Thursday, 9th March 1876.—Dr CLEGHORN, Vice-President, in the Chair.

The following paper was read :--

Observations on Mr Darwin's Views of Climbing Plants. By THOMAS A. G. BALFOUR, M.D. Ed., F.R.C.P.E., F.R.S.E.

"The Movements and Habits of Climbing Plants." Such is the title of a volume from the pen of Mr Darwin which. as you are all aware, has recently issued from the press. It is a work of no ordinary merit, for, while we cannot but differ from this distinguished naturalist in his views regarding "the evolution of species," and fail to see the cogency of the illustrations of that doctrine which he adduces, we most willingly accord to him our high admiration of his skill and ability as a most accurate observer of nature. The very history, indeed, of the book before us affords us the best proof of the statement just made. In 1865 Darwin's observations on climbing plants were first recorded in the "Journal of the Linnean Society," and it was in this periodical that we read with intense pleasure the account of the numerous observations and experiments on that class of plants; and, though ten years have elapsed since that publication appeared, we do not observe that a single correction of any of the then recorded facts has been needed. Some additions have been made in the present volume, and the theory of the cause of twining movement in these plants has been somewhat modified in accordance with the views of Drs De Vries and Sachs; but his observations, which were then recorded as facts, are in almost every instance proved to be such. Nor is this anything else than what we should have expected if we consider, on the one hand, that the most minute particulars claim his attention, for nothing in nature is considered by Darwin to be beneath his observation; and, on the other hand, reflect on the mode in which he varies his experiments, and subjects his observations to the strictest scrutiny.

To attempt a review of this interesting work is scarcely possible, as almost every page teems with facts for the establishment of which no one, who has not been engaged in similar investigations, can form any estimate of the amount of research required. We must, therefore, only give a short sketch of some of the most interesting passages, which may perhaps prove acceptable to those who have not yet procured for themselves this able treatise, and may not, I trust, be altogether unprofitable to others who have already perused it.

Among plants, as among men, we have two distinct classes determined by opposite characters: one, with widespread roots and strong erect trunks, is independent of others and entirely self-reliant; while the other class, destitute of that noble feeling of independence, cannot maintain its position without help; and we regret to add that the analogy extends farther, for the kind support thus supplied is too often ill requited, and, as the viper in the fable bit the man who had cherished it in his bosom so the stem-climbers often strangle the trees around which they have twined. This is specially the case in tropical forests, and such climbers have no ordinary interest attached to them, even in an economical point of view, and have attracted the attention of Indian authorities, as their Blue Books testify.* In a practical as well as scientific aspect this class of the vegetable kingdom is thus seen to have claims on our regard. It is in its scientific bearings that Darwin treats his subject, and 206 pages are not more than sufficient for expatiating on the wonderful adaptations for their various functions with which these plants have been endowed by the beneficent Creator. At present I intend adopting the course of a climbing plant, and, by availing myself freely of the erect and strong stem which Darwin has formed, to attain my object at the expense of a small amount of tissue on my own part.

Darwin divides climbing plants into two great classes,— 1st, Those which twine spirally round a support, unaided

^{*} In the working estimate of the Teak and Sál Forests, large sums are assigned for cutting *Bauhinia* and other destructive climbers, and in Mysore various species of *Convolvulus* are cleared away from the young Sandalwood trees.

by any other movement; and 2d, Those which are endowed with irritable organs, which grasp the object which they touch, such as happens in the case of leaf-climbers and tendril-bearers. These are the chief divisions; but he has two subordinate ones, on which he touches only slightly, viz., the plants which ascend by means of hooks, and those which do so by rootlets, such as the ivy, &c.

No scientific generalisation can be strictly accurate, but merely approximately so, for Nature refuses to submit to such abrupt distinctions, and glories in the endless varieties which she continually presents to our view, and hence, though the above divisions are well suited for Darwin's purpose, yet even among the facts which he himself records we are supplied with illustrations of the inadequacy of the classification proposed; for we find that in a Bignonia and in the early stage of a species of Tropæolum we have examples of stem-climbing, leaf-climbing, and tendril-bearing plants; while in another species of Bignonia we have, besides these, ascent also by rootlets.

1. Twining Plants.—These are found in the three great divisions of the vegetable kingdom,-Dicotyledons, Monocotyledons, and Acotyledons. Thus the common Hop (Humulus Lupulus) and the common Honevsuckle (Lonicera Periclymenum) are examples of the first division; the Black Bryony (Tamus communis) of the second; and a Fern belonging to the Polypodium family (Lygodium scandens) of the third. Some twining plants move from right to left, while others take the opposite direction. So far as observation has gone, the greatest number of plants take the latter direction, i.e., as Darwin puts it, opposed to the course of the sun; for in judging of the direction, he regards the plant as being in front of the individual, but we think it would have been better had he added when the back of the individual was towards the sun.* In regard to twining plants, there are three distinct movements which Darwin. and Dutrochet before him, have described: the first is a revolving movement, which is, "in fact, a continuous self-

[•] It is important that we should bear this in mind, for others regard the observer as being in the centre round which the plant twines, which would lead to the plant being described as climbing in the very opposite direction from that in which Darwin would describe it.

bowing of the whole shoot, successively directed to all points of the compass, and has been well designated by Sachs as a revolving nutation." The design of this is evidently to enable the shoot to find a support. The second is the spiral twining of the shoot round the support; the spire thus formed is sometimes very close, and sometimes an open one; and, on some occasions, both of these features are exhibited by the same twiner. The third kind of movement is that of *torsion*, or twisting on its own axis. As this torsion does not occur when a stem twines round a smooth support, such as a glass rod, and as it manifests itself when rough sticks are used as the support, or when, in the case of glass rods, it has surmounted the summit and become free, Darwin thinks that the stem becomes more rigid by this axial twisting, just as a much twisted rope is stiffer than a slackly twisted one, and that thus it is enabled to get over inequalities in its spiral ascent, and to carry its own weight when at the top it revolves freely in the air.*

