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VI.—*Mechanism of Movement in Cucurbita, Vitis and Robinia.*

By D. P. PENHALLOW, B. Sc.

(Read May 27, 1886.)

The valuable contributions of Darwin[1] to our knowledge of the movements of plants, about ten years since, led to an examination of this most interesting question, and eventually, to the particular form of it to be discussed in the present paper. At that time, the idea of the individuality of the cell prevailed, although Sachs had already demonstrated the continuity of protoplasm through the sieve plates of Cucurbita[2] and had formulated an expression in which he indicated a strong belief in the continuity of all living cells. It is only within very recent years, however, that sufficient reason has been given for a general change of opinion on this question. The additional light which has of late been thrown upon our knowledge of the cell, in its mutual relations, has presented many new and important subjects for consideration with reference to the physiology of movement in plants.

In the motile organs of plants—as represented by those now under consideration—we have to deal with organs which on the one hand are modified as a whole, with reference to their external form, and are thus adapted to a particular purpose, as in Cucurbita and Vitis; or which, on the other hand, show these modifications to be strictly localized, as in the pulvinus of Robinia. In each case, moreover, the internal structure is usually modified in an important way, and to a striking degree. In the tendrils of Cucurbita and Vitis, this occurs in the excessive thickening of the hypodermal tissue, which becomes almost entirely collenchymatous; in the localized development of active fundamental tissue lying in the outer hypodermis; and in the excessive formation of some vascular element—usually bast—which thereby produces a more or less continuous zone or vascular cylinder, internal to the softer parts of more active growth. In the pulvinus of the Robinia, the modification is chiefly found in the excessive hypertrophy of the hypodermal tissues, either at the base of the petiole, or throughout the entire length of the petiolule. In all of these cases, the true relative positions of the tissues, as found in the unmodified organ, e. g. stem or petiole, are fully maintained, but the special change developed in each of the component tissues causes an unusual relation to be established between them, so far as their mutual tension is concerned. This at once introduces an impo 'ant factor in the conditions of equilibrium which would otherwise be maintained, with the result that some disturbance of this condition must sooner or later occur, and this disturbance then becomes outwardly manifest in the form of motion.

Since variations of this character can occur in living tissues only, they must be

[1] Journal Linnean Soc., Vol. ix, 1865.

[2] Text-book, p. 89.

referred primarily and in general terms to conditions of growth, of which they are the result. They may arise, however, as already pointed out,[1] either from unequal growth and nutrition of parts, or from special conditions of turgescence, one or both combined Or, as Sachs[2] states, "in those movements which occur during growth, the tension of the tissues is concerned only so far as any change in it reacts on growth and modifies it Periodic movements, and those due to irritation, on the contrary, depend entirely on changes in the the tension of the tissues, which, in this case, are fully developed only when the organ has attained maturity."

These general principles apply to all the subjects now under consideration, and accepting them as tenable, we shall not in the present paper concern ourselves more particularly as to the special physiological changes involved, and whatever references are made to growth are to be accepted in the general meaning of that term, unless otherwise specified. Two general considerations are of importance in this connection, viz., the mechanical value of the tissues, and the continuity of protoplasm.

Of the various tissues which enter into the composition of motile organs, parenchyma, collenchyma, bast and wood, are of chief value. Of these, the parenchyma probably stands first as capable of the most rapid growth and the most extreme variations of tension from turgescence or other cause. The collenchyma undoubtedly stands next in both of these respects; while the bast, from its more permanent character, as well as from the results obtained by both Schwendener[3] and Haberlandt,[4] in which the great elasticity of this tissue appears, is in all probability the most important mechanical element, by reason of the retarding influence it exerts upon the growth of the more rapidly extending and external parts.

The inference which naturally follows from this is, that the principal conditions of tension with reference to elongation, are established and maintained primarily between the parenchyma and collenchyma on the one hand, and the bast and other vascular elements on the other; and secondarily, between the parenchyma and the collenchyma. It will also follow that, whenever one of these last-named tissues is in excess, it must exert a preponderating influence in changes of tension, without special reference to its particular capacity for such variations.

One of the most important factors in the physiology of motion, particularly that due to irritation, is the continuity of protoplasm. This fact has now been observed in so many widely different cases, and involves so little difficulty in its determination in almost any living tissue, that we can no longer regard its application as a general law, with reasonable doubt[5]. This law is of so recent origin, however, that at present but little is known as to its precise relation to motion; but that it is connected with it in those cases where there is distinct transmission of impulse to parts somewhat remote from the centre of

[1] Darwin, Movements of Plants, p. 2. Sachs, Vorlesungen über Pflanzen-Phys. p. 775.

[2] Text-book, 2nd Ed. p. 878, etc. Morren, La Sensibilité et la Motilité des Veg. Bruxelles, 1885, p. 52, etc.

[3] Das Mechanische Princip. im Anatomischen Bau der Monocotylen. Leipsig, 1874.

[4] Physiologische Pflanzen Anatomie.

[5] Bot. Centralbl. xiv. 89—121. Proc. Royal Soc., xxxv. 163. *Ibid*, xxxiv. 272. Jahrb. Wiss. Bot., xii. 170. Vorlesungen über Pflanzen-Physiologie, Sachs., 102. Nature, xxx. 182. xxxi. 337, 290, 390. Quart. Jour. Mic. Sci., Oct. 1882. Phil. Trans. Royal Soc., 1883, 817. Flora, 1863, 68. Hanstein, Die Milchsaftgefässe, 1864. Wilhelm, Zur Kenntniss des Siebröhrengefässe Dicotyler. Pflanzen, 1880.

irritation, can hardly be doubted in the light of observed facts [1] It remains to determine in what way these transmissions occur through the protoplasmic medium. At present, therefore, we must confine our considerations to continuity of protoplasm, in its structural relations to the tissues of the motile organs.

In both the grape and the squash, the continuity appears most prominently in the collenchyma tissue of the rather thick hypodermis. It may also be observed without difficulty in the active parenchyma of all parts external to the xylem portions of the vascular bundles. The same treatment, however, does not answer equally well for its detection in each case, owing to the different character of the tissues involved. In the pulvinus of Robinia, Gardiner [2] has already pointed out the clearly defined continuity which may be observed both in the parenchyma and in the bast. In the latter tissue we have found it to be most strikingly prominent, its exhibition being much less difficult than in the softer tissues, probably owing to the presence of numerous channels in the cell walls, which serve to localize and more sharply define the connecting filaments.

The method employed for the exhibition of continuity must depend upon the character of the particular tissue involved. Any one of these methods, all of which have been employed by Gardiner and others, may be used according to circumstances. The first we may distinguish as the salt method. For the purpose there should be prepared a 10 p. c. solution of common salt. This has been recommended by Gardiner [3] as giving the best results in most cases, an opinion fully confirmed by our own experience. Perfectly fresh and thin sections are immersed in a suitable quantity of the solution and allowed to lie until wanted for the final staining. The action of the salt is to contract the protoplasm gradually into a compact, rounded mass, towards the centre of the cell, and thereby preserve intact the original connecting filaments, which then become drawn out into long, slender threads. There is, however, no appreciable change in the cell wall. A distinct development of continuity will generally be formed within a period of ten minutes, but, for good results, at least half an hour should be given; and since, with continued action, the salt consolidates all the contracted parts and thus renders all the filaments more distinct, an immersion of the sections for twenty-four or thirty-six hours may often prove desirable. If the solution be stronger than 10 p. c., the action is too rapid and many of the more delicate filaments snap during development, so that we then observe only their contracted remains upon the cell wall, with corresponding processes from the main protoplasmic mass. Treatment of this description answers admirably for all unmodified parenchyma tissue, such as that in the squash fruit the flesh of the apple and pear, and in the pulvinus of the Robinia. It does not answer so well, however, in the case of thick-walled cells, whether collenchyma or bast. Then one of the following methods is to be preferred.

The second method may be distinguished as the sulphuric acid process [4]. Very thin sections, freshly cut—one or two at a time, according to size—are placed upon the end of a glass slide or platinum foil. Surplus moisture is now removed in order to secure uniform action of the acid. A drop of concentrated sulphuric acid is then placed on the slide

[1] Janczewski, Etudes Comparées sur la tubes Cribreux, 1881. Russow, Sitzberg. Dorpater Naturf. Ges., 1882, 23, 257—327. Tangl, Pring's Jahrb., xii. Strasburger, Bau und Wachsthum, 23.

[2] Proc. Royal Soc., xxxv. 163—166.

[3] *Ibid.*, xxiv. 272—274.

[4] Bot. Centralb., xiv. 89—121.

or foil, immediately above the sections, and allowed to flow down over them quickly. Very careful attention is now needed to control the action at the proper moment. In the course of three or four seconds the sections acquire a faint brownish color, which rapidly deepens as the dehydrating action of the acid proceeds. Its first appearance indicates, in most cases, that the action has been continued long enough. The slide is, therefore, quickly plunged in a dish of water which must be ready for that purpose, and the sections thoroughly washed. They are then ready for staining.

The action of the acid, dependent upon its dehydrating properties, is first to contract the protoplasm. It next causes the cell wall to swell strongly and partly dissolve, thus rendering it so transparent as to permit the threads of protoplasm which traverse it to be seen distinctly when stained. The swelling of the wall also tends to aid in the contraction of the protoplasm, while the channels become longer, and further aid in defining the filaments. If great care be not used in this process, the section will be quickly and wholly dissolved. This process is of special advantage as a quick method, while it gives most gratifying results, and it has been chiefly relied upon by us. It may be employed in ordinary parenchyma tissue, and also with great advantage in collenchyma and bast, to the treatment of which latter two, it is best adapted. This is one of the oldest of all the methods now in use.

The third method, and that which Gardiner seems to regard with the greatest favor is the chloriodide of zinc process. This admits of two variations; in the first, the sections are immersed for a short time in an ordinary aqueous preparation of iodine, until the characteristic reaction is developed. They are then transferred to the chloriodide, when they quickly turn dark brown, owing to the intensity of the iodine reaction. After about ten to thirty minutes in this latter reagent, they are washed out in distilled water until the brown color disappears. This method is said by Gardiner to have the special advantage of causing the protoplasm in all its parts, to take a much deeper stain when finally colored with aniline. The second variation simply omits the preliminary treatment with iodine. Preparations by this method, show the filaments very distinctly, and the walls of the cells so strongly swollen as to render them quite transparent. It may therefore be used instead of the last process by sulphuric acid.

Sections treated by any one of these methods, require subsequent staining, in order to differentiate the delicate filaments from the surrounding cell wall. The method originally employed by Tangl[1], in the case of endosperm cells, was to stain with iodine. Our present methods, however, permit of much more accurate results. The stain recommended by Gardiner[2] as used by us, gives most satisfactory results. It is prepared as follows:—To a 50 p. c. solution of alcohol, add picric acid to saturation. To this add aniline blue (we used BB with good results) until the residual color imparted to a section, is deep blue. To facilitate solution, one or two drops of acetic acid may be added to the stain with advantage. Sections previously treated and well washed, are immersed in the stain for a few moments and then washed out in fresh alcohol until the yellow is all discharged and the color of the section changes from green to clear blue. It will then be found that the picric acid, in passing out from the section, has withdrawn all the aniline from the cell walls, but that it has left it in the protoplasm, for which it has a special affinity. The colorless cell walls

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[1] Pringh's, Jahrb., 1880, 170.

[2] Phil. Trans., clxxiv. 817.

and the colored filaments are thus brought into sharp contrast, and the latter may easily be recognized under a sufficiently high power. Sections so prepared may be placed in 25 p. c. glycerine for future examination. For permanent mounts, glycerine jelly should be used. Balsam will answer for exhibition of continuity in the bast tissue, and will even preserve it for several months in the softer tissues, but in the latter case, the protoplasmic filaments gradually break up, and ultimately disappear.

I.—CUCURBITA MAXIMA AND PEPO.

