The Mechanism of Curvature of Tendrils.

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With Plate XIX.

HISTORICAL AND GENERAL CONSIDERATIONS.

IN 1891 the writer began a series of experiments dealing with the features of growth and irrito-contractility of the tendrils of the Passifloreae. In 1892 a paper, concerning the principal features of the anatomy and morphology of the tendrils of *Passiflora coerulea* was published, and in the following year a second followed on the external phenomena of irritability and the coiling movements. In the course of the work many facts of significance in the determination of the mechanism of the movements, the localization of the motor zones, and the conduction of stimuli were brought to light. These facts, especially those concerning the first-named features, were much at variance with the generally accepted theories of tendril-curvature, and were not sufficiently verified by repeated observations at that time to justify their publication with my other work. With the accession of later results by myself and others, the conclusions which follow seem entirely warranted.

It may be useful in the following discussion to recall that complex organs of the higher plants which have the power of

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curvature effect the movement either by elongation of the tissues of the side of the organ becoming convex, or the contraction of a tissue on the concave side. As belonging to the first class, stems, petioles, and other organs which respond to geotropic and heliotropic stimuli, &c. may be mentioned; and to the second class, the pulvini of *Mimosa* and other plants, the tentacles of *Drosera*, the leaves of *Dionaea*, and other structures. It may as well be stated in the beginning, that my conclusions justify the assumptions of Charles Darwin, that the clasping-movements of such highly specialized, initially dorsiventral tendrils as those of *Passiflora* are produced by a contraction of the elements of a tissue on the concave (lower) side of the tendril. He says (I, p. 181): 'At first I attributed this movement to the growth of the outside; black marks were therefore made, and the interspaces measured, but I could not thus detect any increase in length. Hence it seems probable in this case and in others, that the curvature of the tendril from a touch depends on the contraction of the cells along the concave side.' A similar conclusion had previously been reached by Knight: 'The external pressure of any body on one side of a tendril will probably drive the fluid from one side of the tendril which will consequently contract, to the opposite side which will expand, and the tendril will thence be compelled to bend around a slender bar of wood or iron' (VI). From the above it is apparent that while the conclusion that tendrils effected contact curvatures by means of the contraction of the irritated side of the organ is to be accredited to Knight, yet it is clear that to Darwin must be ascribed the first comprehension of the real nature of such contraction. De Vries, by a series of comparative measurements of the growth of the convex and concave sides of tendrils (II), and later by a series of plasmolytic tests, was led to the belief that the curvature and coiling of these organs was due to an increased osmotic activity of the convex side resulting in an accelerated growth-extension of the tissues of this side. Sachs (XX) adheres in the main to De Vries' conclusions, yet he points out that a contraction of the lower side

may occur during curvature, and may amount to one-third of the original length of the organ ; and furthermore admits that in consequence of the relaxation and loss of water of the parenchyma of the concave side, the elastic contraction of the cell-walls may co-operate in producing curvature or coiling.

The mechanism by which the attachment of tendrils and other climbing organs to supports is accomplished, has undergone widely different methods and degrees of development in different groups. In some instances, attachment is made by means of disc-like suckers or outgrowths adapted to the surface to which adhesion is desirable. In others, the same purpose is accomplished by means of mucilage-masses secreted by groups of specialized cells. In others, attachment is by means of curvatures which more or less encircle the support. In the last-named group the tendrils may possess the power of contact-irritability over almost their entire surface, and be able to curve in any direction ; or the seat of irritability may lie on one side alone, which always forms the concavity of the curvature. After attachment to a support, the tendril generally throws its free portion into a number of loose coils, which results in shortening the distance between the shoot and support. In this manner as each internode successively develops, it is drawn up and fastened to the support. In order that this fixation may be effected economically, it is important that exact correlations should exist between the activities of the tendril and those of the shoot. It will be found, therefore, that rapidly growing plants are, in the majority of instances, furnished with tendrils of greatest sensibility and rapidity of reaction to contact, and conjointly the consequent free coiling of the tendril will be rapid and strong because of this power of rapid growth extended to the tendril. As examples of the smallness of stimuli which may cause a reaction may be mentioned the experiments of Charles Darwin (I, p. 171), in which it was found that a tendril of *Passiflora gracilis* responded when a weight of 1.23 mg. was gently laid upon it. Pfeffer found that while a stream of

water directed against a tendril would not cause a reaction, yet if some substance in the form of fine powder were suspended in the water, the repeated impact of these particles induced reaction, although their diameter was only $\cdot 04$ mm., and their weight must have been only a fraction of that used by Darwin. In further experiments by Pfeffer, a rider weighing $\cdot 00025$ mg. placed gently upon a tendril gave no reaction, but when it was moved by the wind, curvature resulted (XVII). It has come under the author's observation that a spider's thread, 43 cm. long, suspended above a tendril of *Echinocystis*, caused such reaction that the tendril coiled around and fastened to it. It will be found that a reaction in some of the more highly irritable tendrils of the Passifloraceae may be obtained in twenty-five seconds, while Müller (XIV) noted a curvature in the tendrils of *Cyclanthera* five seconds after stimulation. In many forms the latent period may extend over sixty to one hundred minutes.

The forces which act as stimuli upon the different types of tendrils sensitive to contact, appear to offer no means of distinction of the mechanism by which the reaction is accomplished. In general it may be said that clasping tendrils are sensitive to contact or repeated impact of solid bodies, but not to static pressure, or to shock such as that given by jarring the soil in which the plant stands, and to which *Mimosa* responds so readily, a generalization first stated by Pfeffer (XVIII, pp. 517-524). The distinct and important mechanical, anatomical, and physiological conditions to be found among tendrils which apparently react in a similar manner to identical stimuli, does not warrant the assumption that the reactions in all classes of tendrils are identical. Not only does this apply to the actual mechanism of movement, but also to that of the transmission of the effects of stimulation. Thus Pfeffer (XVIII) has found that the excision of certain tendrils, viz., *Sicyos angulatus* and *Passiflora gracilis*, was followed by the exudation of a drop of water from the exercised surfaces, a result which I have also obtained in all species of *Passiflora* and Cucurbitaceae examined. On the

other hand, this exudation does not occur in *Cobaea scandens* and other plants which exhibit a high degree of contact-irritability. When a stimulus is given to the perceptive zone, the region stimulated curves; if the stimulus is continuous the curvature strengthens, but the stimulus is not conducted farther than 2 or 3 cm. in either direction, according to Pfeffer and to my own observations. I have recently found that when tips of actively nutating tendrils of *Passiflora incarnata* were quickly cut away by means of a razor-stroke given from above, without otherwise touching the organ, a curvature of 90° was induced at a distance of 1 cm. from the cut surface, an effect which so far has not been obtained in any other plant.

