Observations on *Mamillaria elongata*.

BY

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With Plates XXV and XXVI.

CONTENTS

	PAGE
A. INTRODUCTION—THE PROBLEM	375
B. OBSERVATIONS ON <i>MAMILLARIA ELONGATA</i>	377
(1) Morphology	377
(2) Anatomy	378
a. The stem	378
b. The root	381
c. The tubercle	384
(3) Homology of the tubercle	392
(4) Physiology	395
a. Introductory remarks	395
b. Physiology of <i>Mamillaria elongata</i>	397
c. Comparison with other plants	405
C. CONCLUDING REMARKS.—THE RESULTS	408
LITERATURE.—DESCRIPTION OF PLATES	412

A. INTRODUCTION.

THE species of the natural order Cactaceae show a remarkable uniformity in the plant-form they represent. From this point of view the genus *Mamillaria* may be taken as typical for its natural order.

The Cactaceae occur in desert regions, and are thus subject to the influence generally of adverse conditions. The deviation which they represent, from what we may call the normal dicotyledonous type, makes a study of this order, as representing a definite plant-form, very interesting. This interest is heightened when we find the *Mamillaria* type occurring in another desert genus, belonging to a different natural order, namely in *Mesembryanthemum*, a genus of the Aizoaceae. *Mesembryanthemum stellatum* represents a plant-form of the same type as *Mamillaria elongata*.

In the literature of the subject very little information can be obtained concerning the physiology of *Mamillaria*, as a definite ecological type.

Goebel and Ganong refer to the general biology of the Cactaceae, but we get only a superficial idea of the biological significance of the various organs and structures which characterize this plant-form.

The tubercles, crowned by a set of spines, form a very conspicuous feature in the various species of *Mamillaria*, but the spines are generally very briefly referred to in the literature. Their function is usually, if not always, put down, without further discussion, as that of affording protection for the living plant-body against grazing animals. Ganong, Goebel, Delbrouck, and others have put forward this view.

This explanation of the spines, which form such highly developed structures in many species of the Cactaceae, has never appeared to me to be quite satisfactory. A careful external study of the succulent plants at the Royal Gardens, Kew, still more increased my dissatisfaction with this explanation of their function.

The following paper is an attempt on my part to get nearer a better understanding of that plant-form of which I have taken *Mamillaria elongata* as a typical representative. The problem I put before myself, when I began these observations in 1901, was this: *what is the explanation of the plant-form represented by Mamillaria elongata, and what is, more especially, the meaning of the spines which form so characteristic a feature of this plant?*

A problem which has occupied numerous botanists is only referred to briefly in the following paper. This concerns the homology of the tubercles and spines of the Cactaceae. This question seems to have aroused far more general interest among botanists than their biological significance.

Of course no detailed account of the biology or ecology of any plant-group can be quite satisfactory, which is not based on field-work in the native haunts of the plants concerned.

For this reason great interest attaches to the establishment of a Desert Botanical Laboratory on which D. T. MacDougal reports in the Journal of the New York Botanical Garden of 1903 (18, p. 11). It is hoped that continuous observations will be made of conditions and plants, and with the material thus collected we should finally gain a clearer insight into the life of desert plants with which Volken has already made us familiar to a certain extent. I have no doubt that many general physiological problems will be brought nearer a solution by being thus carefully studied in localities where the functions of the plant are carried out under adverse conditions.

I have, however, attempted to give some physiological explanation of some of the structures met with in *Mamillaria elongata*, although I have never myself visited any of the tropical American deserts.

It was first my intention to examine in detail thirty or forty different species of the Cactaceae, but unfortunately the time at my disposal would

not allow of this. For this reason I selected *Mamillaria elongata* as a good type. Of a few other Cactaceae I was able only to make a more or less superficial examination. The observations made on these latter, however, generally confirmed the opinions which I arrived at concerning *Mamillaria elongata*.

In order to make out the structure of the plants I cut numerous sections, a large number of which were obtained by the aid of the microtome.

The spines unfortunately cut very badly. This is not due to their hardness so much as to the air which they contain. All efforts to remove the air by an air-pump failed entirely. The resulting sections were generally therefore much torn, but did nevertheless help very much in making out the structures met with.

The sections were stained with Kleinenberg's haematoxylin or with brasilin, and mounted in Canada balsam, or they were mounted unstained in glycerine jelly to which some Fuchsin in a watery solution had been added. This last treatment gradually shows up very clearly all lignified, cuticularized, and suberized cell-walls which are well stained, the other walls being but faintly stained.