Let us now take the case of the Hop as Darwin has given it. When its shoot springs up, two or three of the first formed internodes are straight and do not move, the next formed, when young, exhibit the revolving nutation. In one instance, where he tied up the shoot and left only a young internode free, he found that this revolving movement seemed to increase in rapidity as it progressed-" vires acquirit eundo;"-24 hours were probably required for the first revolution, but the second was completed in 9 hours, the third in little more than 3 hours, and when it reached its maximum velocity only 21 hours were required. first the internode was not twisted on itself, but ultimately it became so; but while there were 37 revolving nutations, there were only three axial twistings. When a revolving shoot meets a support, "its motion is necessarily arrested

• Dutrochet believed that the twining movements were due to an expansion of one set of cells and a contraction of another set, and Darwin seems to think that this theory best accounts for the rapidity of movement displayed by sensitive tendrils on being touched; though in other instances he adopts the views of Dr De Vries and Prof. Sachs, who attribute the phenomena to increase of growth. As regards the torsion or axial twisting, Sachs believes that it results from "growth continuing in the outer layers after it has ceased, or begun to cease, in the inner layers."

at the point of contact, but the free projecting part goes on revolving. As this continues, higher and higher parts are brought into contact with the support and are arrested, and so onwards to the extremity. . . . As each internode loses from age its power of revolving, it likewise loses its power of spirally twining." So that, while there is no *neces*sary connection between the axial twisting and the revolving nutation, this last is intimately connected with the spiral twining. The twining process, however, is performed more slowly than the revolving one, probably owing to the retardation by contact with the support; thus a Ceropegia performed its revolution in 6 hours, but required 9½ hours for its spiral twining once round a stick.

In speaking of Ceropegia (which is one of the Asclepiadaceæ, to which Natural Order several other twiners belong, e.g., Hoya, Stephanotis, Dischidia), I may mention that Mr Lindsay and I studied the Ceropegia repens with considerable care, though the season of the year at which we did so was not favourable for observing all the phenomena; yet some of our observations were interesting, and as they illustrate some of the topics referred to by Darwin, I shall enumerate a few, which extended from November 26 to January 13. Darwin speaks of the spirals being drawn up, and on some occasions we noticed this, as we did also in Stauntonia latifolia, where we had good examples of the pushing or drawing upwards of the spirals to which Darwin refers-one being pushed up 1 inch, another 1 inch, and some even 1 inch; the eighth circle seemed to have been pushed off the end of the stick, and stood about 1 inch above it. But our first observation on Ceropegia seemed to indicate that the spirals are sometimes pushed down; this seemed to be the case with two spirals which were apparently pushed downwards before, or while the third was forming, and when a fourth spiral had formed the third one was itself displaced downwards for 1 inch, and in two days afterwards the second circle was pushed backwards for about $\frac{1}{2}$ inch.

Another fact, to which Darwin also refers, was noticed by us, viz., that on the fourth day after the third spiral had formed it *untwined* itself, and stood stiff and erect at the side of the stalk. It must, however, have slipped downwards, as the mark placed on it was found to be on the same level when it stood erect at the side of the stick, as it had been when spirally twined round it.

Another point noticed was, that on the portion of shoot corresponding to the third circle, which was now standing erect, we found that the mark which had been on the convex surface previously was on the concave one, evidently in consequence of its revolution. A similar change was observed a few days afterwards at the part of the shoot which was at the top of the stick, the mark which had been on the outside of the shoot was now resting against the stick.

Another observation of some interest was this, that when the shoot surmounted the stick it formed two spirals. This took place in a different shoot from the last, and unfortunately we were unable to observe the subsequent course of the free internodes, as some green paint was used for marking which killed the end of the shoot. The shoot was not growing very well when the spirals were formed, which corroborates what Darwin, Palm, and Mohl have shown, that where free internodes of vigorously twining plants cease to revolve they become straight, and do not show any tendency to be spiral; and I suspect that Darwin's ingenious explanation must be applicable to my case, and that the lower parts of the terminal internodes were gradually and successively losing their power of movement, while the portions above were in like manner losing their power as they moved onwards, so that an irregular spiral would be formed.

In another instance we found that a spiral was formed on the free portion above the top of stick, which in a few days changed to a triangular form, and was turned vertically, and in five days afterwards the upper free shoot was merely curved thus A and was neither spiral nor triangular. In the case of another shoot which was growing very vigorously in spring, I found that after reaching the top of the stick it had grown quite straight for $1\frac{1}{2}$ foot; at this point it caught another stick, and twined three times round it, then it circled another shoot from its own plant, then reached the branch of another plant round which it made two circles, and again became free and straight to its termination, which was $1\frac{1}{4}$ foot.

Views of Climbing Plants.

One other point was noticed. I began to measure the internodes, and having put a red mark at the base of the first internode measured, which was at that time the penultimate one, it was found to be 2 inches long, and the second or ultimate internode was only about $\frac{1}{4}$ inch. On the 7th day afterwards the first internode was found to be 5 inches long, the second was 1 inch, while the third, which had been newly formed, was about $\frac{1}{4}$ inch.

On the tenth day after this the measurements were as follow:—first internode (which is now the fourth last one) is $5\frac{1}{3}$ inch; second (which is now antepenultimate) is $4\frac{1}{3}$ inches; third (which is now the penultimate) is about $\frac{1}{3}$ inch; while the fourth (or new and ultimate one) is $\frac{1}{3}$ inch.

On the sixth day after last date the measurements were these:—first. 5§ inches, which is same as before; second, $4\frac{1}{2}$ inches, which is also same as before; third (which is now the antepenultimate), which was $\frac{1}{2}$ inches; fourth (now penultimate), which was $\frac{1}{2}$ inch, is now $\frac{3}{2}$ inches; fifth (newly formed or ultimate) is about $\frac{1}{2}$ inch.

On the eighth day after last date, the first, second, and third were the same as at last date; the fourth (now antepenultimate), which was $\frac{2}{3}$ inch, is now $2\frac{1}{4}$ inches; the fifth (now penultimate), which was about $\frac{1}{4}$ inch, is now $\frac{1}{4}$ inch; and the sixth (new or ultimate) is $\frac{1}{4}$ inch.

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It will thus be seen that the growth is mainly confined to the internodes which are penultimate and ultimate at the different periods. This seems to correspond to Darwin's results, for he speaks of the *growth* of the penultimate internode as being the cause of the pushing up of the spire formed on a stick by the terminal internode (p. 18).