The forms embraced under the general term of tendrils embrace organs of widely different anatomy and morphological derivation. This and the fact that the degree of vegetative activity, as well as the condition of, and manner in which, these organs accomplish the fixation of the plant-body to a support, will show the futility of the attempt to assign the mechanism of curvature to one type which shall apply to all those organs. The conclusions reached in this paper are therefore restricted to the actual forms of the Cucurbitaceae and Passifloreae examined. In any case, however, it is to be noted that it cannot be assumed *a priori* that the curvature of tendrils is similar to that of stems. An essential difference between the curvature of stems and of tendrils is based upon the primal fact that the curvature of a stem implies minor physiological changes in the curved organ, while this process in a tendril entails a complicated series of complete alterations in functions of the first magnitude. Furthermore, a sharp distinction is to be made between the processes of the formation of curvatures and that of loose coils. The first is a reaction to the stimuli to which a tendril will respond, while the second is consequent upon the maturity of the organ, a fact pointed out by Penhallow (XVII, p. 72). It has been repeatedly demonstrated that contact-stimuli are not conducted farther than 2 or 3 cm. at the most, and the formation of loose

coils in a tendril whose tip is attached to a support often begins at a point 25 cm. distant from the point of reception of the stimulus at the tip. The attachment of the tip of a tendril to a support by curvature exerts no direct influence on the free portion of the tendril, except by the traction exerted by the weight of the plant-body thrown upon it. The formation of the free coils of an attached and of an unattached tendril is found to differ only in so far as the effect of this mechanical strain is concerned. This is emphasized by reference to No. IV of the dynamometric tables, in which it is shown that a young tendril continued to elongate after its tip had clasped a support, and did not form coils until it had attained maturity. It is therefore necessary to exercise great care in the delimitation of the processes of curvature by which a tendril reacts to stimuli, and the processes of growth by which permanent coils are formed, in the analysis of the movements of these organs.

RESULTS OBTAINED BY VARIOUS METHODS OF EXPERIMENTATION.

In the research directed toward the determination of the mechanism of curvature, two methods of experimentation have been used in securing the data upon which conclusions have been based :—First, estimation of the relative turgidity of the tissues of the convex and concave sides by means of plasmolysis :—Secondly, measurement of the distance between two points on the convex and on the concave surface of the curving organ before and after contraction. In addition to a revision of the results obtained by these methods, it is proposed to throw additional light on the subject by an examination of the structure, form, and arrangement of the cells of probable motor zones in the convex and concave sides of the tendrils before and after induced curvature.

Measurement of elongation. Independently of his plasmolytic researches, De Vries found by measurements that in encircling a support the growth in length of the convex side of a tendril

was increased, and the growth in length of the concave side was lessened. Thus in a length of 1 mm., the increase on the convex side was 1.4 mm., on the concave side .1 mm., and in a neighbouring unstimulated portion, .2 mm. on both sides. These figures express the total amount of change during the formation of the contact-curvatures around the support, and the ensuing growth during a period of twelve to forty-eight hours. Further, both Sachs and De Vries agree that at times an actual contraction of the concave side occurs in many instances. In the tendril of the Gourd, the actual shortening of the concave side amounted to one-third the length of the tendril at time of stimulation (I, II, XX), a fact which is not adequately explained; and it may be shown that the changes in length of the portion of a tendril which are caused by a contact with a support, and which follow upon curvature around it, have been persistently misinterpreted.

In order to obtain the general features of growth-extension, a number of developing tendrils of *Passiflora coerulea* were marked off at intervals of 1 cm. by means of india-ink and a camel's hair brush. These intervals were re-measured each day during the period of nutatory movement and irritability. The marks were placed on the convex sides of the organs, which were held firmly during measurement by means of gelatine-coated clamps in such a manner that they were not stimulated. The data obtained are given in the table below. The figures expressing the length of the portion or portions in the region of maximum growth are given in thicker type.

By a consideration of the table on p. 380 it may be seen that the entire period of development of such tendrils occupies from 110 to 130 hours. The elongation in twenty-four hours of certain portions amount to 150 per cent. of their length; the elongation of the entire tendril during the same length of time amounts to 20-40 per cent. of its length; and the elongation of the region of maximum growth must have greatly exceeded the above rate during the twelve hours inclusive of the period of most rapid growth. The comparisons of De Vries of the growth of the portion of a tendril

Table of measurements of growth of tendrils of *Passiflora coerulea*.

I

Length of intervals.	Base.											Tip.	Total lengths.
Mar. 2, 10 a.m.	1	1	1	1	1	1	1	1	1	1	1	.5	11.5 cm.
„ 3, „	1.6	1.6	1.9	1.9	1.9	2	2.1	1.8	1.4	1.4	1.4	.6	18.8 cm.
„ 4, „	1.7	1.9	2	2.4	2.3	2.5	2.9	2.3	1.9	1.9	2	.8	24.5 cm.

II.

Length of intervals.	Base.							Tip.					Total lengths.
Mar. 2, 10.15 a.m.	1	1	1	1	1	1	.5						6.5 cm.
„ 3, „	1.9	1.9	1.7	1.9	1.7	1.6	.7						11.4 cm.
„ 4, „	2.1	3.4	4.2	3.8	2.6	2.5	1.						19.2 cm.
„ 5, „	2.4	3.8	4.9	4.4	3.7	3	1.1						23 cm.

III.

Length of intervals.	Base.				Tip.								Total lengths.
Oct. 4, 9 a.m.	1	1	1	1									4 cm.
„ 5, „	2.2	1.6	1.2	1.2									6.2 cm.
„ 6, „	3.	2.5	1.7	1.4									8.6 cm.
„ 7, „	5.	3.8	2.	1.8									12.6 cm.
„ 8, „	6.6	4.7	2.5	2.3									16.1 cm.