HISTOLOGY.—The tendrils of the squash externally present the form of long, slender filaments, well rounded, but with a somewhat greater transverse than vertical diameter, and on the upper side flattened and slightly grooved for almost their entire length. The surface is generally smooth, though soft scattering hairs usually appear towards the upper side. The prevailing color is a very pale or whitish green, due to the deeply seated chlorophyll-bearing layer, which is internal to the collenchyma. This pale hue, however, is found to be interrupted along three lines, extending from base to tip of the tendril, in which the color is a strongly marked green, thus bringing these bands into strong prominence by contrast with the surrounding and lighter parts. These three lines or bands of tissue, always occupy the same positions, which are found to be, one on each side, just at the horizon of the major axis of transverse section, and the third in the position of the channel along the upper side of the arm, at the upper extremity of the minor axis. Aside from their more special value in circumnutation, these bands serve as most valuable means of noting certain changes incident to movement, e. g. those of torsion. The tip of the tendril is invariably turned slightly backward, or towards the lower side of the tendril arm, though during certain phases of the circumnutation, changes due to torsion often cause it to point upward.

Internally, the tendril presents several important features. Transverse sections disclose the form and relation of parts shown in Plate IV, Fig. 1. From this, the following details may be gathered :—

The epidermis consists of a single row of cells, which are either of the same size in both directions, or somewhat elongated in a direction perpendicular to the general surface. The epidermal hairs, so far as they may be present, are confined almost wholly to the upper and lateral surfaces at *b*, being absent from the surface below the horizon of the major axis *b'*. The hypodermal tissue consists of a rather thick layer of collenchyma (*b b'*), which is almost continuous throughout the entire circumference of the tendril, its continuity being interrupted in the three regions *a*, *a'*, and an opposite to *a'*. These areas of interruption correspond to the three green bands already referred to. The collenchyma itself is thus separated into three distinct bands, which traverse the tendril throughout its entire length, one being larger and inferior in position at *b'*, and two smaller and superior as at *b* and its corresponding part on the other side. The first is usually distinguished by being somewhat thicker, and also of much greater lateral extent than the other two combined. The detailed structure of this tissue is shown in Fig. 3, from which it appears that the collenchymatous thickening is somewhat general over the entire surface of each cell.

At the three points a, a', a'', the continuity of the collenchyma is interrupted by groups of parenchyma tissue, which extend as longitudinal bands throughout the entire length of the arm. This tissue has certain important distinguishing characteristics. The cells are usually large, well rounded, and thin walled (Fig. 1, *a a'*, and Fig. 5). They contain an abundance of protoplasm and chlorophyll, and possess all the features of cells in an active condition of growth. Indeed, the act. vity of this tissue is conspicuous from the earliest period of circumnutation until long after the surrounding parts have become hard and woody, and all motion has ceased. Within the area of this tissue are to be found intercellular spaces (not shown, however, in the figure) together with their corresponding stomata, which latter are confined to the epidermis of these bands. The very large amount of chlorophyll here present, is the means of that outward distinction to which we have already referred. Inwardly, each of these groups of cells connects directly with the pith region of the tendril, thus causing a further break in the continuity of the interior tissues. From the very prominent part which this tissue evidently takes in the circumnutations of the tendril, and the frequency with which pointed reference must be made to it, we have deemed a descriptive term essential. We have, therefore, applied to it the name of "Vibrogen" or "Vibrogenic tissue," as signifying that the origin of the ordinary circumnutation is to be found there.

Immediately internal to the collenchyma is a zone of rather large, thin-walled parenchyma tissue, c, usually disposed in three or four rows, of which the innermost cells are the smallest. This tissue, which is essentially the mesophlœum of the stem, forms a continuous zone through each of the vibrogen bands. The cells are filled with protoplasm, and contain some granular matter and a small amount of chlorophyll, which imparts the subdued green color to the tendril as a whole. The tissue presents all the characteristics of active growth, but it in all probability is inferior in this respect to the energy of the vibrogen bands—as will appear later—though it undoubtedly contributes its part as a factor in the general circumnutation. Directly interior to this tissue is the bast zone of the liber. At a very early period in the growth of the tendril, the bast portions of the vascular bundles establish conjunctive growth, and thereby form a zone (d), the continuity of which is interrupted only at those three regions where the vibrogen establishes its connection with the pith. In its earlier period of growth, the bast cells are all thin walled (Fig. 2 A). They are then in a condition of active growth, and are capable of conforming to the general and rapid elongation of the organ as a whole. It is this condition which essentially characterizes these cells during the greater portion of the tendril's active period, but most conspicuously so during the earlier portions of it, since we find that, with the growth of the organ, the bast cells gradually increase in thickness and assume more and more completely their true character as permanent structure. And this becomes more conspicuous towards the end of the active period, when the motion of the tendril is gradually retarded, and becomes continually more spasmodic, until finally it ceases altogether We then find that from thin-walled cells the bast has changed to thick-walled, permanent tissue, as shown in Fig. 2 B. This, then, defines the hard and woody character of the tendril, which is so conspicuous a feature after coiling.

It is important to point out in this connection that as soon as this woody character in the tendril is fully developed, all motion must cease; and since the lignification is a gradual process, and will be completed within a definite period—assuming constant conditions of nutrition,—we must recognize the probability of a gradual modification in uniformity, as also of a gradual cessation of motion and the impossibility of the activity being prolonged or even shortened; unless conditions of permanent contact and irritation are established, when maturity is accelerated. As will appear later, the motion resolves itself into an expression of the resultant of activity in two tissues, one of which is continually growing, while the other is as continually becoming less active, and the cessation of motion must then be determined when the latter gains complete ascendancy over the former, and thus permanently destroys the equilibrium of growth.

Internal to all the histological elements thus far discussed, lie the xylem portions of the vascular bundles. These, however, are widely separated. They are seven in number, the three largest traversing the lower region of the tendril arm. As elements of permanent structure, they must undoubtedly serve in a degree to supplement the mechanical value of the bast, but to this they are obviously very subordinate. Within the vascular zone is the somewhat large pith which, especially at the base of the tendril arm, early develops what De Bary [1] designates as a "lysigenetic intercellular cavity," to the extent that the organ becomes hollow for a considerable distance from its base. This also characterizes the petiole of both tendril and leaf, in each of which the same structural elements appear, and in much the same relative positions.

Of the elements thus considered, we must regard the vibrogen, collenchyma and bast as of primary importance, and that they bear a definite relation to the circumnutation of the tendril, and to its behaviour under the influence of irritation, can hardly be doubted in the light of the facts to be presented in the following pages.

Growth in Length.—In vigorous vines, the largest tendril arm often exceeds 30 cm. in length. The extreme lengths of the tendril arm, during the entire period of circumnutation, may generally be taken as ranging from 8 cm. to 35 cm. As this great elongation must occur within the very limited period of two days, it indicates a most rapid organizing process, as the following determinations will show. Moreover, it must be borne in mind that the cessation of growth in length and of circumnutation is simultaneous. The following determinations have been obtained. An arm just uncoiled from the bud measured 12 cm. in length. One day later it had increased to 14.8 cm., and on the following day to 18.3 cm., thus giving a total increase in length of 6.3 cm., or one-half the original. August 8th, five tendril arms, but a short time in action, were measured and marked. The Monday following (10th) all except one were found to have coiled about themselves or other objects. The coils were drawn out and measured with the following results:—

	1.	2.	3.	4.	5.
August 8th.......	12.0	12.4	17.7	10.4	17.5 cm.
" 10th.	24.5	19.0*	25.0*	20.5*	33.0*
Gain.............	12.5	6.6	7.3	10.1	15.5

* Indicates those which could not be fully straightened.

[1] Comparative Anatomy of Phenogams and Ferns. Eng. Ed. 200.

Coils 2, 3, 4, 5 could not be fully straightened for measurement, allowance for which had to be made. Thus if we add to the above numbers as follows: 1.0, 3.0, 5.0 and 1.0 cm. respectively, we then get as the total lengths of all the tendrils, 12.5, 7.6, 10.3, 15.1 and 16.5 cm. We thus get as the extreme range in elongation, from 50 per cent. to 100 per cent. of the original length, and the mean ratio of increase would be as 1 : 1.14, showing that the tendril at least doubles in length after the uncoiling from the bud, and during the period of circumnutation.

Coiling.—When brought in contact with an object near the tip, the tendril, at once affected by the irritation, coils about the support with a firm grasp. The effect of irritation does not immediately extend along the remainder of the tendril, as is shown by the fact that, when the tip is brought in contact, the basal portion of the tendril continues its movement and passes by as a curve, the sensitive surface thereby becoming convex instead of concave, as would occur if it felt the influence of contact. After a time, however, the effect of contact extends to all the cells of the basal portion, which then draws itself into a closer and closer spiral. When brought in contact with an object, the tendril does not immediately lose its power of nutation, but often retains it for a very considerable period, this being dependent upon the age of the tendril, and especially upon the particular state of lignification in the bast. It becomes evident, therefore, that when the tip is arrested, the bands of vibrogen, still continuing to act in the basal portions, tend to bow the tendril in all directions as before. Their power to do so being modified by fixation of the tip, the natural result would be for the centre to pass by the point of support as a curve having the sensitive side outermost. Continued circumnutation of the free central portion between two fixed extremities must result in torsion, which will be right or left hand as the case may be, from both ends towards the centre, and when such torsion becomes excessive, its compensation is of necessity found in a double spiral [1], which always characterizes the fixed tendril. If coiling in the free central portion were primarily due to the irritation of contact, we should expect to find the coiling first developed as the direct result of simple contraction along one side, and this would not immediately give rise to torsion Tendrils which have not suffered contact, always coil upon themselves at the completion of their period of circumnutations. Such coils, however, are always somewhat loose and quite irregular, and are the direct result of excessive inequality of tension between the bast and vibrogen, therefore of unequal maturity in the tissues.

Circumnutation.—The circumnutations of the tendrils commence as soon as each arm uncoils from the bud condition. The central and largest arm generally uncoils first, and later, the laterals. The whole period of circumnutation in a rapidly growing vine, under favorable circumstances, is usually about two days—rarely three days. During this period, the motion is at first by grand and regular sweeps, but it gradually becomes slower as the end is reached; and in the later periods, the movement is spasmodic, often exhibiting rest periods alternating with those of great activity. Ultimately the end is reached in the formation of a spiral, which is more or less loose and irregular if free, or

[1] Darwin, Climbing Plants, 163, etc.

compact and well formed if developed after contact. In each case the structural modifications are the same, i.e. the parts become hard, dry and woody.[1]

The figure described by the nutating tip is approximately ellipsoidal (Plate III), the major axis being transverse. This axis not infrequently reaches a length of 24 to 27 cm.; that of the minor axis being from 13 to 22 cm. in length. In *Echinocystis lobata*, the diameter of the figure, according to Darwin[2], is even larger than this, measuring from 38 to 41 cm. While the tendril thus describes a figure, the vertical plane of which is parallel with the axis of the plant, the space through which the tip moves is greatly augmented by a supplementary movement in the growing end of the vine on which the tendril is found. This secondary movement causes the tendril to describe a double motion, which increases the possibility of its contact with surrounding objects.[3] It is of short duration, however, since the movement of the vine is confined to the few internodes at the end, and at any one node continues for two days only after the tendrils are in motion; so that, by the time the first arm of the latter has grasped a support, the movement of the vine at that particular node may have ceased entirely. So long as there is no contact the tendril continues to revolve, until a gradual increase of permanent tissue arrests its activity.

Circumnutations do not belong to the tendril arms alone. Not only does the petiole of each tendril perform a definite circumnutation but the leaves exhibit a similar movement in a marked degree, as demonstrated by G. E. Cooley during the past summer. The motion of the tendril petiole is best observed by Darwin's method of a fine glass filament with a small black bead at its extremity, inserted into the end of the petiole where the arms separate. The circumnutation of the leaf is to be determined from its tip, as in tendril motion. In this manner, we have obtained, from a leaf of medium size, a figure of twenty different changes of direction, within the space of three hours. The movement was found to be much slower, and the figure much smaller than in the case of the tendrils. This, however, would appear to be the case from theoretical considerations, when we compare the structural features of the two and have due regard for the difference in size. The figure described by the leaf, so far as formed, was quite regularly ellipsoidal, though the curve was retraced before the ellipse was fully completed, in all of these respects showing striking similarity to the movement of the tendril.

