ON THE

MOVEMENTS AND HABITS

OF

CLIMBING PLANTS.

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I WAS led to this subject by an interesting, but too short, paper by Professor Asa Gray on the movements of the tendrils of some Cucurbitaceous plants*. My observations were more than half completed before I became aware that the surprising phenomenon of the spontaneous revolutions of the stems and tendrils of climbing plants had been long ago observed by Palm and by Hugo von Mohl†, and had subsequently been the subject of two

* Proc. Amer. Acad. of Arts and Sciences, vol. iv. Aug. 12, 1858, p. 98.

† Ludwig H. Palm, Ueber das Winden der Pflanzen; Hugo von Mohl, Ueber den Bau und das Winden der Ranken und Schlingpflanzen, 1827. Palm's

memoirs by Dutrochet*. Nevertheless I believe that my observations, founded on the close examination of above a hundred widely distinct living plants, contain sufficient novelty to justify me in laying them before the Society.

Climbing plants may be conveniently divided into those which spirally twine round a support, those which ascend by the movement of the foot-stalks or tips of their leaves, and those which ascend by true tendrils,—these tendrils being either modified leaves or flower-peduncles, or perhaps branches. But these subdivisions, as we shall see, nearly all graduate into each other. There are two other distinct classes of climbing-plants, namely those furnished with hooks and those with rootlets; but, as such plants exhibit no special movements, we are but little concerned with them; and generally, when I speak of climbing plants, I refer exclusively to the first great class.

Part I.—Spirally twining Plants.

This is the largest subdivision, and is apparently the primordial and simplest condition of the class. My observations will be best given by taking a few special cases. When the shoot of a Hop (*Humulus Lupulus*) rises from the ground, the two or three first-formed internodes are straight and remain stationary; but the next-formed, whilst very young, may be seen to bend to one side and to travel slowly round towards all points of the compass, moving, like the hands of a watch, with the sun. The movement very soon acquires its full ordinary velocity. From seven observations made during August on shoots proceeding from a plant which had been cut down, and on another plant during April, the average rate during hot weather and during the day was 2 h. 8 m. for each revolution; and none of the revolutions varied much from this rate. The revolving movement continues as long as the plant continues to grow; but each separate internode, as it grows old, ceases to move.

To ascertain more precisely what amount of movement each internode underwent, I kept a potted plant in a well-warmed room to which I was confined during the night and day. A long inclined shoot projected beyond the upper end of the supporting

Treatise was published only a few weeks before Mohl's. See also 'The Vegetable Cell' (translated by Henfrey), by H. von Mohl, p. 147 to end.

* "Des Mouvements révolutifs spontanés," &c., 'Comptes Rendus,' tom. xvii. (1843) p. 989; "Recherches sur la Volubilité des Tiges," &c., tom. xix. (1844) p. 295.

stick, and was steadily revolving. I then took a longer stick and tied up the shoot, so that only a very young internode, $1\frac{3}{4}$ of an inch in length, was left free; this was so nearly upright that its revolution could not be easily observed; but it certainly moved, and the side of the internode which was at one time convex became concave, which, as we shall hereafter see, is a sure sign of the revolving movement. I will assume that it made at least one revolution during the first twenty-four hours. Early the next morning its position was marked, and it made the second revolution in 9 h.; during the latter part of this revolution it moved much quicker, and the third circle was performed in the evening in a little over 3 h. As on the succeeding morning I found that the shoot revolved in 2 h. 45 m., it must have made during the night four revolutions, each at the average rate of a little over 3 h. I should add that the temperature of the room varied only a little. The shoot had now grown $3\frac{1}{2}$ inches in length, and carried at its extremity a young internode 1 inch in length, which showed slight changes in its curvature. The next or ninth revolution was effected in 2 h. 30 m. From this time forward, the revolutions were easily observed. The thirty-sixth revolution was performed at the usual rate; so was the last or thirty-seventh, but it was not quite completed; for the internode abruptly became upright, and, after moving to the centre, remained motionless. I tied a weight to its upper end, so as to slightly bow it, and thus to detect any movement; but there was none. Some time before the last revolution the lower part of the internode had ceased to move.