Another point which interested us much was the following. When a shoot of Ceropegia came into contact with a long slender stick, it took long sweeps up the stick before completing the spire, but after having taken one or two such, it was generally approaching the top of the support, and immediately the subsequent two or three spires formed were very near each other; when a fresh stick was fastened to the first one, so as to increase its height considerably, the first formed spiral or spirals were much elongated, but became shorter when the end of the stick was approached; a third stick was added to the end of the second one, and a similar course was pursued by the shoot. It reminded us much of the doings of some young man who had come into possession of a fortune, and who, thinking that it could never be exhausted, most lavishly expended vast sums of money, but at length finding his resources beginning to fail, immediately commenced retrenching, and kept his expenses within his annual income. This peculiarity was noticed in more than one shoot of Ceropegia repens -evidently with the design of getting quickly to the light, and yet of holding firmly to supports.

We have already spoken of plants twining in the direction of the course of the sun or against it; and while species of the same genus almost always climb in the same direction, yet we have some exceptions; thus, *Mikania scandens* moves from left to right, but another species climbs from right to left. In *Solanum Dulcamara* (Bittersweet) we find that both directions are sometimes taken by the same stem, as Dutrochet had pointed out. Among several plants of *Loasa aurantiaca* some twined in one direction and some in the opposite, while others adopted one course at first and afterwards reversed it, as happened also in *Loasa Herbertii*. Another interesting point is the thickness of the supports of twining plants. Darwin remarks that while tropical twiners and those in

the warmer temperate regions can ascend thick trees, and instances Fritz Müller, who has seen in the forests of South Brazil one of the Menispermaceæ surrounding with its spiral a trunk which was about 5 feet in circumference, vet in our temperate climate Darwin has only seen one instance of twining round a tree, and that was in the case of a honevsuckle, which encircled a beech tree 41 inches in diameter. A Phaseolus multiflorus in the open air could twine round a support of 3 or 4 inches in diameter, but failed in doing so when the diameter was 9 inches; and as the final cause of this arrangement he adds, "This power would evidently be almost necessary for twining plants inhabiting tropical forests, as otherwise they would hardly ever reach the light. In our temperate countries twining plants which die down every year to the root would suffer if they were enabled to twine round trunks of trees, for they could not grow tall and gain the light." As illustrating these remarks, I may mention the Bauhinia Vahlii, which twines around and overtops the highest trees in the forests of India, and which attains the length of fully 300 feet.

Light has a powerful effect on the rapidity with which revolutions are executed. On this subject our author gives us a most instructive example in *Ipomæa jucunda*, which made a complete revolution in 5 hours and 30 minutes; now, in accomplishing this circle, the semicircle *from* the light took 4 hours and 30 minutes, while that *towards* the light occupied only 1 hour. Temperature also, as might have been expected, influences the rate of revolution.

Some twining plants exhibit striking peculiarities: the Combretum argenteum Darwin found to have two kinds of shoots; most of the shoots did not exhibit any revolving propensities, but one of them revolved and turned most vigorously. The same is true of *C. purpureum*, which for months has looked quite shrubby, but within a few days has sent out several twining shoots with little developed leaves, which have most vigorously twined around sticks. Leon had before shown that certain varieties of *Phaseolus multiflorus* give out some shoots which are thick and upright, and others which are thin and twining. In *Polygonum convolvulus* the season of the year seems to determine this twining property, which is only

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manifested during the middle of summer; for, though it may grow vigorously in autumn, it exhibits no tendency to twine. Again the main stem of *Tamus elephantipes* does not twine, the branches alone do so. A species of Ipomœa in South Africa is almost always firm and erect, attaining the height of 1 or $1\frac{1}{2}$ foot, while seedlings of this plant raised near Dublin twined up sticks 8 feet in height.

2. The second class has two subdivisions. viz., leafclimbers and tendril-bearers. The leaf-climbers accomplish their object either by means of the petioles or of the prolonged midrib. Several observations are recorded very fully on eight species of Clematis and on seven of Tropæolum, besides others on Maurandia, Solanum, Fumaria, Gloriosa, Nepenthes, &c. These investigations have been prosecuted with great care and skill, and reflect the highest credit on the patience and ability of the observer. He has shown that if the petioles of Clematis are left to themselves they do not twist or bend, and hence when we find old petioles so affected we may be sure that, in their young state, they must have come into contact with some object which has subsequently been removed, and we may be also certain that that removal must not have been effected immediately after the contact, else the petioles would have again assumed their straight condition. The clasping tendency of the petioles is owing to their sensitiveness or irritability, which is found presenting peculiarities in degree and situation in different species; thus in Clematis glandulosa it is found on both sides of the petiole, but it exists in a greater degree on the under surface. In Clematis montana, again, the petioles are much more sensitive than in the last species: the main petiole has the sensitiveness extending along its whole length, but this property is not communicated to the three leaflets which it carries. In Clematis Sieboldi the petioles of the lateral and terminal leaflets are also sensitive; while in Clematis calycina a curious compensating property is displayed, for the main petioles are highly sensitive in their young state, and lose this property when they are old; while, on the other hand, the three divided leaflets have scarcely distinct petioles, and no sensitiveness connected with them, while the main petioles are strongly so; but no sooner has the main petiole ceased

to be sensitive than the petioles of the lateral and terminal leaflets elongate, and acquire the property which the main petiole has lost. Such are a few of the interesting observations recorded. The amount of sensitiveness in these cases was determined by minute portions of thread of different weights—some of them only $\frac{1}{15}$ th of a grain—being brought into contact with the petiole, and observing the amount of weight to which the bending response was given, and also the time in which that was accomplished. In many of the species, however, the stem also performed feats of climbing, though in some instances, when the petiole had clasped a support, the stem remained erect, presenting the appearance, as Darwin has well expressed it, of a man standing beside a stick with his whole arm thrown around it. I have, however, seen both petioles firmly grasping a stick; and in another portion of the same plant I have witnessed one petiole twined twice round a neighbouring stem of the same plant, while the other petiole was twisted twice round its own stem.