During a series of observations extending over a period of nearly one week and embracing both day and night, almost the entire circumnutations of each tendril observed were secured. Temperature and other conditions were noted at each of the observations, which were taken at intervals of from two minutes to one hour, according to the condition of activity. The following are the results:—

Tendril No. 1.—Aug. 12th, at 9.30 a.m., one of the longest arms was selected after it

[1] My observations confirm those of Darwin with regard to other members of the Cucurbitaceæ, that when a spiral develops freely, it is always simple; that it only reverses when the tip is attached to a suppo

[2] Climbing Plants, 128, etc.

[3] The fact that there is this double motion as a result of tendril vine action, shows that the true figure is to be obtained only when the tendrils revolve about the inner surface of a glass globe and the changes of direction are recorded from the outside. This, however, was not practicable in our case, nor was it essential to the accuracy of the conclusions to be obtained. For our purpose, the plane recording surface was amply sufficient.

had been sometime uncoiled, and its movements were noted until there was no further motion. The entire period of observation was ten hours and thirty minutes. During that time, the tendril tip traversed a distance of 343.15 cm., giving an average rate of 0.54 cm. per minute.

The greatest rate of movement, at any one time, was 2.06 cm. per minute, and occurred two and one-half hours after the wave of maximum temperature had passed. The waves of most rapid movement extended from 2.30 to 4.30 p.m., closely following the greatest heat wave. The waves of slowest movement covered the time from 10 a.m. to 2.30 p.m., coincident with a rising temperature. The absolute minimum of motion occurred just before the maximum of temperature, at the rate of 0.21 cm. per minute. At four o'clock in the morning, a heavy rain ceased. The air was surcharged with moisture, and the sky was entirely overcast with heavy clouds. It was while this condition lasted, that the waves of slowest motion occurred, the absolute minimum being found during the period from 12.15 to 1 p.m. At the latter hour, the clouds broke and the sun came out brightly and so continued until 6 p.m., when the sky again became overcast and rain set in at 7 o'clock. While the sun was out, the tendril was most active—the absolute maximum of motion taking place within the five minutes from 3.25 to 3.30 p.m., the distance travelled in that time being 16.30 cm.

The first direction of movement was to the right. This, however, was obviously accidental, since the direction first recorded must depend upon the time of first observation with relation to the entire movement—dextrorse alternating with sinistrorse movement during the whole period of activity. The total motion to the right was 190.8 cm.; that to the left, 152.35 cm.; and the ratio therefore, as 1 : 0.79.

Tendril No. 2.—Selected for observation, August 13th, at 8 o'clock. It was a shorter arm than No. 1, and somewhat nearer the end of activity. The time of observed movement was six hours and fifteen minutes, and the whole distance travelled 136.00 cm., thus giving an average rate of 0.36. cm. per minute.

The absolute maximum of motion was 1.76 cm. per minute and occurred from 10.15 to 10.20 a.m., forty-five minutes before the maximum temperature for the day was reached. The waves of most rapid motion covered the period from 8 to 10.50 a.m., coincident with increasing temperature. The waves of least motion occurred between 10.50 a.m., and 2 p.m., during a slight depression of temperature. The absolute minimum was reached between 10.50 a.m. and 12.25, and amounted to 0.179 cm. per minute. It directly succeeded the maximum of temperature. During the entire time of observation, the weather was very pleasant, though somewhat cloudy. At 12 o'clock, the leaves began to droop from the effects of excessive heat and transpiration. This continued until after the close of observations. It was during this time of depressed activity, that the minimum motion occurred. During the entire morning, all the leaves and flowers showed great vigor, and it was while in this condition that most active movement took place. The first motion observed, was to the left, and was not replaced by dextrorse for some time. The entire sinistrorse action was 94.2 cm.; the dextrorse, 41.8 cm.; and the ratio of the latter to the former was therefore, as 1 : 2.25.

Tendril No. 3.—The time of observation was ten hours and thirty minutes, commencing at 10 o'clock, a.m., on August 13th. The whole length of movement was 329.30 cm., and the rate per minute, 0.52 cm. The times of greatest movement were from 1 to 3.15 p.m., and again from 5.15 to 8 p.m., the former occurring at the time of the maximum temperature, the latter on a diminishing temperature. The absolute maximum of motion was 3.55 cm. per minute, and occurred from 1.50 to 1.52 p.m. succeeding the wave of maximum temperature by two hours and fifty minutes, at a time when there was a slight temporary depression of heat. The distance travelled in that short interval was 7.10 cm. The time of least movement was from 12.15 to 1 p.m., during the time of greatest heat, and again from 3.15 to 5.15 p.m., following a diminution of temperature. The absolute minimum of motion was 0.013 cm. per minute, and occurred from 12.15 to 1 p.m. on a decreasing temperature, following the maximum wave by one hour and fifteen minutes. During that time, the weather was pleasant but somewhat cloudy. From 11 a.m. until 5 p.m., all the leaves and flowers were drooping, indicating a weak vital action through excessive transpiration. The first movement recorded was to the right, soon succeeded by a reverse to the left. The entire amount of the former was 261.5 cm.; of the latter, 67.8 cm.; and the ratio as 1 : 0.25.

Tendril No. 4.—This tendril was taken August 14th at 8 o'clock a.m., but so late in its growth that only twelve movements were obtained, covering seven hours and fifty minutes in all. The whole length of movement was 66.20 cm., and the average rate per minute, 0.14 cm. At no time was there any exhibition of very great activity, the tendril appearing to move as if in the last stages of growth, which it really was. The most rapid movement appeared from 9.41 to 9.50 a.m., the extremity passing through 7.7 cm. in nine minutes—an average rate of 0.85 cm. This coincided with the highest temperature, and was just prior to a fall of two degrees. The time of least activity was from 9.50 a.m. to 3.50 p.m. The absolute minimum of motion was from 2.10 to 3.50 p.m., amounting to 0.031 cm. per minute. It occurred on a decreasing temperature, five hours and fifty minutes after the maximum temperature had passed. During that time the sun was shining brightly, though its effects were somewhat modified by numerous clouds. From 12 o'clock to the close of observations, during the time of least activity, the leaves and flowers were all depressed from the effects of the heat.

The movements first recorded were to the left, but after two courses changed to the right. The total dextrorse movement was 18.4 cm.; the sinistrorse 47.80 cm., and the ratio 1 : 2.6.

Tendril No. 5 a.—This was taken Aug. 14th, at 4 o'clock p.m., as soon as it had emerged from the bud condition; thus very nearly the first nutations were secured. Observations were interrupted after a few hours, and not resumed until the next morning. The entire length of movement was 107.60 cm., occupying four hours and thirty minutes, thus giving an average rate per minute of 0.39 cm. The greatest movement was at the rate of 1.44 cm. per minute, and occurred from 4 to 4.05 p.m., at the very commencement of action and observation. The times of greatest movement occurred from 4 to 4.35 p.m., and again from 5.30 to 7 p.m., coincident with decreasing temperature.

Least activity was noticed at 7.55 to 8.10, when the tip moved at the rate of 0.13 cm. per minute. This occurred at the time of lowest observed temperature, the mercury standing at 21° C. The times of least movement were found to extend from 4.35 to 5.30, and again from 7 to 8.30 p.m., when the observations ceased.

At the commencement of observations, the sun was shining brightly, and the effects were sufficiently strong to cause a depression of all the leaves and flowers. Shortly after observations ceased, the sky became cloudy, and at 9 o'clock there was a heavy shower which revived the whole plant, and once more brought all the parts into active condition.

The first movement recorded, was to the left, action in that direction predominating during the entire period of observation. The total movement to the right was 18.80 c.m.; to the left 88.8 cm.; and the ratio, therefore, as 1 : 4.72.

Tendril No. 5 b, c.—This represents the same as the preceding tendril, observations upon which were interrupted Aug. 13th at 8 p.m., and resumed the next morning (14th) at 8 o'clock, being continued through the 14th and 15th. During the night, the arm was quite active, and in the morning showed no tendency whatever to discontinue its nutations. From the time indicated, observations were continued for twenty-four consecutive hours. The entire distance travelled during that time was 511.7 cm., thus giving an average rate of 0.37 cm. each minute. 5 b-c. indicates a change of paper, which occurred at 6.20 p.m., at a time when the tip had dropped to the ground, where it remained without change of position until 8.35 p.m., when its nutations were resumed.

The time of most rapid movement, was during the two minutes from 4.55 to 4.57 p.m., on a decreasing temperature, and five hours after the maximum wave had passed. The rate of movement was 4.55 cm. per minute. the times of most rapid movement occurring from 8 to 10.20 a.m.; 1.30 to 2 p.m.; 4 to 5.30 p.m., and 10.53 to 11.05 p.m.; the maximum of these being from 4 to 5.30 p.m. The absolute minimum of motion occurred from 4 to 5.04 a.m., when the tip traveled at the rate of 0.043 cm. per minute, this being at a time of low temperature. The times of least activity were from 10.20 a.m. to 1.30 p.m.; 2 to 4 p.m.; 5.30 to 10.53 p.m.; and from 11.05 during the remainder of the night, and until the end of the experiment at 7 o'clock in the morning. In these observations, there appears a very sharp division at 5.30 p.m., between the waves of more rapid diurnal, and those of slower nocturnal movement.

The experiment commenced with very pleasant weather and all parts of the plant in vigorous condition—the leaves being erect and the flowers open. From 12 m. to 4 p.m., the leaves were drooping and the activity of the plant small. This, with the exception of one-half hour from 1.30 to 2 p.m., was a time of slow movement. At 4 o'clock p.m., the leaves began to resume their normal, fresh appearance and so continued until the close of observations. Towards morning, a very heavy fog gathered and reached its maximum at four o'clock, the time of minimum motion.

Sinistrorse movement was first noticed. The entire dextrorse motion was 282.1 cm.; the sinistrorse 229.6, and the ratio 1:0.81, thus showing a greater tendency to equality than previously observed.

The figure described during the movement of this tendril—reduced to one-half the actual size—is shown in Plate III, the position of the observer corresponding to the base of the tendril. The following table relating to these movements will convey a fairly accurate idea of the general features of circumnutation with reference to time and distance :—

Number.	Distance in cm.	Time.	Temp. deg. C.	Number.	Distance in cm.	Time.	Temp. deg. C.
1	.0	8.00 A. M.	24.4	29	9.1	4.57 P. M.	....
2	11.6	8.25 "	....	30	10.0	4.60 "	....
3	8.7	8.40 "	....	31	5.7	5.02 "	3.05
4	20.6	9.15 "	35.5	32	3.2	5.05 "	....
5	14.8	9.40 "	....	33	1.9	5.10 "	....
6	29.6	10.00 "	35.5	34	20.8	5.30 "	....
7	10.1	10.15 "	....	35	6.0	5.32 "	....
8	7.0	10.20 "	....	36	8.1	5.40 "	....
9	18.2	11.00 "	36.6	37	14.1	6.20 "	27.2
10	7.0	11.25 "	....	38	6.3	8.35 "	22.2
11	7.2	12.00 M.	36.6	39	4.6	8.47 "	....
12	7.8	1.00 P. M.	33.3	40	14.7	9.00 "	22.2
13	8.0	1.15 "	....	41	6.8	9.50 "	21.1
14	7.3	1.30 "	....	42	18.8	10.55 "	....
15	18.8	1.35 "	....	43	7.5	11.05 "	21.1
16	5.7	1.45 "	....	44	9.0	12.00 "	20.0
17	5.3	1.55 "	....	45	15.1	12.35 A. M.	....
18	8.8	2.00 "	32.2	46	7.2	1.00 "	20.0
19	7.4	2.20 "	....	47	25.9	2.00 "	19.0
20	5.7	2.45 "	....	48	8.2	2.20 "	....
21	4.1	3.00 "	32.2	49	9.7	4.00 "	18.0
22	6.4	3.20 "	....	50	2.8	5.04 "	19.0
23	17.5	4.00 "	32.2	51	9.4	5.30 "	....
24	3.5	4.10 "	....	52	6.0	5.45 "	19.0
25	9.9	4.30 "	....	53	6.6	7.00 "	20.0
26	10.2	4.45 "	....				
27	6.8	4.50 "	....	Totals..	511.5	23 h.	577.8
28	6.0	4.55 "	....				
				Means..	9.8	26.5 m.	26.3

Tendril No. 6.—Selected Aug. 1, at 1.45 p.m., when but a short time from the bud. Observations were continued consecutively for eighteen hours and fifteen minutes. The distance through which the tip moved during that time, was 327.8 cm., an average rate per minute of 0.29 cm.