A few more remarks will complete all that need be said on this one internode. It moved during five days; but the more rapid movement after the third revolution lasted during three days and twenty hours. The regular revolutions, from the ninth to thirty-sixth inclusive, were performed at the average rate of 2 h. 31 m.: the weather was cold; and this affected the temperature of the room, especially during the night, and consequently retarded a little the rate of movement. There was only one irregular movement, when a segment of a circle was rapidly performed (not counted in the above enumeration); and this occurred after an unusually slow revolution of 2 h. 49 m. After the seventeenth revolution the internode had grown from $1\frac{3}{4}$ to 6 inches in length, and carried an internode $1\frac{7}{8}$ inch long, which was just perceptibly moving; and this carried a very minute ultimate internode. After the twenty-first revolution, the penultimate internode was $2\frac{1}{2}$ inches long, and probably revolved in a period of about three hours. At the twenty-seventh revolution our lower internode was $8\frac{3}{8}$, the penultimate $3\frac{1}{2}$, and ultimate $2\frac{1}{2}$ inches in length; and the inclination of the whole shoot was such, that a circle 19 inches in diameter was swept by it. When the movement ceased, the lower internode was 9 and the penultimate 6 inches in length; so that, from the twenty-seventh to thirty-seventh revolutions inclusive, three internodes were at the same time revolving.

The lower internode, when it ceased revolving, became upright and rigid; but as the whole shoot continued to grow unsupported, it became nearly horizontal, the uppermost and growing internodes still revolving at the extremity, but of course no longer round the old central point of the supporting stick. From the change in the position of the centre of gravity of the revolving extremity, a slight and slow swaying movement was given to the long and horizontally projecting shoot, which I mistook at first for a spontaneous movement. As the shoot grew, it depended more and more, whilst the growing and revolving extremity turned itself up more and more.

With the Hop we have seen that three internodes were at the same time revolving; and this was the case with most of the plants observed by me. With all, if in full health, two revolved; so that by the time one had ceased, that above it was in full action, with a terminal internode just commencing to revolve. With *Hoya carnosa*, on the other hand, a depending shoot, 32 inches in length, without any developed leaves, and consisting of seven internodes (a minute terminal one, an inch in length, being counted), continually, but slowly, swayed from side to side in a semicircular course, with the extreme internodes making complete revolutions. This swaying movement was certainly due to the movement of the lower internodes, which, however, had not force sufficient to swing the whole shoot round the central supporting stick. The case of another Asclepiadaceous plant, viz. *Ceropegia Gardnerii* is worth briefly giving. I allowed the top to grow out almost horizontally to the length of 31 inches; this now consisted of three long internodes, terminated by two short ones. The whole revolved in a course opposed to the sun (the reverse of that of the Hop), at rates between 5 h. 15 m. and 6 h. 45 m. for each revolution. Hence, as the extreme tip made a circle of above 5 feet (or 62 inches) in diameter and 16 feet in circumference, the tip travelled at the rate (assuming the circuit to have been completed in six hours) of 32 or 33 inches per hour. The weather being hot, the plant was allowed to stand on my study-table; and it was an interesting spectacle to watch the long shoot sweeping, night and day, this grand circle in search of some object round which to twine.

If we take hold of a growing sapling, we can of course bend it so as to make its tip describe a circle, like that performed by the tip of a spontaneously revolving plant. By this movement the sapling is not in the least twisted round its own axis. I mention this because if a black point be painted on the bark, on the side which is uppermost when the sapling is bent towards the holder's body, as the circle is described, the black point gradually turns round and sinks to the lower side, and comes up again when the circle is completed; and this gives the false appearance of twisting, which, in the case of spontaneously revolving plants, deceived me for a time. The appearance is the more deceitful because the axes of nearly all twining-plants are really twisted; and they are twisted in the same direction with the spontaneous revolving movement. To give an instance, the internode of the Hop of which the history has been recorded was at first, as could be seen by the ridges on its surface, not in the least twisted; but when, after the 37th revolution, it had grown 9 inches long, and its revolving movement had ceased, it had become twisted three times round its own axis, in the line of the course of the sun; on the other hand, the common Convolvulus, which revolves in an opposite course to the Hop, becomes twisted in an opposite direction.