I would like to refer here to a method I adopt for marking the glass slides on which microtome-sections have been mounted. The old method of writing on the glass with a diamond, or the not quite safe plan of labelling the slide, both appear to me to be too cumbrous. I now merely write with a pen, dipped into the white-of-egg mounting solution, on one end of the glass slide, which must, however, be quite clean, a few distinguishing numbers or marks. Almost any stain will colour this albumen, and when dried it shows at once what the slide is. It is not easily removed during staining or even after. The writing can of course be replaced by a proper label later on when the slide is quite finished.

B. OBSERVATIONS ON MAMILLARIA ELONGATA, P.DC.

1. Morphology.

Mamillaria elongata, P.DC., according to Schumann (26, p. 518, Fig. 83) occurs in dense clumps, and is commonly met with in the Mexican state of Hidalgo. It forms patches which may be 1 m. in diameter. Each separate upright shoot is cylindrical in form. Its height may be as much as 30 cm., its diameter 1.5–8 cm. The plant-body, always unbranched, is usually however about 7–8 cm. high (Pl. XXV, Fig. 1).

As with all other species of this genus the surface of *Mamillaria elongata* is studded with numerous and very regularly arranged outgrowths which have been called mammae, warts, or tubercles (Pl. XXV, Figs. 2, 3). They project about 2–4 mm. from the main body of the plant and are

surmounted by a set of spines. A single central spine may be separated from the marginal spines, which are so numerous as to obscure almost entirely from view the body of the plant. A dense mass of hairs is found in between the spines.

The plant is attached to the soil by a rather short and stout root (Pl. XXV, Fig. 3).

2. Anatomy.

I propose now to describe the structure of the main body of the plant-shoot, then to discuss the structure of the root, and finally in greater detail that of the tubercles and their spines.

(a) *Anatomy of the Stem.*

The specimens which I had the opportunity of examining anatomically were not more than about 4-5 cm. in height, and 1.5 cm. in diameter. They were obtained from Mr. F. A. Haage, junr., Erfurt, Germany, and appeared to be seedlings.

Disregarding for the present the structure of the projecting warts or tubercles, the main body of the shoot-part of the plant consists of a mass of fairly uniform parenchymatous ground-tissue, traversed by vascular bundles (Pl. XXV, Fig. 3).

The parenchymatous cells measure about 80-120 μ in diameter and in cross-section they appear roundish. Of this size they are found near and around the vascular bundle, in the cortex, the pith, and the broad medullary rays. They may be 380 μ long. Further away from the vascular bundles and nearer the epidermis the measurements for the cortical cells would be 60 to 70 by 180 to 250 μ . They all contain little cytoplasm, but a large nucleus. Intercellular spaces are found very extensively bordering on these cells in the cortex. They are, however, very shallow.

The epidermis, even in older parts of the plants I examined, which were themselves however not very old, was not replaced by cork, except in cases of injury or in that region where the root joins on to the stem. That part of the plant which is exposed to the air and to the light is almost entirely covered with the projecting tubercles. The remaining portion lower down is in the soil. Stomata are present here and there on this buried part, but very possibly they no longer function. Protoplasmic contents were not discernible. The radial walls of the epidermal cells are wavy and strongly cuticularized.

As just mentioned, the lower end of the plant frequently develops cork. The lower rounded end of the shoot in the plants I examined was covered by 6-10 layers of cork. The passage of any adventitious root through the ground-tissue of the stem is lined completely with a similar mass of cork. Those parts of the lower end of the plant which are actually in contact

with the soil are generally protected by cork. The epidermal layer does not, however, seem to be thrown off till fairly late, if it is got rid of at all. It can in fact generally be distinguished even outside the deepest masses of cork by the sinuate radial walls of its cells. The phellogen takes its origin in the layer of cells immediately inside the epidermis. The cork-cells are frequently very much flattened and stretched. They may thus attain a length of 100μ , being at the same time 20μ and less in radial diameter (Pl. XXVI, Fig. 27).

The main axis of the plant is traversed by a ring of bundles, which in my plants at least remained separate, fairly large medullary rays connecting the pith with the cortex (Pl. XXV, Fig. 2). At any given point we can find between eight and twelve or fourteen bundles in transverse section.

An examination of their structure shows the arrangement already described for the Cactaceae by several authors since the time of Schleiden (25, pp. 20-36). Solereder gives a brief summary of the literature which refers to the structure of the Cactaceae (28, pp. 459-468).

I will, however, briefly recapitulate the structure of our little plant (Pl. XXVI, Figs. 21-27).

The bast forms a small and inconspicuous part of the whole collateral bundle (Pl. XXVI, Figs. 21, 22). Following the nomenclature of Vöchting (32, p. 409) we can distinguish between large clear cambiform cells (*p*), and smaller and darker protophloem elements (*o*). The former measure 35 to 40 by 15 to 20μ , in transverse view, being generally somewhat compressed radially; the latter are more isodiametrical, measuring about 3.5 to 7μ across. In length both kinds of bast-cells measure about 90-100 μ . In the same way as we shall be able to notice in the xylem later on, the transverse walls of the bast elements are all found to be almost at the same height. Both kinds of cells finish longitudinally at the same level, their ends being but slightly drawn out. We might almost distinguish nodes and internodes in the bast, as later on in the wood. The protophloem-cells form groups of two to three to twelve or more cells, which lie embedded in the large cambiform cells. Both contain protoplasm, the protophloem-cells, however, more abundantly.