Most rapid movement occurred from 6.50 to 6.52 pm., at the rate of 6.5 cm. per minute. This was on a decreasing temperature, and six hours and forty minutes after the wave of maximum temperature had passed. The time of the greatest movement was from 3.50 to 7.10 p.m. on a decreasing temperature, and within three degrees of the lowest phase of the thermal wave. The times of least movement were from 1.45 to 3.50 p.m., and from 7 p.m. to the close of observations. As in the preceding case, there was, in this, a marked distinction between the waves of more rapid diurnal, and those of slower nocturnal movement—the time of division being 7 p.m.

The tendril commenced its nutations with a dextrorse movement, and in its entire activity manifested a greater equality between right and left motion, than in even the last case. The dextrorse movement was 166.10 cm.; the sinistrorse 161.7 cm., and the ratio, therefore, 1 : 0.97. At the commencement of observations, the sun was bright, and the temperature high. The vitality of the plant was much depressed, and the action slow—all the parts drooping from excessive transpiration. This continued until 4 p.m., during which time there were slow waves. At 4 o'clock, the plant revived, the leaves became erect, and the normal condition and activity were once more restored. From that time until sunset, the waves of greatest movement occurred. The sky was clear until after midnight, but slow waves continued throughout the remainder of the night, with a slight acceleration just after sunrise.

Tendril No. 7 a.—Observations commenced Aug. 16th, at 9 o'clock, a.m, and were continued for ten consecutive hours. The total distance covered, during that time, was 227.1 cm., or at the rate of 0.38 cm. per minute. The time of most rapid movement was from 5 to 5.20 p.m., when the tip moved at the rate of 0.92 cm., per minute. This occurred just at the outset of a rapid decline in temperature, and six hours after the maximum of temperature had passed. The time of greatest movement was from 3.15 p.m. to the close of the observations at seven o'clock, co-incident with a rapid decline in temperature.

The time of least movement was from 1.42 to 2.25 p.m.; the tip moving at the rate of 0.53 cm. per minute. This was during high temperature, but one hour and forty-two minutes after the maximum had passed. The waves of least motion were found to extend from 9 a.m. until 3.15 p.m., with a marked retardation towards the latter hour. These waves were coincident with the greatest heat wave, the greatest retardation of motion occurring just after the maximum temperature had passed.

The experiment commenced with the sky clear and the plant in active condition. As the heat increased, however, its effect upon the plant was noticed, and at 12 o'clock, with the mercury at 34.4° C., the leaves drooped, and the whole plant was in a very flaccid condition. During this time, the waves of slowest motion occurred. This condition continued until, with considerable fall in temperature during the afternoon, the normal tension and activity of the plant were restored, when the waves of greatest activity were noted. The entire dextrorse movement was 92.90 cm.; the sinistrorse 134.20 cm., and the ratio as 1 : 1.44.

Tendril No. 7 b, c.—This was the same as the preceding, observations upon which were discontinued during the night, but resumed on the morning of the 17th at 8 o'clock, and carried over a period of seven hours and fifty minutes. The entire movement during this time was 94.40 cm., giving an average rate per minute of 0.205 cm. Most rapid movement was at the rate of 0.555 cm. per minute, and occurred from 8 to 8.15 a.m., at the very commencement of observation, and on a rising temperature, six hours before the maximum was reached. The waves of most rapid motion were found from 8 to 11.30 a.m. Least motion took place at 1.30 to 2 p.m., at the rate of 0.08 cm. per minute. This was just at the time of maximum temperature. The waves of least motion were found from 11.30 a.m. to the close of observations at 3.40 p.m., coincident with a rising and maximum temperature.

Observations commenced with a moderate temperature, clear sky and an active condition of the plant, continuing thus during the time of greatest movement, until, at 11 o'clock, the leaves became depressed from the effects of the heat, and from 11.30 on, the waves of slow motion were found. At 12 m., the sky was overcast and the air loaded with moisture. At 1 p.m., the leaves were restored to their normal condition and erect position. At the same hour, rain commenced and continued during the remainder of the experiment. The total movement to the right was 25.10 cm.; to the left, 69.30 cm., and the ratio as 1 : 2.76.

Tendril No. 8 a.—Selected Aug. 16th, at 9 a.m.—The time of observation covered a period of nine hours and fifty minutes, or until 6.50 p.m. The entire movement during that time was 314.50 cm., giving an average rate per minute of 0.516 cm The time of greatest movement was from 3 to 3.15 p.m., and the rate per minute 1.20 cm. This was on a decreasing temperature, four hours and fifteen minutes after the maximum. The waves of greatest movement were found from 2 p.m. until the end of observations, and during a diminishing temperature.

The time of least movement was from 11.25 to 11.40 a.m., and the rate per minute 0.166 cm. This was at the time of maximum temperature. The waves of slowest motion extended from 9 a.m. until 2 p.m., with slight acceleration of movement towards the latter hour. Observations commenced with a bright sun and the plant in active condition. At 12 o'clock, the leaves drooped, with the thermometer at 34.4° C, and this condition continued until early in the afternoon, when they revived with decrease of heat. It was during the passive condition of the plant that the slowest motions were observed, the more rapid waves occurring with renewed vigour and greater tension of parts. The entire dextrorse motion was 143.10 cm.; the sinistrorse 161.40 cm., and the ratio, therefore, as 1 : 1.12.

Tendril No. 8 b.—Observations were resumed at 8 o'clock a.m., August 17th, and were continued for seven hours and forty-five minutes. The distance which the tip travelled during that time was 225.0 cm., or at the average rate of 0.483 cm. per minute. The greatest movement was at the rate of 2.60 cm. per minute, occurring from 3.40 to 3.45 p.m., at the very close of observations and one hour and forty-five minutes after the maximum of temperature. The waves of most rapid movement were from 3.15 to 3.45 p.m. Least movement occurred at 10.15 to 10.30 a.m., at the rate of 0.10 cm. per minute. The waves of least motion extended from 8 a.m. until 3.15 p.m., coincident with a rising and maximum temperature. Observations commenced with a bright sun and the plant active. At 11 o'clock a.m., just thirty minutes after the minimum of motion occurred, the leaves were all drooping as a result of excessive transpiration. At 1 o'clock p.m., it was raining, and the normal activity of the plant was restored. This continued until the close of observations. The entire dextrorse action was 103.50 cm.; the sinistrorse 121.50 cm., and the ratio, therefore, as 1 : 1.17.

Tendril No. 8 c.—Observations upon the tendril were resumed on the 17th of August, at 5 o'clock p.m., and extended over fifteen hours. Apparently, on account of its age, and the time of observation, the entire movements were slow, amounting in the whole period to only 159.0 cm., thus giving an average rate per minute of 0.176 cm.

The greatest movement was from 7.12 to 7.28 p.m., at the rate of 0.65 cm. per minute. The waves of most rapid movement were from 5 to 7.30 p.m., with a slight acceleration in the morning. Least movement was found from 2.30 to 3 p.m., at the rate of 0.023 cm. per minute, occurring at the time of minimum temperature. The extreme variation of temperature during the time of observation was only 2° C. A light rain fell during the greater part of the time, and heavy clouds obscured the sky the remainder. The dextrorse movement was 117.0 cm.; the sinistrorse 41.40 cm., and the ratio as 1 : 0.35.

Tendril No. 9.—The last tendril experimented upon was taken August 17th, at 6 o'clock p.m. It was in the last stages of movement, and exhibited the least horizontal range. The whole length of movement was 191.30 cm.; the time sixteen hours and forty minutes, and the consequent average rate per minute was 0.191 cm.

The greatest movement was from 7 to 7.06 a.m., at the rate of 2.17 cm. per minute. This occurred from 9.30 to 10.00 p.m., at the rate of 0.02 cm. per minute. The waves of slowest motion were found from 6 p.m. until 5 a.m. The temperature varied only three degrees during the entire time of observation. From the commencement until 10 o'clock p.m., light rain fell and the sky was entirely overcast until the close of observations. At 5 a.m., there was a cool east wind, with a very large amount of moisture in the air, and the plant was in a very active condition. At the close of observations, heavy rain commenced to fall. The total dextrorse motion was 160.40 cm.; the sinistrorse 30.90 cm.; and the ratio as 1 : 0.181.

General Summary.

Average Rate of Movement.—From a total of 436 distinct observations upon the motion of the tendril under all conditions of temperature and humidity, it is reasonably safe to assume that the average rate of movement deduced from them, will represent with approximate accuracy, the true normal rate of movement under all the ordinary conditions of growth. This rate we find to be 0.316 cm. per minute.

Maximum Rate of Movement.—By reference to the accompanying table, it will be seen that the maximum rates vary very widely, and also, in the same tendril, that they usually occur in waves, as in 5 *a*, 5 *b*, *c*, etc.

RELATION OF TEMPERATURE TO RATE OF MOVEMENT.

(Deg. C. Distances in cm.)

	1.	2.	3.	4.	5*a*.	5*b*,*c*.	6*a*,*b*.	7*a*.	7*b*.	8*a*.	8*b*.	8*c*.	9.	Means.
Average rate per minute..	0.54	0.36	0.520	0.110	0.39	0.370	0.290	0.380	0.205	0.516	0.483	0.176	0.191	0.304
Max. rate of movement...	2.06	1.76	3.550	0.850	1.41	4.550	6.500	0.920	0.555	1.200	2.600	0.650	2.170	2.216
Temp. for max. rate..	28.30	26.10	27 800	35.500	27.20	30.900	24.400	29.000	20.000	31.700	22.200	20.500	21.100	26.500
Minute rate of movement...	0.21	0.18	0.013	0.031	0.13	0.043	0.047	0.053	0.080	0.166	0.100	0.023	0.020	0.084
Temp. for min. rate..........	31.10	31.70	29.500	32.200	21.70	16.700	21.100	31.100	22.800	34.00	24.000	19.500	20.000	27.300

If we examine these results in their relation to the external conditions of growth, then we find that, of the thirteen observations given, only four show waves of rapid movement during the morning, these occurring between the hours of 7 and 10.20, and in no case—unless we except No. 9—representing the *absolute maximum of motion for the whole life of the tendril*. The remaining nine show the waves to occur in the afternoon, from 1.50 to 7.12 o'clock. If, moreover, we select those figures which represent the true maximum of motion for the entire period of activity in each tendril, we shall find that only one such occurred in the morning, all the others taking place in the afternoon, between the hours of 1.50 and 6.50.

Equalizing the hours of day and night, making the time of division 7 a.m. and 7 p.m., we find the total length of diurnal movement to be 1359.90 cm.; and of nocturnal movement to be 536.90 cm.; thus making the latter in the ratio of 1 : 2.53 to the former, a difference which clearly indicates that temperature exerts an influence which far outweighs any retarding effect due to the greater influence of sunlight.

