ON THE PHENOMENA OF MOTION AND SENSITIVENESS IN CLIMBING PLANTS.

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PREVIOUSLY to Mr. Darwin's elaborate investigations on climbing plants, observations had been made by Palm, Mohl, Professor Asa Gray, and others; but in point of variety and novelty many of his researches far surpass those of the latter botanist. A *résumé* of his deeply interesting paper in the *Journal of the Linnean Society*, vol. ix., Nos. 33 and 34, we purpose submitting to the readers of the POPULAR SCIENCE REVIEW.

Mr. Darwin commences by observing that climbing plants may be conveniently divided into four classes; namely, those which twine spirally round a support (spirally twining plants), those which ascend by the movements of the foot-stalks or tips of their leaves (leaf climbers), those which ascend by true tendrils (tendril bearers), and, lastly, those which are furnished with hooks or rootlets (hook and root climbers).

I. *Spirally Twining Plants.*—This is the largest class, and they apparently indicate the simplest or primordial condition. The first example is that of the hop, the movement of which Mr. Darwin thus describes:—

"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 average rate was 2h. 8m. for each revolution. . . . Each separate internode, as it grows old, ceases to revolve, becoming upright and rigid. . . . Generally, three internodes revolve simultaneously; with all the plants observed, 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 first commencing to revolve."

A point connected with this revolving motion, but not the cause of it, is that the axis of each internode becomes twisted as the plant continues to grow and as each internode assumes a rigid form; thus the first internode of the hop became twisted three times round its own axis, while the internode itself gave no less than 37 revolutions before becoming rigid. It is a curious point in connection with this twisting that it is in a direct relation to the inequalities of, or freedom from the support; for stems do not become twisted if allowed to climb small glass rods, but only rough sticks or when hanging freely in the air. "The most probable view," Mr. Darwin says, "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."

He offers the following in explanation:—"that the lower parts of the 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."

The following is our author's explanation of the purport of this motion:—

> "The purpose of this spontaneous revolving motion, or, more strictly speaking, of the continuous bending movement successively to all points of the compass, is obviously in part to favour the shoot finding a support; . . . but when this is gained, the motion at the point of contact is arrested; while the free part projecting above continues to revolve, and by the very motion cannot fail to twine itself round the support."

Mr. Darwin gives an interesting series of tables showing the direction and rate of motion of several twining plants selected from all parts of the vegetable kingdom, proving that every kind behaves in a nearly uniform manner. We purpose giving some of the more important conclusions deduced.

Of thirty-nine plants, twenty-five revolved in a course opposed to, and twelve with, the sun; two revolved both with and against the sun. No instance is at present known of two species of the same genus twining in opposite directions.

The average rate at which the first circle of revolution is described is about 6h. 10m., computed from thirty-five different plants; the longest period being 26h. 15m., viz., of a young shoot of *Lapagerea rosea* (*Philesiaceæ*); while the most rapid was that of *Scyphanthus elegans* (*Loasaceæ*), viz. 1h. 17m. The average rate of twining plants is 5h. 45m. for five revolutions. It must be borne in mind that young shoots commence slowly, and do not arrive at the maximum time of rotation until they have accomplished several circles or ellipses as the case may be.

Light has a remarkable power in hastening the revolutions. Thus :—

Ipomœa jucunda performed its first circle in 5h. 30m.; the semicircle *from* light in 4h. 30m., and *to* light in 1h. 30m.; the difference being 3h. 30m. It must be observed, however, that the rate of revolution in all plants was nearly uniform during night as well as day; hence Mr. Darwin infers the action of the light to be confined to retarding one semicircle and accelerating the other, so that the whole rate is not greatly modified.

Heat likewise affects the rapidity of revolution, by increasing it; thus, *e. g.*, of *Loasa aurantiaca*, one plant which moved against the sun, completed its first circle in 2h. 37 m. (June 30). Another, which followed the sun, completed its circle in 1h. 51m. (July 11), and its 4th circle in 1h. 48m., that being a very hot day; whereas its 5th circle, on the cool morning of July 12th, was finished in 2h. 35m.

Mr. Darwin describes a peculiar instance of a natural reversal of movement in *Hibbertia dentata*. He found that, although its long flexible shoots were evidently well fitted for twining, yet they would make a whole, or half, or quarter circle in one direction, and then in the opposite one. He could not at first discover for what purpose was this adaptation, until after offering the plant various arrangements of sticks and twigs, &c., he surrounded it with several thin upright sticks; and "now the *Hibbertia* had got what it liked, for it twined up the parallel sticks, sometimes winding round one and sometimes round several. . . . Though the revolving movement was sometimes in one direction and sometimes in another, the twining was invariably from left to right. . . . It would appear that this *Hibbertia* is adapted to ascend by twining, and to ramble laterally over the thick Australian scrub."