When a petiole has entwined itself around an object, it sometimes becomes much thickened and strengthened, a swelling occurs in the course of two or three days, and ultimately the petiole grows nearly twice as thick as the opposite leaf-stalk which has clasped nothing; and while this latter remains quite flexible and is easily broken, the clasping petiole becomes remarkably tough and rigid, which, of course, has the effect of enabling the petiole to support the stem in a strong and durable manner. This change is seen notably in C. glandulosa and C. calycina, In C. montana, so far as I have observed, the increase of bulk was not apparent, but the firmness and toughness were decidedly A rapid and considerable enlargement is acquired by 80. the young petioles of Lophospermum scandens (a Mexican plant of the order Scrophulariaceæ), when these have encircled an object. Perhaps the most interesting illustration of this change is given by Darwin under Solanum jasminoides, of which change he has supplied two most instructive figures. Of the plant itself he says, "In this plant, and in no other leaf-climber seen by me, a leaf grown to its full size was capable of clasping a stick; but the movement was so extraordinarily slow that in the

greenhouse the act required several weeks." And regarding the increase of size and internal changes of the clasping petiole, he thus writes: "When the flexible petiole of a half or a quarter grown leaf has clasped any object, in three or four days it increases much in thickness, and after several weeks becomes wonderfully hard and rigid, so that I could hardly remove one from its support;" and on comparing a transverse section of this petiole with that of one which had clasped nothing, he found its diameter fully doubled and its structure greatly changed, there being, besides other variations from its normal condition, a large development of woody tissue with lines radiating from the centre. After similar careful observations on seven species of Tropæolum, where phenomena not unlike those previously recorded were noticed. Darwin concludes with the remarks: "We have seen in this genus a gradation from species such as Tropæolum tricolorum, which have exquisitely sensitive petioles and internodes, which have rapidly revolving powers, and can spirally twine up a support, to other species, such as Tropæolum elegans and Tropæolum tuberosum, the petioles of which are much less sensitive, and the internodes of which have very feeble revolving powers, and cannot spirally twine round a support; and lastly to Tropæolum minus (the dwarf crimson Nasturtium), which has entirely lost or never acquired" (or rather, been endowed with) "these faculties."

Besides the leaves which twine by means of their petioles, we have those which ascend by the prolonged midrib. A good example of this process is supplied by the highly ornamental genus Gloriosa-a species of which, G. Plantii, Darwin minutely describes ; but we shall here simply allude to one or two points in connection with the growth of this plant which beautifully illustrate a principle of the divin government. The first is the strict economy which is displayed by the Author of nature amid the lavish profusion with which he has surrounded us, for while the plant was only six inches high and could support itself, its climbing powers were not developed, the tips of its leaves were not sensitive, and the stem did not revolve; and, aga n, when it had reached its maximum growth the leaves at the summit were destitute of s nsitiveness and could not clasp

any object. Another illustration of this same principle is afforded us by the withdrawal of a property, once possessed, when the plant has failed to make use of it aright, and when it can no longer be of any avail; thus when a leaf has caught hold of nothing, and has curled inwards so as to form a ring, its sensibility is lost. From this last illustration who can fail to be reminded that in the moral government a like principle is in operation, as the solemn announcement so clearly proves, "He that hath not, from him shall be taken even that which he seemeth to have."

Under this division our attention is directed to the genus Nepenthes or true pitcher plants. At one time the jointed lid of the pitcher was regarded as the modified lamina or blade of the leaf, and all the structures between it and the stem as a phyllode or modified petiole; but the real nature of the structure has been pointed out by Dr Hooker, who shows that the apparent leaf springing from the stem is the true lamina, and that the tendril-like appendage is the prolonged midrib, which, becoming folded on itself at the end, forms the pitcher, which latter organ he regards as the analogue of a secreting gland situated at the end of the midrib in certain plants, such as *Richardia africana*.

In the Nepenthes the climbing or clasping is effected by the prolonged midrib between the lamina and the pitcher, which, when it surrounds a support, becomes thickened and hardened, of which any one can easily convince himself by pressing on the coiled and uncoiled portions. This coiling, however, may be sometimes witnessed in cases where no support has been grasped, and occurs in some midribs which fail to produce pitchers at their ends. Darwin believes that "the chief use of the coiling, at least while the plant is young, is to support the pitcher with its load of fluid," which, in some instances, has no small weight.

We now come to the second division of the second class, which includes tendril-bearers, and which is perhaps the most interesting part of the whole book. True tendrils, homologically considered, are modifications of leaves, flowerpeduncles, branches, and perhaps stipules. The Bignonias supply us with examples of the first modification, as their tendrils are altered leaves; the tendrils of the Vitis vinifera are modified flower-peduncles; the Strychnos has its branches transformed into true tendrils, and if we regard the tendrils as representatives of arms, we have in this last case a happy reversal of the sad fate of Daphne, of whom the poet so plaintively sung, "In ramos brachia crescunt." In the case of Smilax aspera Mohl regards the tendrils which arise from the petiole as modified stipules.

The Bignoniads are the trumpet-flower family, and in some instances these organs are large, numerous, and beautiful, and, as Lindley has said, "are the glory of the places which the species inhabit;" but, with the humility which is ever characteristic of true merit, the plants rather shun than court publicity, for in dark corners rather than in the blaze of light they quietly and unobtrusively perform their appointed duties; they never blow their own *trumpets*, but leave that duty to be discharged by others, and this has been done so effectively by Mr Darwin, that henceforth most of the members of the family will deservedly command the admiring attention and regard of the civilised world. Darwin treats of nine species of Bignonia, and to some of these we must refer.