This naturally raises a question relative to the temperature under which these maxima were obtained. The values for tendrils 1, 3, 5 *b*, *c*, 6 *a*, *b*, 8 *b*, and 9, the six highest rates observed, were obtained when the temperature ranged from 21.1° C. to 30.9°. Of these, the highest rates, viz., 6.50, 4.55, and 3.55, were obtained when the thermometer ranged from 24.4° C. to 30.9°; the other three giving values of 2.17, 2.60 and 2.06, were obtained between 21.1° C. and 28.3°. We thus find that the more active of these waves were formed under the influence of a temperature 3.8° C. higher than that under which the less active were produced. Again, taking the highest rate of each tendril movement —including those just given—we find them obtained under an average temperature of 27.2° C.: while the waves of rapid movement in the same tendrils, but of less amplitude, were propagated under an average temperature of 24.8° C. Of the thirteen maxima of movement obtained, one was found to be coincident with the absolute maximum of temperature. This, however, was a movement at the low rate of 0.85 cm. per minute. Three were found to occur on an increasing temperature, usually several hours before the maximum was reached; and nine were observed on a descending temperature, from two to six hours after the maximum for the day had passed.

Passing to the condition of the atmosphere in other respects, we find that the maximum movements in tendrils 1, 8 *b*, 8 *c* and 9 were reached under conditions of great humidity; of all the remainder, when the sky was clear and the sun bright. The rates of movement in the four tendrils just mentioned were respectively 2.06, 0.65, 2.6 and 2.17 cm., and were attained when, owing to the humidity of the air, transpiration was not very active. Tendrils 2, 3, 4, 5 *a*, 7 *a*, *b* and 8 *a* gave respectively 1.76, 3.55, 0.85, 1.44, 0.92, 0.555 and 1.2 as the maximum of motion. These rates were all reached while transpiration was excessive, and the effect of this upon the plants so great that all the leaves, flowers and buds were drooping. Tendrils 5 *b*, *c* and 6 *a*, *b*, in which the highest maxima were reached, gave respectively 4.55 and 6.50 cm., but these rates were reached under conditions of active, though not excessive, transpiration, clear sky and bright sun, and while the plant was in a normally active condition, as shown by the erect leaves and fine healthy color of all the parts.

MINIMUM RATE OF MOVEMENT.—Of the thirteen minimum movements recorded, we find that five occurred between sunset and midnight, two between midnight and sunrise, three between 10 a.m. and 1 p.m., and three between 1 and 4 p.m. We further find that four occurred during a minimum temperature; four just before the maximum; two just after, and three at the very time of maximum.

As in our previous division, taking the figures obtained for 6 *a*, *b*, 3, 5 *b*, *c*, 1, 8 *c* and 9 as representing the true minima for the entire movement of each tendril, we find the average temperature at which these movements occurred to be 22.9° C., while the average temperature for the whole thirteen is found to be 25.8° C. The remaining seven movements of greater rapidity were found under the influence of an average temperature of 28.2° C. The following table will show the connection between temperature and rate of movement, as just explained:—

Maximum movements		....	13	26.5°	Mean	Temperature.
Minimum	"	....	13	25.8	"	"
Maximum	"	(*a*) rapid.....	6	27.2°	"	"
"	"	(*b*) slow.....	7	24.8	"	"
Minimum	"	(*a*) slow.....	6	22.9°	"	"
"	"	(*b*) rapid.....	7	28.2°	"	"

From this it will appear that a higher temperature is favorable to the more rapid movements, to a greater activity of the whole plant.

Referring to the atmospheric conditions, it is found that tendrils 6 *a*, *b* and 1 gave their minima of movement during pleasant weather, while the plant was apparently in an active condition. The rates per minute were .047 and 0.21 cm. respectively. Tendrils 7 *b*, 9, 5 *b*, *c* and 8 gave 0.08, 0.02, 0.043 and 0.013 cm. respectively, during a time of great moisture and even rain; 8 *c* gave 0.025 cm., during the time of a heavy fog and cold east wind. The remainder, 4, 7 *a*, 2, 8 *b*, 8 *a* and 5 *a*, gave respectively 0.031, 0.053, 0.18, 0.10, 0.166 and 0.13 cm., at a time when transpiration was excessive, as shown by shown by the drooping leaves and terminals, and always during a very bright sun.

DEXTRORSE AND SINISTRORSE MOVEMENTS.—The circumnutations of the tendril tip may commence in a direction with the sun, or the reverse. Movement in either direction is by no means continued during the entire period of activity. Motion in one direction may soon be succeeded by movement in the other direction, one alternating with the other constantly. The dextrorse motion, for all the observations taken, aggregated 1622.10 cm., the sinistrorse amounted to 1400.95 cm., and the ratio of one to the other was, therefore, as 1 to 0.86.

While this shows a tendency to equality of movement in the two directions—a tendency which might have been more pronounced had the observations embraced all the movements—an important relation bearing upon this point is to be observed between the latitudes and departures of movements. Also, the relation which these two directions of motion bear to one another must obviously be directly related to the location of the bands of more active tissue which induce the motion. The following table will exhibit the total latitudes and departures for all the tendrils :—

Tendrils.	Latitudes.		Departures.		Ratios.
No. 1	......	124.30	......	249.70	1 : 2.01
" 2.	......	53.25	......	116.60	1 : 2.19
" 3.........	......	123.35	......	269.40	1 : 2.10
" 4.........	......	21.00	.....	60.83	1 : 2.89
" 5 *a*.......	43.37	285.17	91.10	489.65	1 : 1.71
" 5 *b, c*.....	241.80		398.55		
" 6 *a, b*.....	......	141.75	......	266.55	1 : 1.88
" 7 *a*.......	87.75	135.50	192.80	262.10	1 : 1.93
" 7 *b*..... ..	47.75		69.30		
" 8 *a*.......	106.30	227.15	264.70	612.23	1 : 2.69
" 8 *b*.	67.65		203.03		
" 8 *c*.	53.20		141.50		
" 9.	......	122.40	......	118.15	1 : 0.95
Totals	......	1193.87	......	2145.21	1 : 2.04
Means	......	91.84	......	188.09	

An inspection of this table at once exhibits a most striking relation between latitudes and departures of motion. While in some cases there is a marked variation in the results, e.g., Nos. 4 and 9, yet these, as already seen, were tendrils which were only partially observed, and if we consider the mean result, which agrees with specific cases in which the entire action of the tendril was noted, we find the departures of motion to be just twice the latitudes. This indicates most conclusively, therefore, that the principal energy of circumnutation must be developed along the two sides of the tendril arm, and reference to our figures, as also the description of the histological elements, will at once show that it bears a most important relation to the three bands of vibrogen tissue.

Conclusion.

We may now proceed to sum up the conclusions which the foregoing facts appear to justify.

Temperature.—The observations here recorded are in harmony with the views generally held, that within certain limits and conditions, otherwise favorable, higher temperatures induce more rapid growth. According to the experiments of Sachs upon the germinating seeds of Cucurbita, the most rapid growth occurred under the influence of a temperature of 33.7° C.; the condition, doubtless, being such that the normal tension of parts was fully maintained throughout, or subject to but slight variations. In our own observations, the greatest growth, as represented in tendril movement, occurred under a temperature of 24.4° C.; while the most rapid growth of the vine occurred when the temperature ranged from 29° C. to 36.6°. It is important, however, not to lose sight of the fact that in these cases, there were important modifying influences which would affect growth through the normal tension of the tissues,—a disturbance of which frequently occurs as a result of high temperatures. The general effect of temperature becomes conspicuous at once, if we compare the growth for an even number of hours when the temperature is above 30° C., with growth for the same period when the thermal range is from 25° C. to 30°. We shall then find the growth in the latter case to be greater, as the following table will show:—

Number of Observations	Average Temperature.	Total Growth.	Average Growth per hour.	Relative Humidity.
6	27.0° C.	2.0 in.	0.333 in.	Relatively great.
6	34.9	1.6 in.	0.266 in.	Relatively small.

The relative humidity of the atmosphere, or the degree of saturation dependent upon temperature, exerts a direct influence upon conditions of tension in growing parts, and consequently upon growth itself, by inducing more or less rapid transpiration. Excessive humidity is consistent with more rapid growth. We may, therefore, reaffirm the already accepted principle that increasing temperature promotes growth, so long as it does not disturb the normal conditions of tension.

Light.—Alternations of day and night cause a marked influence upon and variations in the phenomena of growth. Light is generally accepted as exerting a retarding influfluence upon growth,[1] and other conditions being equal, we should naturally expect to find the greatest elongation of the axis and most rapid movement of motile parts during the hours between sunset and sunrise.

From the experiments now under consideration, we find that the growth during hours of darkness was in reality less than that during an equal number of hours of

[1] Sachs' Text-book, 755.

daylight, since, in the case of the tendrils, we obtained a movement of 1359.90 cm., for the day, against 536.90 for the night, and in the growth of the vine, 44.447 cm., for the day, against 34.287 for the night.

Rauwenhoff found that the growth in *Cucurbita pepo*, for twelve hours of day, was 56.9 p. c. of the whole, and only 43 p. c. for the same number of hours of night, thus giving a ratio 1 : 1.32 in favor of the former. Our results in the growth of the vine are in somewhat striking confirmation of this, since, as seen, our ratio is as 1 : 1.29 in favor of day light. In the case of the tendrils, the superior influence of conditions which obtain during the day becomes even more apparent. The one conclusion to be derived from these facts appears to be, that the superior influence of temperature in promoting growth overcomes the lesser and retarding influence which may be exerted by light.

From our previous considerations, it is clear that the movement of the tendril is but a normal manifestation of growth, and therefore subject to the same influences as other vital phenomena. These movements have been found to occur in well defined waves of greater and less activity, which, usually longer and of slower movement at the outset, are of decreasing length and greater activity with advancing age up to a certain period. This, however, is soon reached, and beyond this point the movements become somewhat longer, but more especially slower, with greater maturity. So long as all the tissues remain soft and in an actively growing condition, these waves will succeed one another in accordance with the controlling influence already spoken of. But as there is an advance in age with general hardening of the tissues and large formation of bast, a noticeable and general lengthening of the waves ensues. The tip may even drop toward the ground, as if exhausted, and not resume its nutations for one or even two hours. When it does, it is generally with a more sluggish action.

Growth in Length.—From previous considerations, it is clear that most rapid elongation and most active movement in the tendril, are simultaneous and directly correlated throughout the entire period of movement. It is, therefore, to this very rapid elongation in the first instance that we must look for a true explanation of the circumnutation. On the other hand, the structure of the tendril, presenting, as it does, a diversity of tissues, at once points to the fact that this rapid extension cannot be partaken of by all the tissues in equal degree. The vascular elements are those in which the least extension can occur of all the tissues present. With reference to all the other tissues, therefore, they must be brought into a state of positive tension which continually increases in strength as age advances and the constituent cells become more strongly modified. In the collenchyma also, while capable of greater extension and variation of tension than the wood and bast cells, yet with reference to the unmodified fundamental structure in active growth, there must be a well-pronounced positive tension. This fact is at once demonstrated by the changes which follow the cutting of sections. Transverse sections quickly bulge out in the centre with a strong marginal contraction. Longitudinal sections show a strong curvature with the concavity on the side along which the collenchyma lies. We may also, doubtless, ascribe a certain amount of this contraction to the effect of irritation, which causes a loss of water within the affected area, and thus, through condensation, a further increase of tension. This is essentially the view held by Sachs

(p. 869) and it certainly appears justified. We must, therefore, regard the collenchyma not only as influencing all the movements dependent upon growth, but also as that particular tissue which chiefly determines all movement caused by mechanical irritation, a view which is well supported by its presence in the tendrils of Vitis, Ampelopsis, Cucurbita, Sicyos and other vines, and the relations which it there bears to the movements of those tendrils.

The unmodified fundamental tissue, consisting of large, rounded, thin-walled cells filled with protoplasm and chlorophyll, is that in which the most rapid, general and continuous increase occurs. As the central or pith region early loses its power of growth and shrinks away radially, it may be regarded as having no special value in the movements, and we must look in this respect entirely to that parenchyma which lies without the wood zone. In all of the parenchyma tissue (Plate IV. Fig. 1) at *c* and *a*, there is found to be the greatest activity; and this power of extension is so strongly developed, that even after the vascular elements have assumed their most lignified condition, and the tendril has permanently coiled up, the vibrogen tissue at *a a'* will be found to retain its activity for some days. We must, therefore, infer, from this that the negative tension, as a whole, is developed most strongly in the parenchyma tissue, and particularly in the three bands of vibrogen which lie at *a a' a*."