Mr. Darwin concludes the first part with recording several miscellaneous and curious cases. For example, he observes that "the main stem of *Tamus Elephantipes* does not twine: only the branches." In a species of *Asparagus*, the leading shoot, and not the branches, twine. *Combretum argenteum* produces two kinds of shoots, several of the first formed showed no tendency to climb until "one appeared from the lower part of one of its main branches, five or six feet in length, differing greatly in appearance from its leaves being little developed. It revolved vigorously, and twined." Lastly, a still more remarkable instance occurs in *Ipomœa argyrœoides*, which, in S. Africa, almost always grows erect and compact, from twelve to eighteen inches; whereas seedlings raised at Dublin twined up sticks eight feet high! "These facts," says Mr. Darwin, "are highly remarkable, for there can hardly be a doubt that in the dryer provinces of S. Africa these plants must have propagated themselves for thousands of generations in an erect condition; and yet during this whole period they have retained the innate power of spontaneously revolving and twining, whenever their shoots elongated under proper conditions of life."

II. *Leaf Climbers.*—Mr. Darwin commences his 2nd class by remarking "that it has long been observed that several plants climb by the aid of their leaves, either by the petiole or by the produced midrib." He observed nine different genera; and of two, *Clematis* and *Tropæolum*, eight species of each in order to discover what amount of difference there might be within the same genus; and this, it appears, is considerable.

Clematis glandulosa. The thin upper internodes revolved, against the sun, at an average rate of 3h. 48m. The leading shoot twined round a stick placed near it, first in one direction, then ascending straight, and that portion becoming rigid, twined in an opposite course. This peculiarity was common with other species of this genus. No use is made of the leaves while twining up a vertical stick: "nevertheless if the footstalk of a young leaf be rubbed with a thin twig a few times on any side, it will in the course of a few hours bend to that side; afterwards, however, straightening itself. When first developed, the petioles are upturned, parallel to the stem; they then slowly bend downwards, remaining for a short time at right angles to the stem, and then become so much arched downwards that the blade of the leaf points to the ground with its tip curled inwards, so that the whole petiole and leaf together form a hook. The young leaves are thus enabled to catch twigs when brought into contact with them by the revolving movement of the internodes. The petioles which have clasped any object soon become much thickened and strengthened (as may be seen by reference to Pl. V., fig. 1). If they come into contact with no object, they retain their downward position for some time, and then bending upwards re-assume their original position, which is retained ever afterwards."

Space will not allow us to mention particulars of other species of clematis, to show what amount of variability obtains in this genus; but we introduce a figure of a young leaf of *Clematis viticella* (Pl. V., fig. 2), to compare with that of *C. glandulosa*. In this species, the whole petiole, which with the sub-petioles is sensitive, acts as a hook, being rectangularly bent at the extremity. We may remark that there is a gradation of sensitiveness in the petioles of species of this genus. In *C. montana* it is confined to the main petiole, while in

C. viticella it has spread through the petioles of the several leaflets.

We will conclude our account of leaf-climbers with a short notice of *Solanum jasminoides* (Pl. V., figs. 3 and 4). Some members of the genus *Solanum* are twiners; but this is a true leaf-climber. A long shoot made four revolutions, against the sun, very regularly at an average rate of 3h. 26m. In no other leaf-climber was a leaf grown to its full size capable of clasping a stick, though it took several weeks to do it.

"When a petiole of a half-grown leaf has clasped a support, in three or four days it increases in thickness, and after several weeks becomes hard and rigid. On comparing a thin, transverse slice of this petiole with one from the older leaf beneath, which had not clasped anything, its diameter was found to be doubled, and its structure greatly changed. The sections in fig. 4 will illustrate this peculiarity. In that of the petiole in its ordinary state (A) we see a semilunar band of cellular tissue, slightly different from that outside it, and including three closely approximate groups of dark vessels. Near the upper surface of the petiole, beneath two ridges, there are two other small circular groups of vessels. In the section of the petiole (B), which had during several weeks clasped a stick, the two upper ridges have become much less prominent, and the two groups of woody vessels beneath them much increased in diameter. The semilunar band is converted into a complete ring of very hard, white, woody tissue, with lines radiating from the centre. The three groups of vessels, which, though closely approximate, were before distinct, are now completely blended together. The upper part of the new ring of woody vessels formed by the prolongation of the horns of the original semilunar band is thinner than the lower part, and is slightly different in appearance, from being less compact. The clasped petiole had actually become thicker than the stem close beneath; and this was chiefly due to the greater thickness of the ring of wood, which presented, both in transverse and longitudinal sections, a closely similar structure in the petiole and axis."