Bignonia unguis has an imperfectly twining stem. Each leaf consists of a petiole bearing a pair of leaflets and ending in a tendril which, like the leg (or rather, tarsus) of a bird, divides into three toes of equal length and in the same plane, and which terminate in sharp, hard claws. The petiole and tendril with its three toes are sensitive; and when the toes have clasped a twig, an appearance like that of the perching of a bird is presented, the posterior toe being, of course, absent. Darwin regards this plant as one of the most efficient climbers. I have on several occasions watched with much interest the mode of ascent of a species of M'Fadyena, one of the Bignoniaceæ, which bears the closest resemblance to Bignonia unquis. and I can certify as to the accuracy of Darwin's description of that species. The M'Fadyena presented a most pleasing object with its three toes firmly grasping with their claws the bricks of the walls of a greenhouse, with the two outspread leaflets immediately behind them; the firmness of the hold was very considerable, and my fingers can testify to the sharpness of the terminal claws, and to their admirable adaptation to lay hold of any object which may come

in their way. In one instance where a stick had been placed beside a M'Fadyena, the twining power of the stem did not seem very efficient, for the circles, two in number, were wide and could easily have been withdrawn from their place, but near the top of the stick the tarsus and three toes had embraced it firmly, and gave a fixity to the plant which it could not otherwise have obtained. Even when the leaflets are in a young state the efficiency of the claws is In this genus I found some aërial rootlets proceedperfect. ing from below the attachment of the petioles. But to return to Bignonia unquis, it, as we have just seen, and Bignonia Tweediana, a species introduced from Buenos Ayres in 1838, possess the power of stem-climbing to a greater or less degree, and by means of the revolving movement of the stem the tendrils are brought into contact with sticks or twigs, and as the petiole and tendril (consisting of the tarsus and toes) are all sensitive the object is firmly clasped, while in B. Tweediana, as if to "make assurance doubly sure and take a bond of fate," aërial roots are emitted from the basis of its leaves, and curve partly round and adhere to the twig or stick. When a tendril has clasped an object it ultimately becomes strengthened-a condition which, as we have seen, occurs in other instances; but if it should fail in attaining this end, it seems ashamed of itself and bends slowly downwards, and its power of clasping is lost, and as if disgusted with its inability now to render any further service to the plant, it in a short time afterwards disarticulates itself from the petiole, and drops like an autumnal leaf. This process is peculiar, as in the case of other tendrils under similar circumstances they merely wither away.

Another species, the Bignonia venusta, I have had many opportunities of studying. The petiole, $\frac{5}{2}$ inch, the tarsus, which here is much longer (being on an average about $3\frac{3}{4}$ inches), and the three toes ($\frac{3}{4}$ inch each) lie in different planes. A similar appearance of ternate division at end of tendril occurs also in B. littoralis, B. cherére, a native of French Guiana (whose toes also end in suckers), and in B. Chamberlaynii, which is a variety of B. æquinoctialis, and was introduced from Brazil in 1820. In speaking of Brazil, it is interesting to know that in some of the forests of that country the Bignonias are so numerous, and by their flexible stems and tendrils so pass from tree to tree, as to render these forests almost impassable.

An appearance exactly similar occurs in an unnamed plant in the stove of the Edinburgh Botanic Garden, where the tendril is one of the three branches into which the petiole divides, and is sometimes five inches in length, the three toes being each about § inch long. In this plant there is an interesting illustration of the manner in which leaves may be modified, but on this point I cannot at present dwell. Darwin declares that, though the tendrils of B. venusta can make considerable sweeps, yet even they are aided by the revolving power of the young internodes, and if the stick which has been ascended is thin, the right and left hand tendrils are alternately used. In B. littoralis, on the other hand, which is not a stem-climber, both tendrils seize the stick at the same part and at once. In connection with B. venusta both Mr Lindsay and I noticed that when a young shoot was given off no tendril was formed till the end of the fourth internode, a third leaf supplying the place of that organ at all the previous internodes, thus affording another instance of economy in nature, for when the shoot was able to support itself no tendril appeared. Axial twisting is distinctly seen in some of the internodes. Darwin states that when a tendril has caught nothing it does not contract spirally; here, however, there is apparently some mistake, for I have seen on more than one occasion the spiral twisting where the tendril was quite free. I shall give one instance: a tendril which was given off from the lower portion of the end of the petiole (probably owing to the leaves having risen up towards the light) was seen pointing downwards, and from its termination the three toes were projecting out at right angles to it, and though nothing had been caught, there were on the tarsus two spirals, each consisting of two circles, the first one being situated at 1 inch from the beginning of the tarsus, and the second being 1 inch from the first. Another case that interested me was this: a tendril (or rather the tarsal portion of it) had encircled by its distal extremity an adjoining stem, and other eight fine spirals had formed above this, extending to 1 inch of commencement of tarsus; the toes were grasping nothing; one

of them was in a kind of elliptical form, another formed a semicircle growing gradually thicker towards the point, while the third toe had two beautiful spirals formed on it.

Darwin attributes no power of producing suckers to this species, and on looking at the tendrils which were on the stick in front and facing the light, we could discover no trace of suckers, but, on turning round the portion of plant which was nearest to the wall, we found, on what had been the darkest portion of the stick, three tendrils, from a vigorously growing part, which were grasping a green painted stick (not very rough) by their three toes, and in each case two of the toes were terminated by fine round white suckers. A fourth tendril had a sucker on only one of its toes. All the suckers were at the back except one which was at the side of the stick. Mr Darwin at one time believed that suckers were not formed until the point of the tendril had attached itself to an object. Dr M'Nab, however, pointed out that the tendrils of Ampelopsis Veitchii bore small globular discs before they had come into contact with any object; and Fritz Müller showed that the trifid tendrils of Haplolophium, one of the Bignoniaceæ, did, without contact with an object, end in smooth shining discs. In his recent work Darwin assents to the accuracy of both these observations, though he believes that the discs considerably enlarge when they adhere to some object, and it gives me much pleasure to say that the above statement expresses my experience in the case of B. venusta, for, on examining the suckers referred to, only one was found firmly attached to the stick (though more afterwards became so), the others were easily moved by a slight touch. and some of these had the side of the sucker lying against the stick: but those which were attached were the most developed. Cotton wool and sphagnum were fastened to the stick, but on the second day afterwards there was no indication of any of the tendrils touching it.