Torsion.—Sachs[1] distinctly states that no torsions occur in Cucurbitaceæ. This is not confirmed by our own observations, however, since it has been observed to be a common feature of the circumnutations, that distinct torsions constantly occur. This is readily determined, not only by the vibrogen bands, but by the changes in the direction of the recurved tip. Similar torsion is also readily detected in the petioles of both tendril and leaf, and that it bears a most important relation to the circumnutation itself can hardly be doubted. So strongly are these torsions developed in the tendril arm, that the tip frequently rotates through 180° or 200°. The explanation of this torsion is not difficult, and has been given on many previous occasions by various observers. From what has already appeared with reference to the various tissues in their mutual relations of position and tension, it is clear that torsion must follow as a natural result of excessive elongation in the external layers, thereby exerting a positive tension upon those which are internal.

Irritation.—Of the two sides of the tendril arm, that which is uppermost and slightly channeled is the least sensitive to contact. This bears a direct relation to the distribution of the collenchyma tissue, which we find to be more continuous and strongly developed on the lower and sensitive side. That the vibrogen tissue is not concerned in changes due to irritation, appears evident from the fact that the flexure never coincides with these bands, but is always toward the lower side of the tendril arm, conforming to the position of the collenchyma. The conclusion is justifiable, therefore, that the collenchyma tissue is that which is directly concerned in such movements, through its capacity for strong variations in the contained water.

A tendril subjected to local irritation for about thirty seconds, develops an abrupt curvature at that point within one or two minutes, and the bending continues so long as

[1] Text-book, 866.

the foreign body is in contact, and even for a few seconds after its removal. Puncture with a pin, or the action of a loop of thread, produces similar effects. Irritation over a more extended area causes a correspondingly larger curvature. There is no special evidence in such cases that the impulse has been conveyed beyond the limits of the area irritated, and soon after the irritant body is removed—the growth in the various tissues having become gradually restored to its normal condition—the tendril straightens out and once more resumes its circumnutations.

More violent mechanical stimuli produce a different effect, however. A sharp blow, such as would be given by a pencil, falling upon any part of the arm, produces an effect which throws the latter into a series of long undulations for its entire length. Prolonged irritation at the tip will usually produce the same effect. These facts at once and directly point to the inference that, while the effect is slowly produced, there is, nevertheless, a distinct transmission of impulse to very remote parts. Were concussion alone concerned, it might be possible to refer the whole change to it alone, as directly affecting the turgidity of the collenchyma tissue; but the fact that prolonged irritation will produce a similar result, should raise a question on this point. From what we now know concerning the sensitive nature of protoplasm, the relation which this substance bears to growth and turgidity, and its now well established continuity through living tissues, are we not justified in the belief that such transmissions as above noted are primarily propagated through this means?

CIRCUMNUTATION.—Our attention is first of all called to the fact pointed out by Darwin,[1] and confirmed by our own observations, that the "tendrils revolve by the curvature of their whole length, excepting the sensitive extremity and the base, which parts do not move, or move but little." This clearly shows that whatever force is in operation, acts uniformly through the entire length of the motile organ, and that the movement has not a local origin at or near the base. We must, therefore, conceive, as both Darwin[2] and Sachs[3] explain, that there is a longitudinal band of more actively growing tissue which extends from base to tip, and thus the arm is bent over toward the side of less active growth. So far, our own observations are in strict harmony with these views, but they do not accord with the opinion that these bands "travel round the tendril and successively bow each part to the opposite side." As already shown, the figure described is not one of regular progression through successive points of an ellipse or other figure. (See Plate III.) In fact, the tip may change its direction very abruptly, often retracing the path just passed over (Nos. 36, 37 and 38), or the change may be less abrupt. While, therefore, it appears from the general equality of dextrorse and sinistrorse movement, that the totality of motion in one direction must be compensated by an equal movement in the opposite direction, the facts cited show quite conclusively that the band of growth does not pass regularly through successive points in the circumference, but that it arises irregularly. Again, the relations of the tissues in their mutual tension, and the position which the vibrogen tissue occupies, more especially the relation which this latter bears to the latitudes and departures of movement as already pointed out in a preceding paragraph, serve as a most important indication of the true position occupied by the bands

[1] Climbing Plants, 170. [2] *Ibid.* [3] Text-book.

of growth; and the conviction becomes more firmly impressed upon us that this position is not only fixed, but that it coincides with the vibrogen bands.

According to this view, all movement would be primarily due to these three bands, supplemented by less vigorous growth in the intermediate tissues. Therefore, all departures of motion would arise primarily from the two vibrogen bands traversing the sides of the tendril, and all latitudes of motion would be due to that vibrogen traversing the upper side of the tendril arm. Any deviation from strictly lateral or vertical oscillations must then arise as resultants of activity, either between two vibrogen bands, or between one vibrogen band and intermediate tissue of slower growth. Finally, the torsion already shown is to be regarded as having its origin in, and as compensating excessive growth in, one or all of the vibrogen bands of tissue.

Spasmodic Movement.—It has been noted that towards the end of the circumnutations, periods of rest alternate with periods of activity; that the whole action lacks vigor, and that there is a failure to accomplish those grand sweeps which are so conspicuous in the earlier period of activity.

These features are undoubtedly to be referred to gradually increasing lignification in the wood and bast cells, and the modified conditions of tension which necessarily result from this. As the bast cells, particularly, increase in thickness, their degree of resistance or of positive tension correspondingly increases, while at the same time the growth of the parenchyma tissues continues at a nearly uniform rate. So long as the bast remains thin-walled and capable of its maximum extension or response to conditions of external tension, for such period is the normal relation between it and the more actively growing tissue preserved, and this is marked by regularity and rapidity of motion in the whole organ. With excessive disturbance of the normal relations, the equilibrium is disturbed in the direction of the more resisting structure, and this finds expression, first of all in slow and spasmodic movement, and finally in the completion of the spiral, which is always developed freely, without contact, at the end of the period of circumnutation.

Coiling about a Support.—Coiling about an object with which the tendril comes in contact, has already been discussed indirectly, though it may be well to refer to one or two facts more particularly. The coiling of the tendril tip about the point of contact, is the direct result of irritation, as both Sachs and Darwin have already shown, and as the latter[1] explains, it is developed by a shortening of the side in contact with the object, the same change, i.e., condensation of structure and release of tension, operating here as in previous cases; and with Darwin, we can hardly agree with Sachs,[2] that the coiling is in any way due to accelerated growth in the unirritated side.

When once growth in length is arrested, as it appears to be soon after coiling is effected, the rapid hardening of all the parts appears to be the prevailing change. In this, however, it is difficult to conceive that the mechanical irritation has produced more than a very limited effect in advancing maturity. On the other hand, it rather appears that each tendril arm has a normal period of growth, which is completed only when the wood and bast cells have reached their full degree of maturity. If at the end of this period the

[1] Climbing Plants, 181.

[2] Text-book, 869.

tendril fails to secure contact with a suitable object, it coils up freely, as already shown, and this is the necessary consequence of the normal changes in the tissues. If, however, it comes in contact with an object of support, the tendril coils about it and accomplishes its double spiral within the normal period of its growth. This period cannot be prolonged for the purpose of finding a suitable support or completing imperfect changes. These must all be accomplished before the wood and bast tissue—the latter in particular—reach a certain stage in the development of their permanent character. This is well shown in the fact that old tendrils, which have failed to grasp a support until very near the end of their activity, manifest a striking loss of sensitiveness, and often catch hold but imperfectly, or if they gain a firm hold, fail to perfect their double spiral.

II.—Vitis cordifolia, *Michx.*

In the tendril of Vitis, not only with reference to its sensitiveness and general circumnutations, but more especially in its histological aspects, we have to deal with an organ which presents many features distinct from those of Cucurbita, the common ground of resemblance being found in functional similarity and in the way in which the circumnutations arise.

The tendril of the grape is a modified branch, bearing two smaller branches which serve a similar purpose. These branches, however, unlike those of the Cucurbita tendril, do not proceed from a common point of insertion, but arise successively on the elongating primary axis of the tendril as a whole. In their external aspects, they are well rounded, but somewhat flattened on the inner face toward the extremity, where the tip is strongly recurved. Throughout their length, the prevailing red color (*V. cordifolia*) is broken by ten narrow green lines, which are developed at approximately equal distances through the circumference. These are the bands of vibrogen corresponding to the three bands in the tendril of Cucurbita. Internally, the structure presents the features exhibited in Plate V. Figs. 1, 2, 3 and 4 A—during the earliest period of circumnutation—from which the following details may be gathered. The epidermis consists of a single row of thin walled cells with a strongly corrugated cuticle. Directly beneath this, lies a single row of pigment cells containing the red coloring matter. The hypodermal tissue consists chiefly of collenchyma, in which the angles are but slightly thickened (Fig. 3). As a whole, the tissue is quite continuous in most cases (Fig. 1, *cl*). Within the region of the hypoderma lie the ten vibrogen bundles, *v*, *v*, *v*, etc., which are well defined from the surrounding tissue, but somewhat variable in size These bands, although they frequently penetrate the collenchyma deeply, do not always break its continuity. Next within the collenchyma is a thin layer of very active fundamental tissue, the cells of which are large and regular (Fig. 1, *pr*). It is within this tissue that, at a somewhat later period, the cambium arises as a well defined layer. Directly internal to this is the wood zone, or xylem portion of the vascular bundles. This, in the earliest periods of circumnutation, is composed of somewhat isolated and nascent vascular bundles, the elements of which are all very thin walled and rapidly increasing (Fig. 4 A). The only structural element remaining is the pith, which, as in Cucurbita, bears no special relations to the circumnutations.

As the tendril advances in age, several important structural changes occur. The whole hypodermal tissue increases slightly in thickness, and simultaneously the tissue in the region of each vibrogen band, and for the full depth of the zone, *cl*, becomes so modified that the component cells enlarge strongly—chiefly in a tangential direction—while they also become much more thin walled, and all traces of collenchymatous thickening disappear. This causes a strong localizatior of the collenchyma to the regions between the vibrogen bands, where it retains its original character (Fig. 3) without much change beyond an increase in the size of the cells. Within the region, *pr* (Fig. 1), there arises a layer of cambium which forms a continuous zone. From this arise bast bundles, one for each of the vascular bundles already noted. The former remain quite distinct to the end of their growth, and are usually widely separated. From the inner face of the cambium tissue, there arise new wood cells, which now become develcped so generally as to render the original bundles conjunctive, thus giving rise to a continuous zone of wood which continually increases in thickness.

At a very early period in its growth, each vascular bundle develops from two to three vessels and ducts. Ultimately, all the fibrous elements became highly lignified (Fig. 4 B). That this condition may be hastened in time, and possibly increased by contact, can hardly be doubted: but it is equally true that such changes occur normally where there is no contact, e.g., the sections here exhibited were taken from a freely coiled tendril.

In comparing the tendrils of Vitis with those of Cucurbita, several important structural differences become apparent. The much greater number of vibrogen bands in the former, and their somewhat regular distribution, at once suggest greater regularity in the figure described, as well as a general equality of motion in all directions. Also in Vitis, the inferior development of the collenchyma is consistent with, and may serve as a proper explanation of, the much lower degree of sensitiveness there manifested. While the general changes incident to maturity of parts are the same in any case, it is noteworthy that in Vitis there is no distinct zone of bast which fulfills the function of that tissue in Cucurbita, and upon the xylem portion of the vascular bundles must depend that resistance to general elongation which is so essential a factor in circumnutations; though undoubtedly, in this case, unequal growth of opposite sides is of far greater importance than unequal tension of component tissues, so that torsion would here be of less value as a factor, than in Cucurbita where it is generally more marked.