We must now pass on to—

III. *Tendril Bearers.*—True tendrils are formed by the modification of leaves with their petioles, of flower-peduncles, and perhaps also of branches and stipules.

Of *Bignonia*, nine species, taken at hazard, and observed by Mr. Darwin, afforded connecting links between twiners, leaf-climbers, tendril-bearers, and root-climbers. *B. unguis.*—Young shoots of this species revolve, climbing sometimes in different directions. It is a leaf-climber, though possessing tendrils. Each leaf consists of a petiole bearing a pair of leaflets and terminating in a tendril, a little larger than that represented in Pl. V., fig. 5, and resembling a bird's foot and leg with the hind toe cut off. The toes terminate in sharp and hard claws. The main petiole and tendril are alone sensitive, the sub-petioles of the leaflets being inert; hence, when a shoot grows through branching twigs, its revolving movement soon brings the tendril into contact with some twig, and then all three toes bend, and after several hours seize fast hold of a twig, exactly like a bird when perched.

Of all the species of *Bignonia* examined by Mr. Darwin, *B. Capreolata* seems to offer the most curious points for observation.

The tendril consists of five branches, apparently representing two pairs of leaflets and a terminal one. Each branch is bifid or trifid, the points being blunt, but hooked. The tendrils revolve in an apparently capricious manner, sometimes not at all, or very slightly, but at other times they describe large regular ellipses. A remarkable fact about them is, that although they bent round sticks, the tendrils again loosed it, sometimes repeating the operation three or four times, recoiling from it "in disgust," and then straightening themselves. The tendrils, moreover, avoid the light, and when a rough post with crevices is given to them, the claws of the tendrils crawl into them. But the substance best adapted to the plant is evidently of a fibrous nature, for when—

"Cotton wool or flax was placed in the proximity of the tendrils, the hooked points caught the fibres; which, from the excitement they produced, caused the hooks to penetrate and curl inwards, so that they securely grasped one or two or a small bundle of them. The tips and inner surfaces of the hooks now begin to swell, so that, after a few days, they are converted into whitish irregular balls, rather above the 1-20th of an inch in diameter, and formed of coarse cellular tissue, which sometimes wholly enveloped and concealed the hooks themselves. The surfaces of these balls secrete some viscid resinous matter, to which the fibres of the wool, &c., adhere . . . . As the whole surface of the ball continues to grow, fresh fibres adhere and are enveloped;"

So that a ball with between fifty and sixty fibres of flax, crossing at various angles, all imbedded more or less deeply, were seen by Mr. Darwin. From these curious discoveries, it is deduced that although this *Bignonia* can occasionally adhere to smooth cylindrical sticks, and often to rugged bark, yet its tendrils are specially adapted to climb trees clothed with lichens, mosses, or with *Polypodium incanum*; which Prof. Asa Gray says is the case with the forest-trees where this *Bignonia* grows.

"Finally, it is a highly remarkable fact that a leaf should become metamorphosed into a branched organ which turns *from* the light, and which can by its extremities either crawl like roots into crevices, or seize hold of minute projecting points; these extremities subsequently forming cellular masses which envelop by their growth the finest fibres, and secrete an adhesive cement."

Cobæa scandens furnishes many points for observation worthy of note. We can only give one. The tendril being vertical, sweeps a circle right over the axis of the stem which is turned to one side. As soon as the tendril comes in contact with a stick, the branches commence lifting themselves up and down, and arrange themselves in conformity with every irregularity of the surface, and so bring the hooks with which the extremities of the tendrils are furnished, originally facing in various directions, into contact with the wood. Mr. Darwin thus describes the beautiful adaptation of this plant :—

"A tendril caught a thin stick by the hooks of one of its two extreme branches ; though thus held by the tip, it continued to try and revolve, bowing itself out to all sides, and thus moving its branches ; the other extreme branch soon caught the stick ; the first branch immediately loosed itself, and then, arranging itself afresh, again caught hold. After a time, from the continued movement of the tendril, a third branch became caught by a single extreme hook . . . . the main stem now began to contract into an open spire, and thus to shorten itself ; and so, as it continued to try to revolve, a fourth branch was brought into contact. As the spiral contraction travelled down the main stem and down the branches of the tendril, all the lower branches, one after another, were brought into contact with the stick, and were wound round it and round their own branches, until the whole was tied into an inextricable knot round the stick. The branches of the tendril now became rigid, and even stronger than they were at first. This plant is secured to its support in a perfect manner."