IV.

Length of intervals.	Base.							Tip.					Total lengths.
Oct. 3, 9.15 a.m.	1	1	1	1	1	1	1						7 cm.
„ 4, „	2.5	1.7	2.4	2	1.9	1.3	1.2						13 cm.
„ 5, „	3.1	2.5	3.4	2.6	2.1	1.6	1.6						16.9 cm.
„ 6, „	3.2	2.6	3.7	2.7	2.2	1.8	1.8						18 cm.
„ 7, „	3.6	2.8	3.8	3.1	2.4	2.1	2						19.8 cm.

encircling a support and of a free portion are wholly without significance, since he has failed to indicate the positions of the zones measured with regard to the region of maximum growth, which *in the earlier stages lies in the basal portion of the tendril, and progresses forward in an oscillating manner until it may occupy a position distal to the middle of the tendril, but from which it finally recedes.*

From the numerous measurements of the elongation of the convex surface of portions of tendrils encircling a support, the writer has never found an increase greater than 50 per cent. of the maximum given above, and De Vries' theory, that curvature around a support is due to the accelerated growth of the convex side, is no longer tenable. Furthermore, if the contact-curvature of the tendril were due to growth, it might be expected that the organ would be more highly irritable in the region of greatest growth, but the *zone of greatest growth never at any time coincides with the zone of greatest irritability, which lies near the tip.*

That a difference does exist between the features of growth of a portion of a free tendril and one which has encircled a support, is quite apparent. Such differences consist in a slightly lessened elongation of the convex side and a greatly decreased elongation of the concave side, which are to be considered as consequences, not causes of contact curvature. It is to be readily seen that when a tendril is coiled around a support by any force, whether internal or external, the pressure exerted upon the concave side from the support and the internal strains would exert a very marked effect on the growth of the tissue so affected. The alterations in the growth of a curved tendril, as described by Worgitzky (XXII), are exactly such as might follow from the altered mechanical conditions. These changes consist principally in the tangential division of the epidermal cells, followed by a thickening of their walls which extends in a marked degree to the collenchyma and cortical parenchyma, accompanied by a strong development of prosenchymatous tissue. In the mean time the growth of the

convex side of the tendril has continued unchanged, except for the reaction to the slight traction exerted upon it, and the difference between the two sides in the course of a few hours becomes quite marked.

PLASMOLYTIC INVESTIGATIONS.

The analysis of induced curves by means of plasmolyzing agents has been carried out at great length by De Vries upon tendrils of *Sicyos*, *Echinocystis*, *Bryonia*, *Cucurbita*, and *Passiflora*, as well as upon stems and other organs (II, III). He was led to the conclusion that the cells of the convex side of a curved organ contained a greater amount of osmotic substance than those of the opposite side, and that curvatures are produced by the excessive lengthening of the cell-membranes of this side due to the consequent increased turgidity. His first conclusion has been signally disproved by Wortmann (XXIII–XXVII), by Noll (XV), and by Kraus (VIII) so far as stems are concerned. In further consideration of the conditions of heliotropic and geotropic curvatures of stems, Wortmann believed himself to have proved that in curvature a segregation of the protoplasm on the concave side of the organ occurred, and that the membranes on this side became thickened and more resistant. The action of the uniform turgor stretched the thinner and more elastic membranes of the convex side. Kohl ascribes the curvature of stems to changes in form of the cells of the concave side due to their different elasticity in different directions (VII). Such changes of form were not described as a contraction, but rather as accompanied by an increase in volume. Noll has shown that the segregation of protoplasm on the concave side is a result that has no causal relation to curvature. His conclusions, which are strengthened by his more recent work (XV), point to the variations in the plastic and elastic extensibility of the membranes of the convex side under the regulatory power of the protoplasm as the chief factor. These conclusions, however, relate especially to curvatures of stems, petioles, &c.,

and he calls especial attention to the fact that the elongation of the longitudinal membranes is in no sense growth, since their dry weight does not increase. The only recent work dealing with the mechanism of the tendril alone is that of Penhallow (XVII, p. 75), in which he concludes that 'movements due to irritation depend upon the continued elongation of the opposite side, together with cessation of growth and contraction in the irritated parts.' In support of this conclusion, however, no additional facts, except the accentuated development of the collenchymatous tissue of the concave side, are given.

While, as noted above, it has been proved that the convex side of curving organs does not show a preponderance of osmotic substance, in opposition to the conclusions of De Vries, it is evident that such conditions would be of value only in conjunction with certain mechanical features. Moreover, I have been unable to verify the immediate facts of De Vries' plasmolytic researches on tendrils of *Sicyos angulatus*, *Cucurbita Pepo*, *Bryonia dioica*, *Echinocystis lobata*, and *Passiflora gracilis*. He found that the plasmolysis of freshly induced curvatures of stems and tendrils resulted finally in the lengthening of the radius of curvature, perhaps to such extent that the organ became straightened. At first, however, a minor amount of shortening of the radius occurred. That such may be the case with geotropically or heliotropically induced curvatures of stems and petioles under certain conditions is confirmed; but is by no means invariable, as has been shown by Wiesner (XXI). O. Müller (XIV) found that the plasmolysis of tendrils, stimulated or unstimulated, might be followed either by increased or decreased curvature, in accordance with certain unexplained inward differences.

My own results are completely at variance with those of De Vries, and differ from those of Müller in that with weak solutions plasmolysis invariably resulted finally in the shortening of the radius of curvature, in both stimulated and unstimulated organs, and this decrease continued with minor variations so long as they were alive. The following data,

taken at random from my note-book, will fully illustrate this point.

Plasmolytic experiments. Plasmolysis was effected by means of a 1 per cent. solution of potassium nitrate in a flat porcelain dish, in which the tendrils were gently placed. During the preparation they were unavoidably slightly stimulated, and their stature is noted in the first line of the description of each experiment.

I.