The bundles possess but little cambium, which very slowly adds on new tissue (*r*). This consists only to a very small extent of bast, being chiefly wood.

We now come to the wood, the elements of which occur in four different forms, three of which only are represented in every central bundle of the main stem.

The protoxylem is made up of the long and narrow spiral tracheids (Pl. XXVI, Fig. 21, *l*) so generally met with in this part of the bundle. They vary in diameter from 10 to about 20μ , at which size, however, they are already passing into the metaxylem. The thickening forms a fairly

close spiral, but does not project very far into the cavity of the tracheid. In a tracheid measuring 10μ across, the spiral thickening projected barely 2μ into the cavity, and even in a 20μ tracheid the spiral ledge was but a fraction thicker. Between these lignified tracheids we get a few thin-walled parenchymatous cells. These are of about the same size as the smaller spiral tracheids.

The metaxylem is made up of a different form of spiral tracheid, but the same kind of parenchymatous cell met with in the protoxylem. The spiral tracheids form a very characteristic constituent of cactaceous wood (Pl. XXVI, Figs. 23, 25) and have already been carefully figured by Schleiden (25, Pl. VII, Fig. 1, &c.). Subsequent authors have generally been satisfied with drawing them in a purely diagrammatic way or referring to Schleiden's paper only (28, p. 463, Fig. 91).

These tracheids have angular walls where they adjoin other tracheids, but rounded convex walls where parenchymatous cells are their neighbours. 50μ probably represents the greatest diameter to which they may attain, the average lying between 30 and 40μ for the larger ones, 20 – 30μ for the smaller ones. In length they show a very uniform measurement, this being about 100μ . The ends of adjoining tracheids meet at about the same level as was noticed already for the bast-cells (Pl. XXVI, Fig. 23). The ends are but slightly pointed or drawn out. Each tracheid has a cellulose wall, which is quite continuous, but from this projects a lignified spiral thickening of very large dimensions. The cellulose wall can plainly be made out and is probably about 1μ thick. The spiral band of thickening projects into the cell-cavity a distance of 10 – 12μ in the large tracheids, but never less than about 6μ in the smaller ones. The spiral band is thinner at its point of attachment to the cell-wall and gets slightly thicker towards the centre. In longitudinal section we again usually see the cellulose wall bulging in towards the cavity of the tracheid when the latter is neighbour to a parenchymatous cell. The spiral thickening, however, always protrudes into the parenchymatous cell (Pl. XXVI, Figs. 23, 25).

The tracheids contain no protoplasm, as soon as they have become properly lignified. Frequently we can however see just inside the cambium tracheids which already show a large spiral thickening, which does not however respond to the ordinary wood-stains. Such cells contain cytoplasm and nucleus.

Van Tieghem seems to maintain that the spiral tracheids of the Cactaceae invariably contain protoplasm and should therefore be called parenchymatous cells (28, p. 462). It seems very likely, however, that his observations were made on some such younger tracheids as I have just referred to. These peculiar, broad and short, tracheids with their very well developed single spiral band form the bulk of the bundle of the main axis.

The parenchymatous cells found in between the spiral tracheids are

living cells, and they are practically of the same breadth and length as the tracheids. In breadth they are not unfrequently compressed, but their length may be said to be identical with that of the lignified cells.

Another kind of cell is found in the small plants of *M. elongata* towards the lower end of the main stem. In the later additions to the metaxylem we get in the latter, apart from the large spiral tracheids and parenchymatous cells, some libriform cells, which have very much thickened walls. In length they are about equal to the spiral tracheids, but in the region where they occur, the position of the tracheids with regard to one another has become rather irregular and they may be longer than at other points. The libriform cells measure up to about 90 and 120 μ in length (Pl. XXVI, Fig. 25, *q*). The transverse walls of the neighbouring cells still remain at about the same level. The libriform cells contain cytoplasm and nucleus, both of which can be made out clearly in transverse and longitudinal sections (Pl. XXVI, Fig. 26). The cells are angular in outline, and measure about 15 to 30 μ across (Pl. XXVI, Fig. 24). The thickening, which is continuous except for a number of pits, is not more than 4–5 μ in depth. The walls of these cells are flat and not rounded even when abutting on a parenchymatous cell. They have very distinct crossed pits. The opening of the pit towards the cell-cavity is a long and narrow slit, which widens out towards the middle lamella. At the latter point, the pit may be 2 μ across. The slit-like opening to the cell-cavity is about 3–4 μ long. The slit in any given cell lies at right angles to the corresponding slit of a neighbouring cell. The pits are found on all the walls (Pl. XXVI, Fig. 26).