Bignonia speciosa next claims our attention. Here also we find the same principle of economy illustrated by the non-development of tendrils when the plant is young and has no need of a support. Even after the tendrils have appeared, they, in their early stage, exhibit a fickleness and capriciousness somewhat akin to that which is not uncom-

monly displayed at comparatively early periods by our own They are impatient of restraint, unsettled in their race. habits, and seem bent on proving that they have a will of their own, and hence we find them sometimes refusing to clasp a stick, or, after having grasped it, loosening their hold and relinquishing their task. With maturer years, however, a greater steadiness of purpose seems to be developed. The tendrils in this species, and also in B. picta and B. æquinoctialis, which is a shrubby plant, end in a sharp and nearly straight point, which exhibits a strange peculiarity in searching out holes into which it may insinuate itself, and when such a crevice has been found the point bends at a right angle in order to enter it, and may even bend again to gratify its desire to explore some other hole which may open into the crevice; and though, by its frequent withdrawal of itself from these holes and inserting itself into others, a slight reappearance of its early unsteadiness might by some be suspected, yet it is not really so, for it seems to be anxiously engaged in seeking a proper field for the display of some potential energy which it possesses, as the analogy in the case of Bignonia capreolata apparently indicates.

This Bignonia capreolata is perhaps the most interesting and instructive of all the tendril-bearers. The tendrils here are much branched, there being five, or, as I have observed, even seven branches, each of which is bifid or trifid at the point, which ends in a blunt hook. These tendrils seem to be sensitive on all sides, and, unlike leaves, of which they appear to be modifications, they move from the light. This tendency was proved by Darwin by various experiments of a most conclusive kind. Now these tendrils, like those of Bignonia speciosa and B. picta, exhibited a like capriciousness in seizing and abandoning a stick for even three or four times: yet when a fissured post was placed near the plant a very different course was pursued by the tendrils, for their points and the tips of even miniature tendrils crept in a surprising and beautiful manner into the various crevices, and after two or three days, the development of balls by the swelling of the tips and inner surfaces of the hooks commenced. But, as another experiment of Darwin's imitated the natural condition of the plant still more accurately, I shall under it enlarge on the

formation and functions of these disc-like, or rather, globular bodies. Flax, moss, and wool were bound loosely round sticks, which resembled much the lichens. mosses. &c.. which clothe forest trees, and also the Polypodium incanum, which, as Prof. Asa Gray declared, was abundant on those trees in the districts of North America in which this species of Bignonia abounds. Having placed the stick, thus prepared, near a tendril, the hooked points seized and penetrated the fibrous mass. The tips now began to swell, and in a few days "the hooks were changed into whitish irregular balls rather above $\frac{1}{20}$ of an inch in diameter, formed of coarse cellular tissue." The balls by their surface secreted a viscid resinous matter, which is soluble in ether, and which causes the fibres to adhere so that fifty or sixty fibres may be seen crossing a little ball at various angles. Sometimes eight discs are formed on the same tendril. After the discs are developed, spiral contraction of the tendrils occurs, and they become woody and strong. An analogous cellular layer, which secretes a resinous cement, was found by Darwin to be formed by the lower surface of the branches of the tendril of Hanburya mexicana, one of the Cucurbitacese, after it had, for a few days, grasped a In the Ampelopsis, as is well known, a similar stick. appearance is presented, and to that I shall presently refer.

In a fine specimen of B. capreolata which I had an opportunity of studying, I found the main petiole about half an inch long, and the sub-petioles of the two leaflets about one-quarter inch. The tarsus or tendril was evidently the terminal portion of petiole, though it bent down at an angle from the end of the leaf stalk. It ultimately divided into five and sometimes even seven branchlets or sub-tendrils, formed respectively by two or three pairs of representative leaflets with a terminal odd one, and three sub-tendrils ended in a bifid or trifid manner. Thus, on examining a tendril, five of these sub-tendrils were found all twined together, and on carefully separating them, the first pair were trifid at the extremity, the next pair had one bifid, and the other ending in a single point, and the odd or terminal sub-tendril was bifid.

On some portions of the front sticks a few suckers were found, but on the part of the stick at the back which was facing the wall the suckers were numerous, and very firmly attached to it, which was an unpainted one, by no means very rough, and which had no fissures. On a stick at the front where there was a growing shoot with tendrils, but no suckers, a flower-pot was inverted. On taking off the pot on the second day the shoot had grown about $1\frac{1}{2}$ inch, and the tendrils corresponding to the second last internode had, in some instances, at the bifurcations of the subtendrils, small sucker-like bodies formed, which became more distinct and numerous in a few days afterwards. I should have mentioned that the pot was replaced.

The suckers in some cases were attached firmly to the stem of the plant, and even to the edge of a leaf. Here, as in B. venusta, many discs were formed where no object whatever had been grasped, though in these instances the suckers seemed smaller than when an attachment had been effected.

We reluctantly pass over *Eccremocarpus scaber*, a native of Chili, belonging to the Bignoniaceæ, Cobæa scandens, one of the Polemoniaceæ, and some belonging to the Leguminosæ, and shall only touch on the Smilaces. The Smilax aspera var. maculata is well figured and described by Darwin. The tendrils in this case spring in pairs from the petiole, and are by some, as already mentioned, regarded as modified stipules, while others consider them to be changed petioles. It seems a difficult point to determine which party is right. After a careful examination of a dwarfed specimen of Smilax aspera, I was led to conclude that the minute tendrils were really petioles; but in the Smilax officinalis they seemed to be modified stipules, for the base of the petioles seemed thickened by what appeared to be a sheathing stipule, from the end of which the tendrils seemed to spring, or rather to be a continuation; this took place about half-way between the stem and the attachment of the leaf to the petiole. The tendrils of Smilax aspera are, according to Darwin, from 11 to 12 inch long. They are sensitive when rubbed on either side. They at first stand erect, but when old bend backwards and downwards, still, however, retaining their sensitiveness, and do not contract spirally in any case. Its stem is well supplied with spines, hence its specific name.

In contrast to this we have studied a fine specimen of Smilax officinalis, whose enormous leaves measured from the jutting backwards from attachment of petiole to the point of leaf 11 inches, and whose greatest breadth was 6 inches. One tendril was 7³ inches in length, and another was actually 9 inches. The stem and shoots were square, and exhibited twisting on themselves. The spines, which are mostly curved as hooks (but which in some cases are straight), are frequently given off in pairs, but also singly. In three instances the spines between several of the internodes were counted, and it was always found that the first and second internodes were destitute of spines, while on the other the spines varied from 2 to 12, and even 14. For example, a stem had spines on the internodes as follow: -1st, none; 2d, no spines; 3d, 2 spines; 4th, 12; 5th, 14; 6th, 6; 7th, 7; 8th, 7; 9th, 9; 10th, 9 spines. No more were counted, but there were 21 internodes on this stem.