- Dec. 24, 9.15 a.m. Tendril of *Cucurbita*, 18 cm. long, with tip curved through 300° , with radius of 1.5 cm. placed in solution.
 „ 9.30 a.m. 3 complete circles with a radius of 6 cm.
 „ 12 a.m. 4 circles.
 „ 2.30 p.m. $3\frac{1}{2}$ circles.
 Dec. 25, 10 a.m. $1\frac{1}{9}$ circle.
 „ 4 p.m. Same.
 Dec. 26, 9 a.m. Same.
 Dec. 27, 11 a.m. Same. Placed in distilled water.
 „ 2 p.m. $1\frac{2}{3}$ circle.
 Dec. 28, 2 p.m. $3\frac{1}{2}$ circles.
 Dec. 29, 2 p.m. Curves strengthened.

II.

- Dec. 24, 9.15 a.m. A tendril of *Cucurbita*, 25 cm. long, with curve of 250° at tip, with radius of 4 cm. placed in solution.
 Dec. 24, 9.30 a.m. 4 circles with a radius of .2 to .4 cm. were formed at the tip; entire tendril curved through 180° .
 Dec. 24, 12 a.m. 5 circles at tip. Curve of tendril strengthened.
 „ 2.30 a.m. 5 circles. Curve of tendril of shorter radius.
 Dec. 25, 10 a.m. $6\frac{1}{2}$ circles. Curve of entire tendril 320° .
 „ 2 p.m. 7 circles. $1\frac{1}{9}$ circle in entire tendril.
 Dec. 26, 9 a.m. 7 circles. $1\frac{1}{6}$ circle in entire tendril.
 Dec. 27, 11 a.m. 8 circles. $1\frac{1}{2}$ circle in entire tendril. Placed in distilled water.
 Dec. 27, 2 p.m. Curves contracted.
 Dec. 28, 2 p.m. Curves contracted.

III.

- Dec. 24, 9.15 a.m. A tendril of *Cucurbita*, 20 cm. long, was placed in a solution.
- „ 10 a.m. The tip curved 320° with radius of .3 to 1.3 cm. Entire tendril curved 20° .
- „ 12 a.m. No change.
- „ 2.30 p.m. Curves decreased to 240° . Entire organ straightened.
- Dec. 25, 10 a.m. $1\frac{1}{9}$ circle.
- „ 4 p.m. Same.
- Dec. 26, 9 a.m. Same.
- Dec. 27, 11 a.m. $2\frac{2}{9}$ circles. Placed in distilled water.
- „ 2 p.m. Curve $3\frac{1}{2}$ circles.
- Dec. 28, 2 p.m. Curve contracted.

IV.

- Dec. 24, 9.15 a.m. Tendril of *Cucurbita*, 20 cm. long, placed in solution.
- „ 10 a.m. Tip of main tendril in 3 circles of radius of .4 to 1 cm. $1\frac{1}{2}$ circle in branch.
- „ 12 a.m. No change.
- „ 2.30 p.m. No change in main tendril. Curve of 300° in branch.
- Dec. 25, 10 a.m. $1\frac{1}{2}$ circle in main tendril. Curve of 300° in branch.
- „ 4 p.m. Curve of $1\frac{2}{3}$ circle in main tendril. Curve of 300° in branch.
- Dec. 26, 9 a.m. Same in main tendril. 1 circle in branch.
- Dec. 27, 11 a.m. Curve of 350° in main tendril. 2 circles in branch. Placed in distilled water.
- Dec. 28, 2 p.m. 3 circles in main tendril. $2\frac{1}{2}$ circles in branch.
- Dec. 29, 2 p.m. No change.

From the long continuance and variations in changes in the stature of the tendril, both in the plasmolysing fluid and in distilled water, it is evidently unsafe to draw conclusions as to the initial osmotic conditions, since the resulting movements

must also be largely influenced by the degree of development of the mechanical tissues, and the elastic extensibility of the walls of the mobile tissues. In order to ascertain the conditions resulting in the active cells, tendrils of *Passiflora* which had been plasmolysed in 2, 3 and 4 per cent. solutions of potassium nitrate, and allowed to remain in the solution until killed, were carefully hardened by the use of series of alcohol-mixtures and stained. In the parenchymatous tissues of both the concave and convex sides of the tendril, the cells were strongly plasmolysed, so that the protoplasts were in a large number of instances torn completely from the wall. The differences in form and size of the cells of the convex and concave sides make comparisons difficult, but it was apparent that the outer rows of parenchymatous cells of the concave side immediately internal to the collenchyma had lost their oblong ovoid form and become irregularly globoid. In these cells the ectoplasmic layer was barely separated from the wall, while in the cells of the convex side, whose walls retained their normal stature, the separation was quite distinct, and the protoplast enclosed no more than a half or two-thirds of the volume of the cell. The only satisfactory explanation of such conditions is that the solution, while it simply plasmolysed the cells of the convex side which retained their normal stature, acted as a stimulus on the contracted cells of the concave side, upon which the ectoplasm became extremely permeable to water and allowed the sap to escape. The elastically extended walls of the plasmolysed and mechanical tissues contracted simultaneously, indirectly causing the curvature of the tendril, immediately after immersion in the plasmolysing fluid. The solution afterwards penetrated the wall of the contracted cells sufficiently to slightly plasmolyse them. The continued curvature of the organs, when placed in distilled water, can only be due to conditions similar to those prevailing in loosely coiling mature tendrils, the most important feature of which is the loss of the power of growth and turgidity of the parenchymatous cells of the concave side.

STRAINS EXERTED IN CURVATURE AND FREE COILING.

Still farther insight into the amount and character of the forces concerned in the rapid formation of a curvature in response to contact, and the formation of free coils, is offered by the data obtained from a careful measurement of the strains set up during such processes. To this end tendrils of *Cucurbita* and *Passiflora* were placed in horizontal and upright positions with the base firmly fixed to a support, and extended as far as possible, and the tip attached to a Vöchting's dynamometer (X) in such manner that the strain set up by any curvature in the organ would be directly indicated on the sliding scale carried by one of the compass arms of the instrument. In such experiments attention was also given to the relative effect of the turgidity of the plant upon the strain exerted by the free coils, the time necessary for the formation of the coils, and the effect of irritation upon the coiling portions. A large number of such tests were made, of which those detailed below are fairly illustrative.

I.

Sept. 25. After fastening the stem of a Gourd firmly to an iron post at the base of a tendril 35 cm. long, the tip was placed loosely in the attachment hook of the dynamometer, so that the body of the tendril was loosely held between the stem and the dynamometer. After it had formed a strong curve at the point of attachment with the dynamometer, the latter was fastened firmly in a horizontal position, with the tendril vertically extended, and exerting a strain of less than 1 gram.