Corydalis claviculata.—Of this plant we have introduced a figure (Pl. V., fig. 6), because it affords an instance of an actual state of transition from a leaf-climber to a tendril bearer. In a full-grown plant *all* the leaves have their extremities more or less converted into tendrils. All the reduced leaflets have branching nerves, and terminate in little spines like the fully developed leaflets. Every gradation can be traced until we come to branchlets *a*, and *d*, which show no vestige of a lamina. The terminal branches are highly sensitive, the sensibility of the petiole gradually diminishing from the tendril-like extremities to the base. The internodes are not at all sensitive.

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Vitaceæ.—In this, in *Sapindaceæ*, and in *Passifloraceæ*, the tendrils are modified flower peduncles. *Vitis vinifera*, common vine. The tendril is of great size and thickness, sometimes sixteen inches in length. It consists of a peduncle, bearing two branches, which diverge equally from it like the letter Y (Pl. VI., fig. 7). One branch (B) has a scale at the base, and is the longer, and often bifurcated. After a tendril has clasped any object, it contracts spirally. The revolving movement of the internodes is extremely slight.

The diagram of the flowers of the vine (Pl. VI., fig. 8) will show that the tendril here described is a modified flower peduncle.

The two branches above mentioned correspond to B and C (as lettered in the figures), only here the longer (with the bract) bends downwards, evidently to give extra support to the bunch of grapes, which is formed upon what is homologically the other branch of the tendril.

The peduncle, C, increases in length, and loses its sensitiveness in an inverse degree to the number of flower-buds. Thus, the fewer there are, the greater the length of the peduncle, and the more nearly does it assume the character of a tendril.

Similarly, the "flower-tendril," B, occasionally bears flowers, and then "in this state they retain their characteristic qualities of sensitiveness and spontaneous movement, but in a somewhat lessened degree." In fact, a perfect gradation may be seen from the ordinary state of a "flower-peduncle" to that of a true tendril. Mr. Darwin remarks that this affords a good instance of the law of compensation.

Ampelopsis hederacea, or *Virginian Creeper*.—Pl. VI., fig. 9, will illustrate the appearance of the tendril. There is but feeble sensitiveness in the branches, which turn from the light, as their purpose is not to climb by twining round objects, but by means of discs on flat surfaces, as follows:—When they meet a wall they all turn their branches towards it and bring the hooked tips laterally in contact with it. After arranging the branches satisfactorily, the curved tips swell, become bright red, and form on their under side little disks or cushions which apparently secrete some resinous fluid, and so assist in adhering the tendril firmly to the surface, for "the cellular outgrowth of the disk completely envelops every minute and irregular projection, and insinuates itself into every crevice." An attached tendril increases in size, contracts spirally, and becomes highly elastic; and even when subsequently dead, retains its strength and elasticity.

Mr. Darwin mentions one branchlet which had been attached for ten years, yet supported a weight of two pounds. If any entire tendril, or branch of a tendril, do not attach itself, it shrivels up, and very soon drops off (see Pl. VI., fig. 10).

Our author concludes Part III., on Tendril-bearers, by several interesting remarks upon the *Spiral contraction of Tendrils*. This movement begins in half-a-day or a day or two after the extremities have caught some object. It occurs in all tendrils after seizure, with the principal exception of *Corydalis* *claviculata ;* the branchlets of which become deeply sinuous or zigzag, which may be the first indication of the spiral contraction which takes place on the lower surface, as indicated by the abruptly bending of the petiole, when it has not seized an object. This "indication" would seem to corroborate the statement already made, that this plant is an example of a state of transition between a leaf-climber and a tendril-bearer. Tendrils of many plants, if they catch nothing, contract after several days or weeks into a close spire ; whereas when caught, they contract immediately, and in other instances (as *Virginian Creeper*) wither and drop off without contracting spirally; thereby showing the intimate connection between the spiral contraction of a tendril and the previous act of clasping a support.

