant to plant and from animal to animal. The sensitiveness is localised. There is transmission of influence from the excited part to another part at a distance, and there is movement of this last part. It is hardly going too far perhaps to say that the tip of the radicle with its extreme sensitiveness, and its power of directing movements of distant parts acts in a fashion similar to the brain of a low animal. Assuredly it is not too much to say that it acts in a fashion similar to that of the spinal cord of some of the higher animals.

(4) Personal characteristics. Once again the loving patience of the experimenter shines out strongly in this work,

and it is evident that the care and perseverance which have made notable the elder naturalist have descended to the younger. The precautions taken against prejudiced observation are in some instances almost amusing. The directions of curvatures of radicles were noted before the record as to the method in which they had been treated was consulted, so that no wish as to the result of an experiment might be father to the thought

(5) Gradations. In this book as in the others occur many examples of the gradations that are the consequences of the working of evolution. One would think that roots and leafstalks were sufficiently distinct from each other, and yet when the radicle of an Ipomœa was cut off and the cotyledons planted they emitted roots from their bases and the petioles were enlarged into little tubers in exactly the same fashion as an ordinary radicle would have been. The nyctotropic movements of leaves are in some cases exceedingly complex, in others exceedingly simple; but there is every gradation between the most simple and the most complex in the kingdom of plants. So also with the heliotropic movements. On page 436 we read:—

"We have therefore many kinds of gradations from a movement towards the light, which must be considered as one of circumnutation very slightly modified and still consisting of ellipses or circles,—through a movement more or less strongly zigzag, with loops or ellipses occasionally formed,—to a nearly straight, or even quite straight, heliotropic course."

And lastly the gradual evolution of this same heliotropic movement out of the ordinary circumnutation is not difficult of observation:—

"First, we have a succession of ellipses with their longer axes directed towards the light, each of which is described nearer and nearer to its source; then the loops are drawn out into a strongly pronounced zigzag line, with here and there a small loop still formed. At the same time that the movement towards the light is increased in extent and accelerated, that in the opposite direction is lessened and retarded and at last stopped. The zigzag movement to either side is likewise gradually lessened, so that finally the course becomes rectilinear."