During the circumnutations, distinct torsions occur. These are readily determined by tracing the course of the vibrogen bands, from which it becomes apparent that the tendril is frequently twisted to the extent of one-half revolution upon its own axis. If no object is grasped during the active period, the tendril ultimately coils upon itself; but having grasped an object, it perfects a double spiral similar to that in Cucurbita. It is also noted that tendrils which have coiled freely, do not become so hard and dry as those which have secured attachment, from which it would appear probable that contact produces a more or less marked effect in accelerating, or, at least, in increasing the maturity and strength of parts, a view which gains strong confirmation also from the very marked differences in these respects to be found in Ampelopsis.[1]

It would thus appear that the general features of circumnutation in Vitis and Cucur-

[1] Darwin, Climbing Plants, 148.

bita are the same, and that they may be regarded as representing a particular class of movements, so far as their mode of production, as well as their general external features, are concerned. It is not as yet possible to say how far each of these may represent the type for the family; but from the similarity of the structure and circumnutation presented by Sicyos and other Cucurbitaceous vines, it is perhaps safe to infer that, in that case, Cucurbita is the type of the family.

The deductions which the preceding facts justify are as follows:—

1. Movements of circumnutation arise through unequal growth of the tissues, which is chiefly represented by the vibrogen bands.

2. The bands of more active growth are strictly localized.

3. Movements due to irritation depend upon continued elongation of the opposite side, together with cessation of growth and contraction in the irritated parts.

4. The collenchyma tissue is that which is chiefly concerned in variations of tension under mechanical stimuli.

III.—ROBINIA PSEUDACACIA, *L.*

In the Robinia, there is not only an entirely distinct variety of motion, but also a motile organ which differs widely in many respects from the plants that we have previously considered. In this case, the special organ endowed with motion, is the leaf, which, instead of serving as a prehensile organ, is invested with the power of movement, for reasons directly connected with its own preservation against sudden and extreme atmospheric changes. Unlike tendrils, therefore, such motile leaves are found to present certain periodic changes of a most conspicuous character. They are, moreover, in most cases, supplied with a special cushion or pulvinus, through which the motion is primarily determined. As a whole, such movements present a certain relation to those already discussed, in that they may be regarded as modified circumnutations.[1]

PULVINUS OF THE LEAF.—Each pulvinus surrounds the base of its corresponding petiole as a cushion, conspicuously larger below than above. It extends upward from the point of insertion of the petiole, for a distance of 4.5 mm. to 7.0 mm. Its diameter is variable, increasing with age of the leaf, but apparently much more dependent upon the rankness of growth in the plant as a whole, since the largest pulvini are invariably found upon rank growing suckers. Under these circumstances, the diameter has been found to vary from 3.0 mm. to 5.0 mm., the mean size being not far from 4.0 mm. Externally, with a smooth and shining surface and very firm throughout, it possesses all the features of high tension. Of uniform size throughout, its strongest development is on the lower side of the petiole, while above it often but slightly exceeds the petiole itself. At the base on the lower side, just at the point of insertion, there are two triangular depressions in the pulvinus, formed by three ridges, one of which is central and strongly developed, while two are lateral and less strongly defined. All these ridges extend downward from the base of the pulvinus for some distance on the stem, and serve an important mechanical purpose, as braces or supports to the leaf. Directly interior and corresponding to the

[1] Darwin, Movement of Plants, 280, etc.

depressions noted, and thus occupying the extreme base of the pulvinus, is a large intercellular space, into which project numerous coarse, straight, sharp-pointed and thick-walled intercellular hairs. As seen in transverse section, this space lies within the lower half of the pulvinus, while the vascular structure is divided into three bundles, which traverse the projecting ridges referred to above, and thus it passes by the intercellular space on its lower side, in the extreme peripheral portion of the pulvinus. That portion of the pulvinus which lies on the upper side of the intercellular space, is quite uniform both externally and internally, and presents only those internal modifications of the normal tissues which are essential to its character as a pulvinus. In its structural details, other than these, the pulvinus may be characterized as follows :—

The epidermis is simple, the cells of equal diameter or slightly elongated tangentially; the cuticle is thin. The hypodermal tissue, which constitutes the pulvinus proper, and extends, without modification, to the bast zone, is of the same kind throughout, and consists of simple, round-celled parenchyma, with moderately thin cell walls. The cells show no essential variation in form, though in size they are usually much the largest in the central region. Throughout this tissue, continuity of protoplasm may be readily determined by the methods already stated. In the centre of the pulvinus and completely surrounded by it, is the fibro-vascular structure which forms the base of the petiole. In this vascular axis, the various tissues of the stem—pith, wood, cambium and bast—may be readily distinguished. The pith has the outline of an equilateral triangle with its base facing the upper side of the pulvinus, thus conforming to the external configuration of the pulvinus as a whole, as well as to the general outline of the other tissues. The cells of the pith are small and usually with medium-thick cell walls, though in some cases, especially toward the base of the pulvinus, they become very thick. The wood zone is well defined, and completely encloses the pith The medullary rays are very prominent, but the most striking feature is the presence of numerous pitted ducts and vessels, which, from their long diameter, conspicuously thick walls and regular radial arrangement, at once attract notice. Among them, there appear, in much less conspicuous manner, the wood cells, which are small both in length and breadth. Surrounding the wood is a somewhat narrow zone, which, in its earlier periods of growth, is meristematic, and provides for radial extension of the wood zone. It possesses the usual characteristics of such tissue. The bast zone forms a continuous tissue. The cells are of small diameter, but very long and fusiform. The walls are of medium thickness and traversed by numerous pits, which terminate at the intercellular substance. During the activity of the pulvinus these cells are all filled with protoplasm, and from the facility with which the walls swell under the influence of strong sulphuric acid, the tissue presents one of the best opportunities for observing the continuity of protoplasm. The bast, as a whole, is probably to be regarded as one of the most important mechanical elements present.

From what has previously been stated with reference to the sectional outline of the pulvinus and its included vascular structure, it will be seen that the latter is not concentric with the former, and that the minor axis, which passes transversely through the true structural centre, lies considerably above the centre of the section, and since this is a constant feature of the pulvinus, it will be seen that the lower half of the transverse section and the lower side of the pulvinus always exceed the upper half or side. The relations of parts in these respects were determined by making an outline drawing of all the parts by means of the camera, under an amplification of 20 diameters. A line representing the minor axis was then passed transversely through the true centre, and all tissues lying above and below measured by means of a planimeter. The results were as follows:—

	Upper Side.	Lower Side.
Pith	1.50 Sq. cm.	1.50 Sq. cm.
Wood and Bast..............	16.50 " "	23.00 " "
Parenchyma of Pulvinus...........	80.65 " "	171.25 " "

From this it appears that, leaving the pith altogether out of consideration, as of no mechanical importance, whatever tension is produced in the vascular bundles, as opposed to the tension in the surrounding pulvinus, must be developed above and below the true centre in the proportion of 1 : 1.39. Since the vascular elements are of the nature of permanent structure, their tension in relation to surrounding parts must be positive, and any general release of tension must result in a contraction of the organ through the vascular region. It therefore follows that this contraction must be stronger along the lower side of the pulvinus in the ratio given, and hence a tendency to curvature of the pulvinus downward. This, though slight, may often be noticed.

The tension in the tissue of the pulvinus, as opposed to that of the vascular structure, is developed above and below the true centre in the proportion of 1 : 2.12. The parenchyma tissue of the pulvinus is that capable of the greatest and most continued growth, as also that in which the greatest variations of tension must occur through variable turgescence. Its tension, with relation to the vascular structure, must be negative; hence any release of tension must permit contraction of the whole organ, while increase of tension must tend to elongate the pulvinus, and this action will be developed above and below in the ratio given. From this it is obvious that elevation and depression of the leaf, as a whole, depend respectively upon the pulvinus proper and the enclosed vascular structure.

From what has thus far appeared, we are doubtless prepared to gain a true explanation of the large intercellular cavity and its external braces, which occur at the base of the pulvinus. The three braces, of which the central has been seen to be the largest, must doubtless be regarded, first of all, as means of mechanical support through the firmness of their structure; while the pulvinus proper, which still surrounds each, seems to control changes of position to a certain extent, by its variable tension. The depression of the leaf, under any circumstances, however, must cause a much stronger compression of the structure on the under side of the pulvinus, where the flexure occurs, than elsewhere; and this is at once compensated for by the large intercellular cavity, which permits the central brace to bend into it, the leaf thereby hinging chiefly upon the upper side of the pulvinus. This view gains additional weight from the fact that, while very slight curvature may arise through the whole length of the pulvinus, the depression of the leaf is chiefly accomplished by sharp bending at the extreme base of the pulvinus, which thus becomes the true joint or hinge.

Pulvinus of the Leaflet.—The pulvinus of the leaflet bears but little external resemblance to the main pulvinus. It is of uniform width, and extends the entire length of the petiolule, being but slightly flattened along the upper side. The length varies—between leaves just unfolding and in their mature state—from 5.0 mm. to 6.0 mm., while for the same period the diameter varies from 1.0 mm. to 1.5 mm. These dimensions are subject to much less variation, as dependent upon conditions of growth, than in the main pulvinus. Externally, each little pulvinus is minutely and somewhat densely pubescent, a character which at once distinguishes it from the large pulvinus. Both the superior and inferior terminations are devoid of lateral ridges or depressions, nor is there any intercellular cavity. In these facts, there appears a very strong argument in support of the supposed mechanical importance of these structural features. The structure, in all its parts is continuous throughout, so that in most respects relating to their grosser anatomy, the larger and smaller pulvini are quite distinct.

In its internal structural features, the epidermis is simple and the cuticle thin. The tissue of the pulvinus is the same as that in the large pulvinus, though not so strongly developed as a whole. (Plate V. Fig. 5.) The important feature of the organ, as a whole, is the peculiar form of aggregation of the tissues and their mutual relations. The transverse section is nearly round, its vertical diameter exceeding its transverse in the ratio of 1 : 1.06. The wood and bast, instead of forming closed zones, are open along the upper side, where the pith blends with the tissue of the surrounding pulvinus. This peculiar arrangement bears an important relation to the flexibility of the petiolule as a whole, and corresponds with the fact that curvatures of this organ are downward and not upward. Determining the distribution of similar tissues, as in the previous case, with reference to the true centre, we find the following :—

	Upper Side.	Lower Side.
Wood and Bast........	1.9 Sq. cm.	6.6 Sq. cm.
Parenchyma of Pulvinus...........	33.8 " "	51.3 " "

Assigning the same function to these tissues in their relations of mutual tension, as in the case of the main pulvinus, it would appear that the influence of the special tissues concerned, in promoting elevation or depression of the leaflet, must be exerted between the upper and the lower side of the pulvinus in the following ratios :—

	Upper.		Lower.
Wood and Bast....	1	:	3.47
Parenchyma	1	:	1.52

Comparing these values for those obtained in the previous case, it appears that in the lower side of the pulvinus the vascular elements exert a much stronger influence as a contractile tissue, while the parenchyma exerts a much weaker influence as an erectile tissue. Inharmonious with our previously expressed views as this at first sight appears to be, it really offers no ground of conflict if we bear in mind the relative size of leaf and leaflet, and thus realize the very inferior influence of gravitation upon the latter. The intercellular cavity which appeared in the large pulvinus is, in the smaller organ, replaced by the peculiar development of the vascular structure. The open pith which appears along the upper side permits a greater extension of parts in that region, as the pulvinus curves downward.

During the period when the leaflets are folded, just as they emerge from the bud and for a short time afterward, they manifest no nyctitropic movement. During that period, all the vascular elements are in a nascent state (Plate V. Fig. 6 A). As soon, however, as the leaflets unfold and movement begins, the various vascular elements are found to have become strongly developed (Fig. 6 B), and from that time onward they continue to increase in their character as permanent structure. It thus appears true that no movement can occur until the woody tissue reaches a certain stage of maturity.

SENSITIVENESS.—The leaves of Robinia are not sensitive in any marked degree. Incisions and other strong irritations of the pulvinus have, with us, produced no effect. Simple irritations, such as would produce an immediate effect in the tendril of Cucurbita unless very much prolonged, are also without effect, and response appears to be gained from nothing less violent than percussion. Several determinations of the effect of percussion were made. In each case the base of the leaf just above the pulvinus was given a short, sharp blow with a pencil. The following results were obtained (in each case the degrees given represent the depression of the leaflets two minutes after percussion):—

(*a*) 10.05 A.M.—No. 1=87°. No. 2=87°. No. 3=60°.—Recuperation complete at 10.25.—Time required=20 m.—Plant in shade.