On the internodes of a young shoot the spines were— 1st internode, no spines; 2d, no spines; 3d, 2 spines; 4th, 5; 5th, 7; 6th, 10; 7th, 6; 8th, 8; 9th, the spines had not broken through the epidermal covering, but the elevations pointed to their being 6 at least; 10th, which was the last internode formed as yet, was quite smooth, no spines having yet formed. On the internodes of an older shoot—1st, none; 2d, no spines; 3d, 1 spine. The tendrils of this species were seen distinctly spirally contracted when an object was caught.

On the Cucurbitaceæ, though deeply interesting as a whole, and specially so in the case of the North American annual *Echinocystis lobata*, and in that of the Mexican genus—whose name painfully reminds us of the loss we have sustained by the death of a distinguished pharmacologist—*Hanburya mexicana*, on these, I say, time forbids me to dwell, though Darwin's description of them will well repay a careful perusal. Under the Vitaceæ I shall omit all reference to the vine, and shall confine my few remarks to Cissus and Ampelopsis. In *Cissus discolor* the tendrils are formed of a long footstalk, bifurcating at the end, but the branches so formed are generally of unequal length. This disparity in length is much greater in *Cissus albo-nitens*. The long footstalk is sensitive, but not nearly to the extent that the

branches are, for the slightest touch is sufficient to cause these latter to curve; but these are equally sensitive on both sides, so that if they are drawn between the fingers no movement ensues-an important point to bear in mind, as Darwin ingenuously informs us that it once misled him. In one instance we found that a slight touch was followed in about two or three minutes by a distinct bending of the long footstalk, and after curving downwards towards a stick, it gradually moved round about 90°; this movement occupied about one hour; in about one hour and a half the tendril had become quite straight, and was back again to its old In about five minutes after being touched on its position. inner side, the smallest fork was curved slightly inwards. On the following day the footstalk of the tendril had caught the stick, and was closely applied to it for about half of its circumference, while the remaining half of the circle was completed by the branches or forks. The stick was 21 inches from the stem from which the tendril sprung; but in two days after this occurrence, three fine spirals were seen at the portion of the footstalk close to the stick. and now the contraction caused by this spiral movement brought the stem within 14 inches of the stick. On the second day after this three other spirals, but more open than the former, were formed; and on the day following another spiral was added. These spiral contractions which occur in tendrils which have caught a support seem designed to accomplish a twofold object-1st, to draw the shoot nearer the support, and thus facilitate the grasping of it by the subsequently developed tendril; and 2d, to diminish the strain to which a tendril without such an arrangement would be subject. Before performing its revolution in quest of a support, the *tendril* rises up, while the end of the shoot bends downwards so as not to arrest its progress.

Under Ampelopsis hederacea both the description and figures are admirable. Often have we studied the allied species A. tricuspidata and A. Veitchii, whose sucker-like pointed tendrils when fixed against a wall, especially when the branches of these are spirally contracted, present a most pleasing object. The closeness with which the stems are held to the wall, and the strong resistance which they offer to any attempt to remove them, show how admirably

adapted the provisions are for accomplishing the end in The discs consist of enlarged cells, with smooth view. projecting hemispherical surfaces, coloured red, and at first gorged with fluid, but ultimately becoming woody. By the solvent employed Darwin proved that the substance secreted was of a resinous nature, which would aid the cellular outgrowth (which insinuates itself into every crevice) in securely fixing the plant to its support. In proof of the tenacity of the branchlets of the tendrils, Darwin mentions that an old one was able to support a weight of 2 lbs., and he reckons that the whole tendril would, at the same rate, have resisted a strain of 10 lbs. I suspect, however, that the age in this case must have contributed largely to the result, for on selecting the terminal portion of a branch of Ampelopsis tricuspidata (which, however, had at that time been growing on a wall for only two months), which was fixed firmly by three tendrils, and attaching a weight of 4 lbs. to the lowest of the tendrils, the portion of the branch and its tendrils were pulled from the wall; and on examination it was found that the tendril nearest the end of the branch had one of its seven discs pulled away, while the other six were left adhering to the wall; the next tendril had left its six discs sticking to the stone; while the remaining one, which was attached entirely to lime, had six discs pulled off, and one left on the lime. If we could draw a conclusion from this observation, it would be that the discs, when attached to an unyielding surface, are quite able at an early period to resist a heavy pull, but that the other portions of the structure of the tendril require a much longer time for attaining that woody firmness and toughness which, in the case of Darwin's species, exhibited such remarkable tenacity. About five months afterwards four or five additional experiments were made on the same plant, which fully bore out our previous conclusion.

Experiment 1.—A portion of stem was chosen which was fixed by two tendrils, the tendril above having eight suckers, and that below having seven, all attached to stone. At 4 lbs. the centre of the stem broke across, while the tendrils and suckers remained intact.

Experiment 2.—A stronger stem was chosen with a tendril above bearing seven suckers, and one below with

five. With 4 lbs. of traction the lower tendril gave way at its attachment to the stem, but neither the branches nor the suckers yielded.

Experiment 3.—A stem chosen even thicker than the last, the upper tendril having nine suckers, and the lower one eight. In this case a traction equal to 6 lbs. was required before the tendrils gave way at the attachment to stem; the branches and suckers were uninjured.

Experiment 4.—Another tendril with eight suckers was itself subjected to direct traction, and at 4 lbs. two branches broke across just at their commencement, but the suckers did not yield. On trying still further with 4 lbs. weight, another gave way in a similar manner, the sucker still adhering to the stone.