The use of the spiral contraction is varied. If it has caught a twig higher than the shoot which is inclined, it drags it up. Again, when it has once secured a hold, and the internodes of the shoot continue to lengthen, were it not for this contraction, the shoot would be slackened. Another most important service is that the tendrils are thus made more highly elastic. The strain (as in *Virginian Creeper*) is equally distributed to the several attached branches of the tendril, thereby vastly strengthening it. Little can be said upon the exciting cause of the spiral contraction. At present, therefore, it must be called a vital action without any further explanation being attempted.

IV. *Hook Climbers and Root Climbers.*—In this group there is no spontaneous revolving movement ; the former of these, as *Galium Aparine, Rubus Australis,* and climbing roses, apparently depend solely upon the mechanical support gained by their hooks, as is the case with certain palms in the New and Old Worlds. In the latter group are a good many plants which are excellent climbers.

"One of the most remarkable is the *Marcgravia umbellata*, which in the tropical forests of South America, as I hear from Mr. Spruce, grows in a curiously flattened manner against the trunks of trees, here and there putting forth claspers (roots), which adhere to the trunk, and, if the latter be slender, completely embrace it. When this plant has climbed to the light, it sends out free and rounded branches, clad with sharp-pointed leaves, wonderfully different in appearance from those borne by the stem as long as it is adherent . . . ."

The following are Mr. Darwin's concluding remarks :—

"Plants become climbers, it may be presumed, to reach the light, and to expose a large surface of leaves to its action and to that of the free air. This is effected by climbers with wonderfully little expenditure of organized matter, in comparison with trees, which have to support a load of heavy branches by a massive trunk. . . . . . I have ranked twiners—leaf and tendril climbers—as subdivisions of one class, because they graduate into each other, and because nearly all have the same remarkable power of spontaneously revolving. Does this gradation indicate that plants belonging to one subdivision have passed, during the lapse of ages, or can pass from one state to another?"

Mr. Darwin believes that they can and have done so. He believes this to be true from the fact that the internodes of leaf-climbers revolve, and that many are capable of spirally twining round supports. Moreover, "several leaf-climbing genera are closely allied to other genera which are simple twiners." Similarly he believes tendril-bearers to have been primordially climbers. "For the internodes of the majority revolve, and in a very few the flexible stem still retains the capacity of spirally twining round an upright stick." He proceeds to give the advantages a spirally-twining plant gains by becoming a tendril-bearer. Thus:—

"It might be an advantage to a plant to acquire a thicker stem, with short internodes bearing many or large leaves; and such stems are ill fitted for twining. Moreover, it is easy to see how incomparably more securely they grasp an upright stick than do simple twiners. From possessing the power of movement on contact, tendrils can be made very long and thin, so that little organic matter is expended in their development, and yet a wide circle is swept. Tendril-bearers can from their first growth ascend along the outer branches of any neighbouring bush, and thus always keep in the full light."

He then enumerates several of the diverse powers of movement possessed by climbing plants, as follows:—

"In the first place, the tendrils place themselves in the proper position for action.

2nd. If the young shoot of a twining plant, or if a tendril, be placed in an inclined position, it soon bends upwards, though completely excluded from the light.

3rd. Climbing plants bend towards the light; except in a few instances when they bend in a conspicuous manner towards the dark.

4th. Stems, petioles, flower-peduncles, and tendrils spontaneously revolve, the motion being contingent on the youth and vigorous health of the plant.

5th. There exist in tendrils movements, often rapid, from contact with any body.

6th. After clasping, tendrils generally contract spirally."

Finally, Mr. Darwin concludes his long and deeply interesting paper by the following excellent words:—

"We see how high in the scale of organization a plant may rise, when we look at one of the more perfect tendril-bearers. It first places its tendrils