Sept. 27, 8 a.m. A series of wide coils were forming, inducing a strain of 2.5 grams; at 6 p.m. 8.5 grams. The radius of the coils had increased from .5 cm. to 2 cm.

Sept. 27, 8 a.m. The strain amounted to 12.5 grams. The sun shone directly upon the tendril (and upon the terminal portion of the plant, 2 M. in length, all day) during the forenoon.

Sept. 27, 10 a.m. The strain had decreased to 11 grams, and with the shading of the tendril it immediately began to increase.

Sept. 27, 12.30 noon. The strain amounted to 12.5 grams. The temperature of the plant-house at this time rose to 27° C., the leaves of the whole plant assumed a wilted drooping position, and the strain at 3 p.m. fell to 11.5 grams. Four litres of water were then applied to the soil about the roots. After pouring on the water an increase of tension began, which at 3.15 amounted to 12 grams, and at 3.30 to 13 grams; 6 p.m. to 14 grams; 9 p.m. to 15 grams, which was the capacity of the dynamometer. The strain remained fixed at that point at 8 a.m. on the 28th.

II.

Sept. 14. A tendril of *Passiflora incarnata* was attached by the hooked tip to the dynamometer, which denoted a strain of .5 gram. After twenty minutes, when the strain was zero, the entire under surface of the tendril was stimulated by rubbing. A tension of .2 or .25 gram was set up, and the organ was thrown into a number of curves which gave it an undulating outline. In an hour this tension had disappeared.

Sept. 15, 8 a.m. The dynamometer showed a strain of .25 gram. The hooked tip had contracted still further, elongated and encircled the hook of the dynamometer.

At 5.30 p.m. the strain had increased to .5 gram, and the tendril had formed a number of loose coils.

III.

Oct. 9, 1 p.m. A tendril of the Gourd was fastened in an inverted position with the tip attached to the dynamometer, with a strain of .75 gram and a temperature of 30° C.

Oct. 10, 4 p.m. Sunny Temperature 22° C. Readjusted to .5 gm.

Oct. 11, 8.30 a.m. „ „ 16° C. Tension 3 „

„ 12 a.m. Cloudy „ 25° C. „ 4.5 „

„ 3 p.m. „ „ 22° C. „ 7 „

Oct. 12, 8 a.m. Sunny „ 19° C. „ 9.5 „

„ 10 a.m. „ „ 20° C. „ 9.5 „

„ 4 p.m. „ „ 28° C. „ 10 „

Oct. 14, 10 a.m. „ „ 32° C. „ 7 „

Oct. 15, 8 a.m. „ „ 14° C. „ 8 „

IV.

Oct. 6, 8 a.m. A tip of a tendril of *Cucurbita* fastened to dynamometer.

Oct. 6, 4 p.m.	Sunny	Temperature	14° C.	Tension	1.5 gm.
Oct. 7, 10 a.m.	"	"	14° C.	"	3 "
" 11 a.m.	Cloudy	"	14° C.	"	3.5 "
" 12.30 a.m.	"	"	16° C.	"	3.5 "
" 4.30 p.m.	"	"	12° C.	"	4 "
Oct. 8, 8 a.m.	Sunny	"	13° C.	"	4 "
" 10 a.m.	"	"	23° C.	"	3 "
" 11 a.m.	"	"	24° C.	"	3 "

A rapid increase in length made a readjustment of the dynamometer necessary at 4 p.m. The tension was made the same as in the last observation.

Oct. 9, 8.30 a.m.	Sunny	Temperature	15° C.	Tension	2 gm.
" 10 a.m.	"	"	24° C.	"	5.5 "
" 12 a.m.	"	"	35° C.	"	6 "
" 3 p.m.	"	"	35° C.	"	7.5 "
" 6 p.m.	Sunset	"	21° C.	"	11 "
" 10 p.m.	Dark	"	35° C.	"	15 "

V.

Oct. 20, 10 a.m. Branch of tendril of *Cucurbita* attached in horizontal position to dynamometer.

Oct. 20, 4.30 p.m.		Temperature	29° C.	Tension	2 gm.
Oct. 21, 9 a.m.		"	20° C.	"	3 "
Oct. 22, 8 a.m.	Sunny	"	29° C.	"	4.5 "
" 11 a.m.	Leaves wilted	"	36° C.	"	3.5 "
" 12 a.m.	Cloudy	"	31° C.	"	4.5 "
" 1.30 p.m.	"	"	27° C.	"	5 "
" 4.30 p.m.	"	"	20° C.	"	6 "
Oct. 23, 8 a.m.	"	"	31° C.	"	4.5 "
" 3 p.m.	Sunny	"	36° C.	"	5 "
" 5 p.m.	"	"	23° C.	"	6 "
Oct. 24, 8 a.m.	"	"	17° C.	"	5.5 "
" 11 p.m.	"	"	28° C.	"	5 "

VI.

Oct. 31, 8 a.m. Tendril of *Cucurbita* in horizontal position attached to dynamometer. (Cloudy during the entire exp.)

Oct. 31, 10 a.m.	Temperature	18° C.	Tension	1	gram.
Nov. 1, 8 p.m.	"	20° C.	"	3.5	"
" 5 p.m.	"	21° C.	"	4.5	"
Nov. 2, 8 a.m.	"	18° C.	"	7	"
" 11 a.m.	"	17° C.	"	7	"
Nov. 3, 10 a.m.	"	12° C.	"	6.5	"
Nov. 4, 3 p.m.	"	17° C.	"	6	"
Nov. 6, 1 p.m.	"	18° C.	"	6	"

VII.

Oct. 24, 8 a.m. A tendril of *Cucurbita*, 28 cm. long, attached in horizontal position to dynamometer.

Oct. 24, 11 a.m.	Sunny	Temperature	28° C.	Tension	1	gram.
" 2 p.m.	"	"	30° C.	"	1.5	"
" 3 p.m.	"	"	25° C.	"	2	"
Oct. 25, 8 a.m.	"	"	19° C.	"	4.5	"
" 11 a.m.	"	"	28° C.	"	5	"
" 5 p.m.	Dark	"	19° C.	"	9	"
Oct. 26, 8 a.m.	Sunny	"	17° C.	"	14.5	"
" 11 a.m.	"	"	36° C.	"	10.5	"
" 5 p.m.	Cloudy	"	23° C.	"	13.5	"

VIII.