Experiment 5.—Another tendril with eight suckers, at 4 lbs. all were broken similarly to above case, but the suckers remained unaffected.*

* In such a case as this of Ampelopsis, art and nature are strongly contrasted. The gardener with his cloth and nails can never fit the plant accurately to the inequalities of a wall, but in nature this is admirably effected. After the gardener has fixed his branch, every day has a tendency to allow greater latitude to its movements, while by the marvellous provision in nature of the contraction of the branches of the tendril they become day by day more closely drawn inwards. Again, the material used by the gardener is slowly but surely destroyed by constant exposure, while in nature, as we have seen, the longer the exposure the stronger the support becomes. To call these wonderful properties acquirements made by the plant itself, as Darwin would have it, and thus to attribute high mental qualities to the vegetable world, as my friend Dr Lauder Lindsay has done, is in my opinion equivalent to giving God's glory to another. The truth is at once clearly and beautifully expressed by the well-known words of the poet in reference to the coral polypes, which, *mutatis mutandis*, apply equally here :--

> "Omnipotence wrought in them, with them, by them. Hence, what Omnipotence alone could do, Worms did."

Facts similar to those which are supposed to justify the attribution of mind to plants are observed also in inorganic nature; thus the diffusion of gases, which acts in direct opposition to the force of gravity, and which secures the continued respirability of our atmosphere, is no less a proof of mind and design than are the phenomena observed in plants. The operations of mind are undoubtedly manifest throughout all nature, but it is the mind of the Creator who also sustains all things by the word of his power; and our ability to discover these proofs of mind is only a fresh testimony to the old revealed truth, that man was made in the image and likeness of God, in so far as *knowledge* at least is concerned.

Under the Sapindacese Darwin instances the Cardiospermum Halicacabum. We have only had one opportunity of studying a species of Cardiospermum from Mauritius. but as it was in a weakly condition and never flowered, we had no means of observing for ourselves many of the points to which Darwin alludes, but what we did observe fully corroborated the statements made by him. The flower peduncle terminates in three branches, the two lateral being the tendrils which, though at first straight, ultimately curl downwards, and in some cases, as where they caught no object, form a close and beautiful helix. The central branch divides and subdivides, and bears the flowers, but in some instances the homology is still farther declared by the three branches producing flowers. The movements of their upper internodes and of the peduncles bring the tendrils ultimately into contact with some twig or other body round which it curls. The value of having these organs of prehension and support so near the fruit has been well shown by Darwin, for "the seed-capsules, though light, are of enormous size (hence its English name of balloon vine), and as two or three are carried on the same peduncle" they are thus prevented from being dashed to pieces by the wind.

Paullinia thalictrifolia is at present being studied by me, but I have nothing definite as yet to report.

Darwin's account of the tendril-bearers is befittingly closed by introducing the Passifloraceæ. The tendrils in this order are also modified flower peduncles. One of Mr Darwin's sons found a very young tendril of P. floribunda with traces of floral organs at its summit. Passiflora gracilis (if we except P. acerifolia) is facile princeps of all twining plants, as the revolutions of its internodes are more rapid, and its tendrils endowed with more sensibility. Sometimes, indeed, as Darwin has shown, 57 or 58 minutes have sufficed for a revolution. The extreme sensitiveness is manifested only when the tendril is nearly fully developed. and at that period the most delicate touch or pressure causes a response. This effect has been noted when only $\frac{1}{20}$ grain has been placed upon its tip. Nor is this sensitiveness or irritability easily exhausted, for Darwin found TRANS BOT SOC. VOL. XII. 2 н

that in 54 hours it responded to the stimulus twenty-one times.

In *Passiflora punctata* the movement of the tendril was considerably accelerated when approaching the light, the semicircle towards the dark part of the room requiring 15 or 20 minutes longer than that in the opposite direction.

The tendrils in this genus are sometimes of considerable length; thus, one from P. racemosa when the spiral was straightened measured $9\frac{1}{2}$ inches, and the delicacy of the spirals and their perfect uniformity is a most pleasing object to contemplate. In one instance a tendril of P. racemosa had encircled a stick two or three times, and spirals began to show themselves at the part of the tendril next the stick, and in two days afterwards eight or nine spirals had formed.

As regards hook-climbers little need be said; sometimes, as in brambles and roses, &c., they seem to be the only means by which these plants can retain the positions which they may have reached in thickets, but in other cases the hooks are something superadded to some efficient mode of climbing, as we have seen in *Smilax aspera* and *officinalis*, and also in *Smilax deltoides*.

The root-climbers in some instances exhibit most interesting phenomena, and the description by Darwin of the roots of Ficus repens brings some of these most strikingly before us. He found that when it climbed up a wall, the young rootlets emitted a clear fluid of a slightly viscid character, which when removed from the root was very difficult to dry, some remaining still liquid at the end of 128 days. When left in contact with rootlets, however, the watery particles seemed to be absorbed, and a strong cement was formed. The cement was soluble in bisulphide of carbon, and seemed to be a kind of caoutchouc. We know that Ficus elastica, F. indica, and F. religiosa (or Urostigma elasticum, indicum, religiosum, as they are named by some) abound in caoutchouc, so that it is not unlikely that in F. repens, and also in F. barbatus, this substance may exist and be utilised.

Vanilla aromatica gives off aerial roots, which, according to Mohl, wind like tendrils round a thin support should they meet with it. Darwin says the roots are a foot in

length, but Mr Lindsay called my attention to a root of V. planifolia in a hothouse, which passed straight downwards into a water tank, and which on measurement, was found to be 9 feet 7 inches, and though this seemed to be the longest, yet others in its immediate neighbourhood (but not passing into the tank), did not fall far short of it in length, one being 7 feet 10 inches. Hedera Helix is of course the best known among us of the plants whose ascent is secured exclusively by roots; but there are other plants to which the roots merely supply supplemental organs, and sometimes these are comparatively small, as in $M^*Fadyena$, but at other times, as in Hoya carnosa, I have found them covering a large portion of a wall, and from the commencement of one of these roots to its termination, it measured $2\frac{1}{5}$ feet.

Such is a necessarily imperfect sketch of the contents of the last volume from Darwin's pen, but I trust enough has been said to prove that an interest of no ordinary kind surrounds the plants that climb, and I do hope that many of our Fellows who have the time and opportunity may make observations, and record them from time to time to this Society. It is an inviting field, and notwithstanding all that Darwin and others have done, many sheaves may yet be borne from it, for the climbing plants and all their peculiarities are "the wondrous works of Him who is perfect in knowledge," Job xxxvii. 16; and whose "understanding is infinite," Ps. cxlvii. 5.