Hence it is not surprising that Hugo von Mohl (S. 105, 108, &c.) thought that the twisting of the axis caused the revolving movement. I cannot fully understand how the one movement is supposed to cause the other; but it is scarcely possible that the twisting of the axis of the Hop three times could have caused thirty-seven revolutions. Moreover, the revolving movement commenced in the young internode before any twisting of the axis could be detected; and the internode of a young Siphomeris or Lecontea revolved during several days, and became twisted only once on its own axis. But the best evidence that the twisting does not cause the revolving movement is afforded by many leaf-climbing and tendril-bearing plants (as *Pisum sativum*, *Echinocystis lobata*, *Bignonia capreolata*, *Eccremocarpus scaber*, and with the leaf-climbers, *Solanum jasminoides* and various species of *Clematis*), of which the internodes are not regularly twisted, but which regularly perform, as we shall hereafter see, revolving movements like those of true twining-plants. Moreover, according to Palm (S. 30, 95) and Mohl (S. 149), and Léon*, internodes may occasionally, and even not very rarely, be found which are

* Bull. Bot. Soc. de France, tom. v. 1858, p. 356.

twisted in an opposite direction to the other internodes on the same plant, and to the course of revolution; and this, according to Léon (p. 356), is the case with all the internodes of a variety of the *Phaseolus multiflorus*. Internodes which have become twisted round their own axes, if they have not ceased revolving, are still capable of twining, as I have several times observed.

Mohl has remarked (S. 111) that when a stem twines round a smooth cylindrical stick, it does not become twisted. Accordingly I allowed kidney-beans to run up stretched string, and up smooth rods of iron and glass, one-third of an inch in diameter, and they became twisted only in that degree which follows as a mechanical necessity from the spiral winding. The stems, on the other hand, which had ascended the ordinary rough sticks were all more or less and generally much twisted. The influence of the roughness of the support in causing axial twisting was well seen in the stems which had twined up the glass rods; for these were fixed in split sticks below, and were secured above to cross sticks, and the stems in passing these places became very much twisted. As soon as the stems which had ascended the iron rods reached the summit and became free, they also became twisted; and this apparently occurred more quickly during windy weather. Several other facts could be given, showing that the axial twisting stands in relation to inequalities in the support, and likewise to the shoot revolving freely without any support. Many plants, which are not twiners, become in some degree twisted round their own axes*; but this occurs so much more generally and strongly with twining-plants than with other plants, that there must be some connexion between the capacity for twining and axial twisting. The most probable view, as it seems to me, is that the stem twists itself to gain rigidity (on the same principle that a much twisted rope is stiffer than a slackly twisted one), so as to be enabled either to pass over inequalities in its spiral ascent, or to carry its own weight when allowed to revolve freely†.

* Professor Asa Gray has remarked to me, in a letter, that in *Thuja occidentalis* the twisting of the bark is very conspicuous. The twist is generally to the right of the observer; but, in noticing about a hundred trunks, four or five were observed to be twisted in an opposite direction.

† It is well known that stems of many plants occasionally become spirally twisted in a monstrous manner; and since the reading of this paper, Dr. Maxwell Masters has remarked to me in a letter that "some of these cases, if not all, are dependent upon some obstacle or resistance to their upward growth." This conclusion agrees with, and perhaps explains, the normal axial twisting of twining-plants; but does not preclude the twisting being of service to the plant and giving greater rigidity to the stem.

I have just alluded to the twisting which necessarily follows from the spiral ascent of the stem, namely, one twist for each spire completed. This was well shown by painting straight lines on stems, and then allowing them to twine; but, as I shall have to recur to this subject under Tendrils, it may be here passed over.