Oct. 16, 8 a.m. Tendril of *Cucurbita* attached in perpendicular position to hook of dynamometer.

Oct. 16, 11 a.m.	Temperature	38° C.	Tension	2	grms.
" 4 p.m.	"	30° C.	"	3	"
" 6 p.m.	"	26° C.	"	4	"
Oct. 17, 10 a.m.	"	23° C.	"	5	"
" 12 a.m.	"	23° C.	"	5	"
" 6 p.m.	"	21° C.	"	7	"

Oct. 18, 8 a.m.	Temperature	13° C.	Tension	7 grms.
„ 11 a.m.	„	25° C.	„	6 „
„ 5 p.m.	„	24° C.	„	7 „
„ 6 p.m.	„	20° C.	„	8 „
Oct. 19, 8 a.m.	„	18° C.	„	10 „
„ 10 a.m.	„	24° C.	„	8 „
„ 1 p.m.	„	34° C.	„	9 „
„ 4 p.m.	„	33° C.	„	9 „

From the data given in the preceding tables it may be seen that the fixation of any portion of a tendril to a support does not induce the formation of coils in the free portion of the organ by transmission of a contact-stimulus. This is demonstrated by the fact that in a large number of experiments, after the tip of the tendril had clasped the dynamometer-hook, its extension in length made an alteration in the distance from the base of the tendril necessary (see Exp. IV). The formation of coils in the free portion of the tendril depends upon inequality of growth of the convex and concave sides, and may be induced by an artificial mechanical traction, or by the weight of the stem depending upon it, only when the period of growth of the organ has been nearly completed. The application of brief contact-stimuli to the irritable surface of the free portion of the tendril, in no wise modified the manner and time of the formation of the free coils. Such stimuli caused the formation of weak curves exerting an additional strain of .2 to .4 grams, which disappeared with the removal of the stimulus. The increase in the strain exerted upon stimulation speaks simply of a release of tension of the concave side and of a similar amount of unbalanced tension of the convex side. On the other hand, the decrease in the strain exerted by a tendril of a wilted plant must be due to the lessened tension of the entire organ due to an insufficient water supply. The decrease of strain exerted by a fully matured organ may be ascribed to the loss of turgidity of the parenchymatous cells. The lesser strain of old tendrils is due entirely to the elasticity of the mechanical elements which were built up while the organ was held in a coiled position by the turgidity of the

active cells. After a tendril has reached the end of the grand period of growth, the formation of free coils in either an attached or unattached tendril of *Cucurbita* occupies from ten to eighty hours, and is modified only by the traction exerted by the weight of the stem which it supports. The manner in which strains may arise or be induced, and their continuance, point to the conclusion that curvature in response to contact-irritation and the formation of free coils are entirely distinct physiological processes

ANATOMY AND MORPHOLOGY.

The most important facts in the localization and determination of the action of the motor zones would be those obtained by a consideration of the anatomy and morphology of the tendril with especial reference to the structure and arrangement of the parenchymatous tissue lying between the vascular and epidermal systems. Curiously enough an examination of the changes in structure and stature of these cells for the foregoing purpose has not heretofore been made.

Although the work in hand has been extended to cover a large number of species of Cucurbitaceae and Passifloreae, it will be most convenient to restrict the discussion to the above-named features of *Passiflora coerulea*, *P. incarnata*, and *P. Pfordti*, which the author has had under more or less constant observation for several years. The tendrils of these species are tapering filamentous organs of ovoid cross-section, attaining a length of 20 to 30 cm., and a diameter at base of 2 mm. decreasing at the tip to 1 mm., which for a length of .5 cm. is curved into a characteristic hook-form. The tendril makes its appearance as a lateral conical projection from the growing point, in the axil of a leaf (XXII), and shortly by reason of the accelerated growth of the periblem, there is formed, on the summit of the cone, a cup-shaped depression, which becomes more and more marked, and by reason of the excessive growth of the convex (upper) side of the tendril it faces laterally (or downward) when the tendril

has reached a length of 3 cm. This unequal growth also accounts for the hooked-shape formation of the tip. The cup-shaped cavity seems to be confined to tendrils of Passifloreae, and so far as the observation of the author extended, it has been found to subserve no mechanical or other use, although it is possible to imagine it might prevent to a slight extent the slipping of a tendril away from a support before a curvature had been formed. It is altogether probable on the other hand that this cup-shaped cavity is entirely a vestigial structure in the transformation of a leafy branch into a tendril; a conclusion justified by the fact that I have, in several instances, found the walls of this cup extended into a leaf-like lamina. Similar structures were observed by von Mohl (XIII). This is in accordance with the conclusions of Russell (XIX) as to the morphology of the tendrils of the Passifloreae. 'En résumé, la vrille des Passiflores représente un rameau axillaire modifié qui peut avoir à sa base plusieurs rameaux secondaires dépourvus de feuilles axillantes. Celui qui représente la première ramification se développe toujours, et peut donner, soit un rameau feuillé remplaçant le rameau axillaire transformé en vrille, soit un pédicelle floral, simple ou ramifié. Les autres qui n'existent que dans la région florifère deviennent des pédicelles floraux ou bien avortent en tout ou en partie.'

While no attempt has been made to determine the changes in the tissue directly connected with the curvature alone of tendrils, yet much attention has been given to their general anatomy and to the alterations of structure consequent upon curvature and coiling. Penhallow has described the anatomy of the tendrils of *Cucurbita maxima* and *C. Pepo*, and of *Vitis cordifolia* (XVII); A. Fischer, the general structure of the tendrils of Cucurbitaceae (IV); and Otto Müller has devoted considerable attention to several species of the Cucurbitaceae (XIV). Worgitsky has recently made a comprehensive investigation into the comparative value of the mechanical tissues and their arrangement in a large number of species representing many genera (XXII) inclusive of *Passiflora*.

A clear comprehension of the results presented below necessitates the delineation of the general features of structure of the tendril of *Passiflora coerulea*.