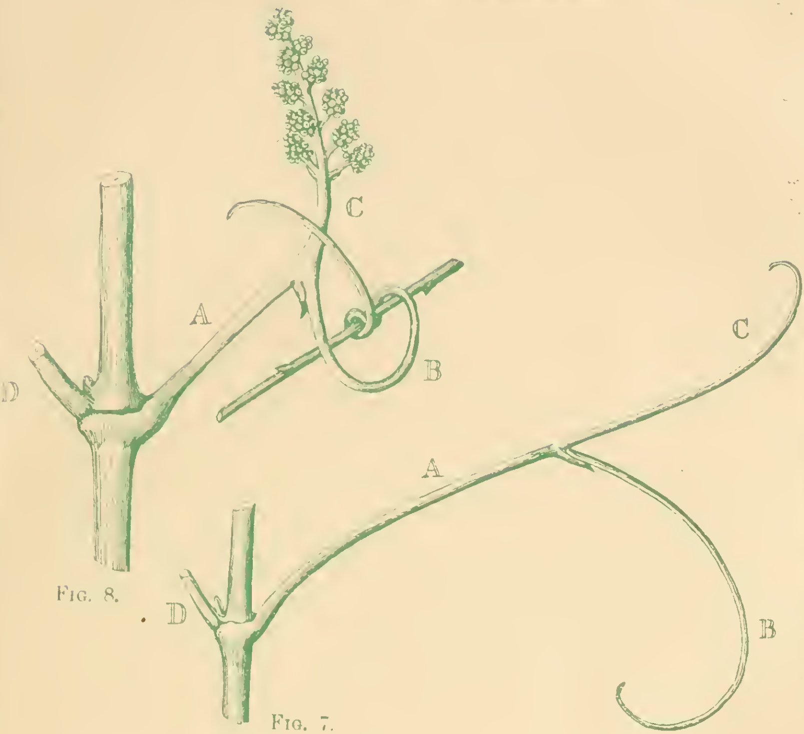

FIG. 8.

FIG. 7.

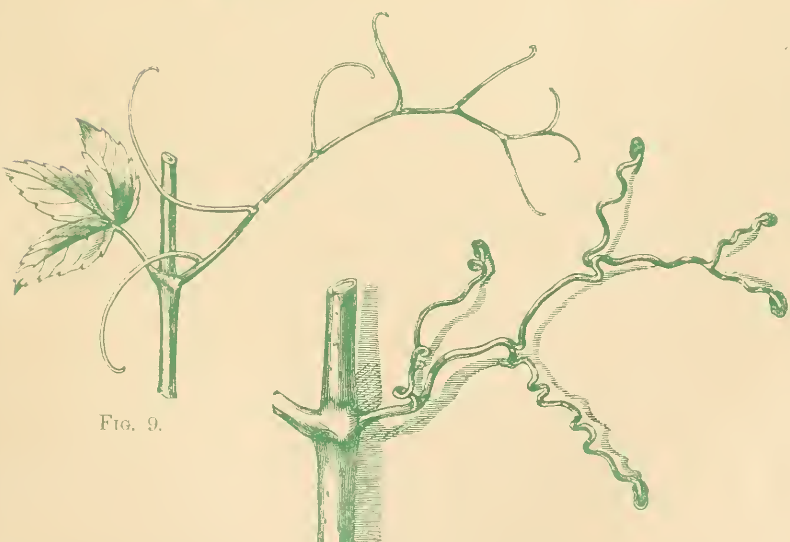

FIG. 9.

FIG. 10.

ready for action, as a polypus places its tentacula. If the tendril be displaced, it is acted on by the force of gravity, and rights itself. It is acted on by the light, and bends towards or from it, or disregards it, whichever may be most advantageous. During several days the tendril or internodes, or both, spontaneously revolve with a steady motion. The tendril strikes some object, and quickly curls round and firmly grasps it. In the course of some hours it contracts into a spire, dragging up the stem, and forming an excellent spring. All movements now cease. By growth the tissues soon become wonderfully strong and durable. The tendril has done its work, and done it in an admirable manner."

EXPLANATION OF PLATES.

Plate V.

Fig. 1. *Clematis glandulosa*, with two young leaves clasping twigs, with the clasping portions thickened.
„ 2. A young leaf of *Clematis viticella*.
„ 3. *Solanum jasminoides*, with one of its leaves clasping a stick.
„ 4. *Solanum jasminoides*. A. Section of petiole ; B. Section of a petiole some weeks after it has clasped a stick, as shown in fig. 3.
„ 5. *Bignonia*, unnamed species from Kew.
„ 6. *Corydalis claviculata*. Leaf-tendril, of natural size.

Plate VI.

„ 7. Tendril of the Vine.
A. Peduncle of tendril.
B. Longer branch, with a scale at its base.
C. Shorter branch. D. Petiole of opposite leaf.
„ 8. Flower of the Vine. A. Common Peduncle ; B. Flower-tendril, with a scale at its base ; C. Sub-peduncle ; D. Petiole of opposite leaf.
„ 9. *Ampelopsis hederacea*. Tendril, with the young leaf.
„ 10. *Ampelopsis hederacea*. Tendril, several weeks after its attachment to a wall, with the branches thickened and spirally contracted, and with the extremities developed into disks. The unattached branches have withered and dropped off.