I have already compared the revolving movement of a twining plant to that of the tip of a sapling, moved round and round by the hand held some way down the stem; but there is a most important difference. The upper part of the sapling moves as a rigid body, and remains straight; but with twining plants every inch of the revolving shoot has its own separate and independent movement. This is easily proved; for when the lower half or two-thirds of a long revolving shoot is quietly tied to a stick, the upper free part steadily continues revolving: even if the whole shoot, except the terminal tip of an inch or two in length, be tied up, this tip, as I have seen in the case of the Hop, Ceropegia, Convolvulus, &c., goes on revolving, but much more slowly; for the internodes, until they have grown to some little length, always move slowly. If we look to the one, two, or several internodes of a revolving shoot, they will be all seen to be more or less bowed either during the whole or during a large part of each revolution. Now if a coloured streak be painted (this was done with a large number of twining plants) along, we will say, the convex line of surface, this coloured streak will after a time (depending on the rate of revolution) be found to lie along one side of the bow, then along the concave side, then on the opposite side, and, lastly, again on the original convex surface. This clearly proves that the internodes, during the revolving movement, become bowed in every direction. The movement is, in fact, a continuous self-bowing of the whole shoot, successively directed to all points of the compass.

As this movement is rather difficult to understand, it will be well to give an illustration. Let us take the tip of a sapling and bend it to the south, and paint a black line on the convex surface; then let the sapling spring up and bend it to the east, the black line will then be seen on the lateral face (fronting the north) of the shoot; bend it to the north, the black line will be on the concave surface; bend it to the west, the line will be on the southern lateral face; and when again bent to the south, the line will again be on the original convex surface. Now, instead of bending the sapling, let us suppose that the cells on its whole southern surface were to contract from the base to the tip, the whole shoot would be bowed to the south; and let the longitudinal contracting surface slowly creep round the shoot, deserting by slow degrees the southern side and encroaching on the eastern side, and so round by the north, by the west, again to the south; in this case the shoot would remain always bowed with the painted line appearing on the convex, on the lateral, and concave surfaces, and with the point of the shoot successively directed to all points of the compass. In fact, we should then have the exact kind of movement seen in the revolving shoots of twining plants. I have spoken in the illustration, for brevity's sake, of the cells along each face successively contracting; of course turgescence of the cells on the opposite face, or both forces combined, would do equally well.

It must not be supposed that the revolving movement of twining plants is as regular as that given in this illustration; in very many cases the tip describes an ellipse, even a very narrow ellipse. To recur once again to our illustration, if we suppose the southern and then the northern face of the sapling to contract, the summit would describe a simple arc; if the contraction first travelled a very little to the eastern face, and during the return a very little to the western face, a narrow ellipse would be described; and the sapling would become straight as it passed to and fro by the central point. A complete straightening of the shoot may often be observed in revolving plants; but the weight of the shoot apparently interferes with the regularity of the movement, and with the place of straitening. The movement is often (in appearance at least) as if the southern, eastern, and northern faces had contracted, but not the western face; so that a semicircle is described, and the shoot becomes straight and upright in one part of its course.

When a revolving shoot consists of several internodes, the several lower ones bend together at the same rate, but the one or two terminal internodes bend at a slower rate; hence, though at times all the internodes may be bowed in the same line, at other times the shoot is rendered slightly serpentine, as I have often observed. The rate of revolution of the whole shoot, if judged by the movement of the extreme tip, is thus at times accelerated and retarded. One other point must be noticed. Authors have observed that the end of the shoot in many twining plants is completely hooked; this is very general, for instance, with the Asclepiadaceæ. The hooked tip, in all the cases which I observed, viz. in *Ceropegia*, *Sphærostema*, *Clerodendron*, *Wistaria*, *Stephania*, *Akebia*, and *Siphomeris*, has exactly the same kind of movement as the other revolving internodes; for a line painted on the convex surface becomes lateral and then concave; but, owing to the youth of these terminal internodes, the reversal of the hook is a slower process than the revolving movement. This strongly marked tendency in the young terminal and flexible internodes to bend more abruptly than the other internodes is of service to the plant; for not only does the hook thus formed sometimes serve to catch a support, but (and this seems to be much more important) it causes the extremity of the shoot to embrace much more closely its support than it otherwise could have done, and thus aids in preventing the stem from being blown away from it during windy weather, as I have many times observed. In *Lonicera brachypoda* the hook only straightened itself periodically, and never became reversed. I will not assert that the tips of all twining plants, when hooked, move as above described; for this position may in some cases be due to the manner of growth, as with the bent tips of the shoots of the common vine, and more plainly with those of *Cissus discolor*; these plants, however, are not spiral twiners.