STRUCTURE OF THE TENDRILS OF PASSIFLORA (IX).

An examination of these organs was first made by Hugo von Mohl (XIII, p. 3, Figs. 4 and 5, Pl. II); he describes the structure, as seen in cross-section, as follows: 'Die Rinde besteht aus regelmässigen grünen Zellen (a); an der Stelle wo sie mit dem jungen Holze (b) zusammenstösst, liegen die Baströhren in getrennten Bündeln (c). Der Holzkörper besteht aus feinen Spiralgefässen und dickwandigen Holzzellen, die Markzellen (e) sind in die Länge gestreckt;' and later by Worgitsky (XXII), in which work it is to be noted that chief attention was paid to the distribution of the tissues in cross-section.

In longitudinal section the epidermal cells are somewhat uniformly rectangular in outline, with the long axis parallel to the long axis of the tendril. The protoplasts occupy a large proportion of the cell cavity. The nucleus, especially on the concave side, generally lies against the inner wall. The protoplasm is richly granular, but more markedly so in the concave side; moreover the proportion of granular substance gradually increases in the cells of the concave side from the base to a point near the tip, in a manner corresponding quite exactly with the degree of irritability exhibited by the respective areas included. This fact may be demonstrated by staining longitudinal sections in eosin and haematoxylin as I have previously shown (IX). When so prepared, the gradation in density is appreciable with a magnification of 50 diameters. The outer walls of the concave side are slightly arched outwardly, and are only cuticularized after maturity. These convexities must greatly increase the delicacy of perception of stimuli. Any solid body applied to their surface would in consequence touch the crest of these convexities, and the shock of impact, or pressure of contact,

would be communicated directly to the ectoplasmic layer on the opposite (inner) side of the wall of the cells touched, which under ordinary circumstances would be several in number. The failure of the impact of liquids at ordinary temperatures to produce a reaction, is probably due both to the smallness of shock and the fact that it is received over the entire outer surface of the wall. Pfeffer has noted an extension of the ectoplasmic layer into the outer wall of the epidermal cells of the irritable surface of tendrils of *Cucumis sativa* (XVIII, p. 525), a structure absent from any other material examined by him or myself. The epidermal layer is broken in places by stomata, which communicate with the cortical parenchyma by very narrow intercellular passages. The collenchyma-layer is one, two, or three cells in thickness. The tangential walls are much heavier, and show a number of perforations. No great difference in these respects can be made out between the concave and convex sides. The protoplasm of the concave side almost completely fills the cells, and is very densely granular, in marked distinction to that of the convex side. Moreover the contents of the collenchyma-cells of the concave side, when treated with a mixture of eosin-haematoxylin, take on a yellowish violet tinge, due to the absorption of the eosin by the innumerable minute granules which it contains. The marked difference between the contents of the collenchymatous tissue of the two sides, favours the presumption that the densely granular condition of those of the concave side bears some connexion with the transmission of impulses transversely or longitudinally; although it is not to be forgotten that the granular contents are used during the thickening of the cell-walls, after continued curvature, and their presence might be solely as reserve substance. The parenchymatous tissue internal to the collenchyma exhibits marked differences in form and behaviour. The parenchyma cells of the concave side are longer in proportion to their width than those of the convex side, and their absolute length is no greater than those of the convex side (IX, Pl. XIV, Figs. 2, 3), while their diameter is less.

Furthermore the cells of the concave side are provided with tapering ends, and the end walls are united over a small area only. As a consequence of this arrangement, the intercellular spaces are large. The cells of the convex side are united more completely across the ends, and the intercellular spaces are relatively smaller. The protoplasm of the elements of this tissue in the concave side is much more densely granular, and occupies a much greater proportion of the cell-cavity than in the convex side. The parenchymatous cells are arranged in four or five layers on both the concave and convex side of the tendril, but owing to the greater diameter of the cells of the convex side, the tissue of this side attains a marked preponderance in thickness. The two outer layers are furnished with chloroplasts varying from 6 to 10 in number in each cell. The parenchymatous tissues of both the cortex and pith exhibit marked infoldings of the walls. In tendrils exposed to strong sunlight, a reddish cell sap is found in numerous cells both in the epidermis and cortex of the convex and concave sides. Previous to the maturity and coiling of the tendril, the prosenchymatous and tracheary tissue are not developed to such extent as to be of great mechanical value. The arrangement of the vascular elements conforms to the outline of the tendril and its mechanical needs. The chief mechanical element during the irritable stage of the tendril is the collenchyma-cylinder, which as well as the epidermis and vascular tissue must be in a state of extreme elastic extension, due to a small extent to their own turgidity and to the excessive turgidity of the parenchymatous cells. Under such circumstances curvature might result from an increase in the extensibility of the walls of the convex side, or by a loss of turgidity or by an active contraction due to the loss of elasticity of the walls of the cells of the concave side. The contour of the parenchymatous cells of the two sides after plasymolysis as already described before curvature, after curvature, and in a mature coil which has fastened around a support, offers some conclusive evidence in favour of the latter view.

Action of the parenchymatous cells in plasmolysis, curvature, and coiling. During the course of my work on the morphology and anatomy of the tendrils of *Passiflora coerulea* I had occasion to examine many hundreds of cross and longitudinal sections of the irritable portions which had been killed by immersion in acetic alcohol. The changes in the stature of the cells of the concave side were marked and significant, and seem to offer a complete solution of the problem. When active tendrils are placed in the acetic alcohol solution, they execute a number of rapid oscillating curvatures and are shortly fixed by the action of the reagent. In such tendrils the parenchymatous cells had all been slightly plasmolysed before fixation. The outer two or three layers of the cells of the concave side had been moreover diminished in length from 20 to 40 per cent in size, and taken on a globoid form quite similar to that attained in simple plasmolysis. By reason of such change of volume and shape, the surfaces of contact with the neighbouring cells had been greatly diminished. The contraction of the protoplast around the central vacuole had almost obliterated it. At the same time numerous aggregation-bodies had been formed. On the convex side of the organ, the more attenuated protoplasts were not so much affected, and only modifications of minor importance had occurred, and the aggregation-bodies were noticeably absent. It seems entirely warrantable to connect the structure and behaviour of the cells of the concave side with the curvature of the tendril, especially since these features correspond almost exactly to certain characteristics of other known contractile cells. The action of the stimulus upon the cells of the motor zone, which are highly turgid, doubtless results in an increase of the permeability of the protoplasm and the consequent escape of water into the intercellular spaces. The outward passage of the fluid is facilitated by the highly-porous condition of the walls. This loss of water allows the elastic contraction of the highly-stretched walls of the cells affected, and also of an amount of contraction of the collenchymatous epidermal and vascular