(*b*) 10.12 A.M.—No. 1=87°. No. 2=50°.—Recuperation complete at 10.30.—Time required=18 m.—Plant in shade.

(*c*) 10.17 A.M.—No. 1=50°. No. 2=45°.—Recuperation complete at 10.30.—Time required=13 m.—Plant in sun.

(*d*) 10.20 A.M.—No. 1=45°. No. 2=45°–80°.—Recuperation complete at 10.31.—Time required=11 m.—Plant in the sun.

(*e*) 10.32 A.M.—No 1=0°. No. 2=0°. No. 3=50.—Recuperation complete at 10.42.—Time required=10 m.—Plant in the sun.

(*f*) 10.38 A.M.—No. 1=50°. No. 2=45°. No. 3=45°.—Recuperation complete at 10.53.—Time required=15 m.—Plant in the shade.

(*g*) 10.42 A.M.—No. 1=55°. No. 2=45°–50°. No. 3=45°–60°.—Recuperation complete at 10.59.—Time required=17 m.—Plant in the shade.

(*h*) 10.47 A.M.—No. 1=0°. No. 2=0°. No. 3=2°–3°.—Plant in the sun.

In all these observations it was noticed that the basal leaflets, hence those nearest the percussion, responded first and most strongly; also, that the effect of percussion did not appear until fifteen or twenty seconds had elapsed, after which the motion became an accelerating one until the maximum of change was reached; the time for recuperation, as indicated above, thus embraces both depression and subsequent elevation to normal position. In all these cases one fact is conspicuous, viz., the relation of recuperation to direct action of the sunlight. Whenever the plant was in the sun the leaves were much less depressed from percussion, and their recuperation was much more rapid as compared with leaves in the shade.

NYCTITROPISM.—The nyctitropic, or true sleep movement, is that which essentially characterizes the leaves of Robinia. They may also manifest during the day, under the influence of bright sunshine, a paraheliotropic movement, during which the general tendency is for the edges to be turned upward to the sun, as if to check its influence. As Darwin has already pointed out,[1] the object of this movement is totally different from that of sleep movement, and is doubtless designed to lessen the destructive influence of too intense sunlight upon the chlorophyll.

[1] Movements of Plants, 355, 445.

Our observations have been almost wholly confined to the true nyctitropic movement, the principal data of which we have collected in connection with M. Chapman and G. E. Cooley.

Sleep-movement usually begins within half an hour after sunset, though this period appears to become longer as the season advances. In all cases, it has been most conspicuous that leaves at an elevation, e.g. those on the tops of trees, assume the sleep position much sooner than those at a lower level. No general rate of change, however, can be stated for all the leaves, since it is found that the leaflets fall into the nocturnal position at very irregular intervals, some assuming this position very early in the evening, while others remain in their diurnal position until quite late. The sleep-movement is generally completed by 10.30 p.m. From that time on there is no change in position, until the actual awakening occurs, which begins just before dawn. With reference to this, the following extract from our notes will give the general features of the change :—

"At 2 o'clock a.m. the maximum darkness and minimum temperature have just passed, and the older leaves show the first signs of awakening, many of the leaflets being expanded 5° or 10° from their former sleep position. At 3.30 the leaflets have opened to to an angle of 45°, and at 4 o'clock they are well expanded, the most marked change occurring within the latter hour. From an examination of the accompanying table the general conditions throughout the night may be obtained. The temperature was taken from an exposed thermometer, hung at the height of, and among, the plants observed. This will account for the variations of temperature noted in one or two instances :—

Hour.	Temp.	Remarks.
7.30 p.m.	16.00° C.	Leaves closing.
8.00 "	16.50	Sky clear all night.
8.30 "	16.25	
9.00 "	15.25	
9.30 "	15.50	
10.00 "	16.00	
10.30 "	16.25	Leaves all closed.
11.00 "	16.75	
11.30 "	15.00	
12.00 "	14.30	
12.30 a.m.	12.75	
1.00 "	11.25	
1.30 "	11.20	Max. darkness.
2.00 "	12.75	Leaves begin to open.
2.30 "	13.00	
3.00 "	13.50	
3.30 "	13.50	
4.30 "	13.25	Leaves all open.

The leading features of the awakening are, that the process begins at or immediately following the periods of maximum darkness and minimum temperature, and that it is completed before the sun rises above the horizon. As in going to sleep, the first change is noted in those leaves which are highest, so in the awakening the same fact is conspicuous. Important as these facts are to the general question of nyctitropic movement, we can only introduce them incidentally at this time, since it is not our present purpose to determine the precise influence of external causes upon the processes of growth whereby these changes are effected, but simply to det mine the mechanism of movement through the various tissues involved. We are, therefore, more intimately concerned in considering the various changes which occur in the leaf and leaflet during the process of sleeping and waking.

As the period of sleep approaches, the most conspicuous indication is to be found in the change of position which the leaflets assume. From a horizontal or slightly elevated position, they gradually droop, until they assume a position at right angles to their normal diurnal position; thus, assuming the leaf as a whole to be horizontal, each leaflet becomes vertical. Two important facts are here to be noted, viz., the relation of these changes to gravitation, and the indications they give of the operation of an active force. Whatever the position of the leaf as a whole may be, the leaflets are found to be influenced in certain directions by the action of gravitation upon their mass. Thus, if the leaf as a whole be horizontal, the drooping leaflets will finally assume a position perpendicular to its length. If it be raised or depressed above or below the horizontal, the leaflets no longer hang perpendicular to the leaf—with reference to its length—but fall vertically. Thus each leaflet is seen to turn laterally upon its petiolule as an axis, in direct response to the influence of gravitation upon its mass, and in this respect it is independent of the position of the leaf as a whole. In harmony with this, it will always be found that, in petiolules of a depressed leaf, there is a distinct torsion conforming to the relation which the leaflet bears to its main rachis. In leaves which hang almost vertically from drooping limbs, the leaflets thus often come to lie nearly parallel with the rachis.

When the leaflets fall into the sleep position, there is always a strong tendency for them to pass by the vertical plane passing longitudinally through the leaf; or in other words, the movement of the leaflets, with respect to the width of the leaf, is independent of gravitation. As the sleep movement progresses, the leaflets of each pair hang quite parallel, being separated throughout by a distance of 5 or 8 mm., representing the combined width of the rachis and length of the two petiolules. Soon, however, each leaflet bends in at the tip toward the other, so that they finally touch. This is effected in part by a curvature throughout the entire length of each leaflet, but much more by a continued curvature of the pulvinus of the petiolule, the result being that each tip is carried several millimetres beyond that point which would be determined by gravitation alone. Removing the opposite leaflet of each pair, does not seem to affect the movement of that remaining. In the terminal leaflet, the sleep position is assumed precisely as if it were a lateral leaflet, with the difference that its change of position is much greater, and it is carried much farther past the vertical. Without any regard to the position of the leaf as a whole, the terminal leaflet drops until it forms an acute angle with the rachis on its lower side. If the leaf be horizontal, the terminal leaflet bends several degrees past the vertical. If, however, the leaf be drooping, then the leaflet still establishes the same relation to the rachis, and thus often becomes horizontal or even turns up past the horizontal. In the case of leaves which were hanging vertically, this reflex position of the terminal leaflet was often found to be 10° above the horizontal, or about 100 from the position which would be established by gravitation alone. These facts, therefore, show that the true sleep movement is not passive, similarly to that previously discussed, but that it is due to an active force, the measure of which is partly expressed in the degree to which it overcomes gravitation.

In assuming the sleep position, each leaflet droops: first, by curvature of the petiolule through its whole length; secondly, by a sharper bending at the junction of petiolule and leaflet; thirdly, by a slight curvature through the entire length of the leaflet itself. In this connection it is important to note that, when leaflets are removed by cutting away at the extreme base of the petiolules, the latter almost immediately curve, the curvature conforming to that which is produced during the normal sleep movement. There is, in all this, a strong indication that the change is due to release of tension in the tissue of the pulvinus.

In the leaf as a whole, there is comparatively little movement. Darwin[1] has shown that there may be an actual elevation during sleep, to the extent of 3° or 4°. Our own observations show, and probably with greater frequency, a depression of the whole leaf to the extent of 35° or 50°. The same change may sometimes be induced by irritation, occasionally in a more marked degree. In all such changes of position, they appear to be accomplished at the extreme base of the pulvinus which thus acts as a hinge. As the leaf drops, the central ridge on the lower side of the pulvinus recedes slightly, the cushion around it becomes somewhat wrinkled, but on the upper side the pulvinus is drawn quite tense and smooth. It is important here, to note the difference between the pulvinus of the leaf and of the leaflet during the sleep movement, as it will be found to be correlated in a most significant manner, to the internal structure in each case.

Conclusion.

The deductions which can reasonably be based upon the foregoing facts, may be briefly stated.

By comparison with Cucurbita and Vitis, the absence of any marked sensitiveness in Robinia, would imply the absence of a tissue in which variation of tension under external irritation is a special function. This we find quite in accord with the presence of collenchyma in the former, its absence in the latter, and the relation which it bears to the sensitiveness of the organ itself. Whatever transmission of impulse there may be, can be readily determined as in the previous cases through the continuity of protoplasm.

In the leaf, the soft tissue of the pulvinus proper is that in which the variations of tension under external influences is determined. Moreover, the fact that this tissue is greater below than above the centre, points to its serving as the true erectile tissue wherever its internal tension is augmented sufficiently—becoming simply passive when its tension is reduced below a certain point. This is a more important factor in the pulvinus of the leaflet than in the large pulvinus, since the changes in the leaflet are greater, and require a relatively greater erectile force. As the pulvinus determines the upward movement, the included fibrous elements determine the downward and reflex movements.

[1] Movements of Plants, 355.

Being in a state of positive tension, any release of tension in the surrounding pulvinus at once permits contraction in the bast. Under irritation, and possibly other influences, this may also be increased by loss of water, as occurs in a more marked degree in the collenchyma of Cucurbita. The direction of bending, as determined by this contraction, depends upon the distribution of the bast in the organ. In the case of the leaflets, we have seen the bast to be so disposed below the axis of the petiolule, that the latter can only curve downward, this being facilitated, moreover, by the vascular structure being open along the upper side. In the main pulvinus, the closed cylinder of vascular structure preserves a condition of rigidity in all parts except at the extreme base, where we find the vascular structure to become branched in such a way as to produce a true joint in connection with an intercellular cavity.

Explanation of Plates.

Plate III.

Figure, half natural size, showing movement of tendril tip. The figure is seen as if the observer were at at the base of the tendril looking toward the tip.

Plate IV.

Fig. 1.—Half section of tendril arm of *Cucurbita pepo* × 66.
(*a*) Vibrogen.
(*b*) Collenchyma.
(*c*) Active parenchyma.
(*d*) Bast.
(*e*) Vascular bundles.
(*f*) Central pith parenchyma.
" 2.—Bast cells × 266.
A. During active period.
B. After coiling of tendril.
" 3.—Collenchyma × 266.
" 4.—Continuity of Protoplasm in collenchyma × 266.
" 5.—Vibrogen × 133.

Plate V.

Fig. 1.—Half cross-section of tendril of *Vitis cordifolia*, Michx., × 66.
cl. collenchyma.
pr. parenchyma.
w. wood.
p. pith.
" 2.—*v.* vibrogen tissue × 266.
" 3.—*cl.* collenchyma × 266.
" 4.—wood tissue × 266.
A. During activity of the tendril.
B. After cessation of motion.
" 5.—Cross section of smaller pulvinus of leaflet, *Robinia pseudacacia* × 66, showing relation of central vascular structure to the pulvinus tissue.
" 6.—Structure of vascular zone × 266.
A. Before nyctitropic activity.
B. During nyctitropic activity.