The purpose of the spontaneous revolving movement, or, more strictly speaking, of the continuous bending movement successively directed to all points of the compass, is, as Mohl has remarked, obviously in part to favour the shoot finding a support. This is admirably effected by the revolutions carried on night and day, with a wider and wider circle swept as the shoot increases in length. But as we now understand the nature of the movement, we can see that, when at last the shoot meets with a support, the motion at the point of contact is necessarily arrested, but the free projecting part goes on revolving. Almost immediately another and upper point of the shoot is brought into contact with the support and is arrested; and so onwards to the extremity of the shoot; and thus it winds round its support. When the shoot follows the sun in its revolving course, it winds itself round the support from right to left, the support being supposed to stand in front of the beholder; when the shoot revolves in an opposite direction, the line of winding is reversed. As each internode loses from age its power of revolving, it loses its power of spirally twining round a support. If a man swings a rope round his head, and the end hits a stick, it will coil round the stick according to the direction of the swinging rope; so it is with twining plants, the continued contraction or turgescence of the cells along the free part of the shoot replacing the momentum of each atom of the free end of the rope.

All the authors, except Von Mohl, who have discussed the spiral twining of plants maintain that such plants have a natural tendency to grow spirally. Mohl believes (S. 112) that twining stems have a dull kind of irritability, so that they bend towards any object which they touch. Even before reading Mohl's interesting treatise, this view seemed to me so probable that I tested it in every way that I could, but always with negative results. I rubbed many shoots much harder than is necessary to excite movement in any tendril or in any foot-stalk of a leaf-climber, but without result. I then tied a very light forked twig to a shoot of a Hop, a *Ceropegia*, *Sphærostema*, and *Adhatoda*, so that the fork pressed on one side alone of the shoot and revolved with it; I purposely selected some very slow revolvers, as it seemed most likely that these would profit from possessing irritability; but in no case was any effect produced. Moreover, when a shoot winds round a support, the movement is always slower, as we shall immediately see, than whilst its revolves freely and touches nothing. Hence I conclude that twining stems are not irritable; and indeed it is not probable that they should be so, as nature always economizes her means, and irritability would be superfluous. Nevertheless I do not wish to assert that they are never irritable; for the growing axis of the leaf-climbing, but not spirally twining, *Lophospermum scandens* is, as we shall hereafter see, certainly irritable; but this case gives me confidence that ordinary twiners do not possess this quality, for directly after putting a stick to the *Lophospermum*, I saw that it behaved differently from any true twiner or any other leaf-climber.

The belief that twiners have a natural tendency to grow spirally probably arose from their assuming this form when wound round a support, and from the extremity, even whilst remaining free, sometimes assuming this same form. The free internodes of vigorously growing plants, when they cease to revolve, become straight, and show no tendency to be spiral; but when any shoot has nearly ceased to grow, or when the plant is unhealthy, the extremity does occasionally become spiral. I have seen this in a remarkable degree with the ends of the shoots of the *Stauntonia* and of the allied *Akebia*, which became closely wound up spirally, just like a tendril, especially after the small, ill-formed leaves had perished. The explanation of this fact is, I believe, that the lower parts of such terminal internodes very gradually and successively lose their power of movement, whilst the portions just above move onwards, and in their turn become motionless; and this ends in forming an irregular spire.