tissues equal to the stretching force previously acting upon them. The contraction is not due directly to a muscular contraction of the protoplasts as has been suggested by MacFarlane in connexion with his work upon *Dionaea* (XI), but to the release of an expansive force exerted up to the moment of the movement of contraction. The action of the stimulus in either instance doubtless results in the sudden release of chemical energy, due to new affinities set up, and is accompanied by the excretion of carbon dioxide, water, and other substances. The great volume of the intercellular spaces of the motor tissues would admit of an extension of a much greater quantity of water than that necessary to allow the ordinary amount of contraction, and the return of the motor cells to their normal stature would be accompanied by the reabsorption of the intercellular fluid. *The greater density of the protoplasm of the concave side, the richness of its granular contents, the formation of aggregation-bodies, and the alterations in stature and volume of the parenchymatous cells of the concave side, lead to the conclusion that it is to the action of these cells that contact curvatures are due.*

RECAPITULATION.

The contents of this paper may be briefly summarized as follows:—

1. The power of curvature is characteristic of organs of such widely different morphological value and physiological function that it cannot be assumed *a priori* that the mechanism of reaction is similar or identical in them all.

2. Two general methods of curvature are known to prevail in various organs of different species. The curvature of stems, petioles, and peduncles, in response to heliotropic and geotropic stimuli, is supposed to be due to elongation of the convex sides of these organs. The movements of pulvini, tentacular hairs of *Drosera* and the leaves of *Dionaea*, and similar phenomena in other plants, is known to be due to the action of cells on the side becoming convex.

3. Tendrils, irritable to contact, exhibit the greatest difference in morphological derivation, anatomy, and degree of irritability, and it cannot be assumed that their mechanism is identical.

4. The curvature of such highly developed, initially dorso-ventral organs as the tendrils of the Passifloreae is due to the contraction of the tissues of the concave side.

5. The curvature of a tendril around a support as a direct reaction to irritation, and the coiling of a free portion of a tendril are entirely distinct, and to a great extent independent processes. The first is due to the action of tissues on the concave side of the organ, the second to the excessive growth of the convex side, and is probably preceded or accompanied by the relaxation of the tissues of the concave side consequent upon loss of irritability.

6. The curvature of a tendril around a support does not accelerate the growth of the convex side. The growth-extension of a coiled portion of a tendril is rarely equal to that of a similar region in a freely nutating organ.

7. The region of maximum growth lies between the middle of a tendril of *Passiflora* and the tip, and never at any time coincides with the region of greatest irritability.

8. The plasmolysis of stimulated or unstimulated tendrils generally results in a shortening of the radius by the contraction of the outer layers of parenchymatous cells of the concave side.

9. The attachment of a tendril to a support influences only in a minor degree the growth and formation of coils of the free portion of the organ. Such influence is due primarily to the traction exerted upon the organ by the weight of the shoot, not to a conduction of the contact stimulus.

10. The amount of strain capable of being exerted during the coiling of the free portion of a tendril is a specific characteristic, and generally is greatly in excess of the weight of the shoot to be supported and drawn upward by the organ. A tendril of *Passiflora* may exert a strain amounting to 10 grams, while that of *Cucurbita* may exert a strain of 30 grams.

11. The strain exerted by a tendril during contact curvature is less than .5 grams. Rapidity, not force, is essential to the effectiveness of such curves.

12. The time of formation of coils in the free portion of a tendril extends over 6 to 40 hours.

13. The latent period of a contact-reaction varies from 5 seconds to an hour in different species.

14. Marked differences exist between the structure of the protoplasm of the convex and concave sides. The protoplasm of the concave side is more richly granular, and occupies a greater proportion of the cell-cavity than on the convex side. The density of the protoplasm of the convex side increases from the base toward the tip, and apparently corresponds with the degree of irritability to contact exhibited.

15. The parenchymatous cells of the concave side are markedly different in outline, structure, and form from those of the convex side. When plasmolysed they undergo a decrease in size amounting to 20 to 40 per cent. of their original volume, and changes in contour from oblong-ovoid to irregularly globoid or ovoid. During curvature they undergo similar alterations. After curvature they are found in such condition, and to their action must be ascribed the contact-curvatures of the tendrils under examination. This action consists in an increase in the permeability of their protoplasts, a consequent extrusion of water into the intercellular spaces, and a release of the stretching tension exerted upon their walls of the vascular, collenchymatous, and epidermal tissues. The elastic contraction of these cell-walls causes the resultant curvature. This action ensues in free portions of attached tendrils upon maturity, and early in the process of the formation of loose coils in an unattached tendril.

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EXPLANATION OF FIGURES IN PLATE XIX.

Illustrating Prof. MacDougal's paper on the Mechanism of Tendrils.

All the figures were made freehand from longitudinal sections of tendrils of *Passiflora coerulea*, and with the exception of Fig. 5, include the epidermis, collenchyma, and cortical parenchyma.

Fig. I. Showing size, arrangement, and contour of cortical parenchyma-cells of concave side in free coils. Prepared from fresh material. $\times 350$.

Fig. II. Showing tissues of convex side in free coil. Prepared from fresh material. $\times 350$.

Fig. III. Tissues of concave side of active tendril before stimulation. Killed with acetic-alcohol and imbedded in paraffin. $\times 550$.

Fig. IV. Showing tissue of convex side of active tendril before stimulation. Killed with acetic-alcohol, and imbedded in paraffin. $\times 350$.

Fig. V. Infolded end-walls of pith. Prepared from fresh material. $\times 300$.

Fig. VI. Showing contour of tissues of concave side after curvature. Killed in acetic-alcohol and imbedded in paraffin. $\times 350$.

Fig. VII. Tissues of convex side after curvature. Killed in acetic-alcohol and imbedded in paraffin. $\times 350$.

I

V

II

VI

III

IV

VII

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