The cells of the ground-tissue, which immediately surround the bundle, are very much compressed (Pl. XXVI, Fig. 21), so that their cavity is often very small as compared with their whole bulk.

(b) *Anatomy of the Root.*

The few small plants of *M. elongata* which I have examined were evidently grown from seeds. The whole root-system in these consisted of a distinct tap-root, with a small number of lateral roots. The former extends into the soil for a distance which is about equal to the height of the shoot above the soil.

The tap-root is usually very much thicker than the lateral roots, more particularly near its junction with the shoot (Pl. XXV, Fig. 3).

The structure of the root-tissues is very simple, but shows several important differences as compared with the shoot, apart from its general arrangement as a normal dicotyledonous root.

The growth of the root-tip and the origin at this point of the various tissue systems has been described by v. Breda de Haan for *Melocactus* (4, pp. 9–11). Pretty much the same condition of things, I imagine, will obtain

here, but my examination has been very cursory with regard to this question.

I will here merely describe the structure of a younger, and then that of an older root.

We can take first a young lateral root with a diameter of about 1 mm. The roots which I examined were all pentarch, with the exception of one, which was tetrarch (Pl. XXVI, Figs. 33, 34).

A few parenchymatous cells in the centre of the root, about eight to twelve in number, form the pith, in the outer part of which lie the small groups of protoxylem, consisting of 5–8 elements (Pl. XXVI, Figs. 31, 32, 4). The cells of the pith are more or less round in transverse section, but rather elongate in longitudinal view. They measure about 12–18 by 100–150 μ . Their ends fit on to one another square, i.e. at right angles to the longitudinal direction of the cell, and the cells themselves contain a fair amount of cytoplasm and a distinct and fairly large nucleus (Pl. XXVI, Fig. 32).

The protoxylem-elements appear to be tracheids and not vessels. They are annular throughout. They measure about 10–15 μ across, but I have been unable to ascertain their length. The thickened ring is 1.5 to 2 μ thick, and projects about 1.5 μ into the cell-cavity. The distance from one ring to the next is very regularly about 8 μ . The very thin unthickened part of the tracheidal wall consists of cellulose.

Radiating outwards from the protoxylem-bundles may be seen the primary medullary rays. The cells of the primary medullary rays are usually much compressed tangentially, measuring occasionally as much as 50 μ in radial direction, and 19 μ in tangential direction. They become less compressed towards the periphery of the transverse section. The medullary ray as a whole naturally becomes slightly broader towards the outside, the rows of living cells radiating outwards very regularly. Finally they pass into the cortical tissue (Pl. XXVI, Fig. 31).

The large wedge-shaped masses of metaxylem fill up the space between the medullary rays. The elements of the metaxylem are tracheids and wood-parenchyma. Both are arranged in regular rows, but the distribution of the two kinds of wood-elements varies. Some of the radiating rows will consist almost entirely either of tracheids or parenchymatous cells, or both may be equally represented. The parenchymatous cells, whether merely xylem-parenchyma or belonging to the secondary medullary rays, are smaller than the tracheids. Their diameter varies between 10 and 20 μ ; their length, like that of the cells of the primary medullary rays, may reach as much as 200 μ . They are of course living cells. The tracheids exhibit annular thickening throughout, although in a few cases two neighbouring rings may be connected by a band of thickening—thus forming a short spiral. They measure 10–26 μ in diameter, and seem to attain a length of 200 μ , but only in a few cases could the transverse walls be made out. The

narrower ones are generally found nearest the centre of the root (Pl. XXVI, Figs. 31, 32).

The projecting ring of thickened wall-substance is a very conspicuous feature. It may project as much as 8μ all round, but generally only as much as $5-7\mu$. The separate rings are regularly about 3μ high and separated from one another by a distance of about $18-20\mu$. In cases where an annular tracheid adjoins a parenchymatous cell the tracheidal wall collapses slightly, thus becoming concave towards the cavity of the former (Pl. XXVI, Fig. 32).

A layer of cambial cells, slightly compressed radially, surrounds the metaxylem, but does not seem to be very actively dividing opposite the primary medullary rays (Pl. XXVI, Fig. 31, *r*).

The elements of the bast are of the same structure as already described for the main axis of the shoot. Small groups of protophloem (*o*) are dispersed in between the large cambiform cells (*p*).

Then follow a few layers of large cells, which form the cortex. Their diameter is $18-30\mu$ in a radial direction, and $40-50\mu$ in a tangential direction. Their length seems to be about 150μ . They are of course living cells.

The outer portion of the root is made up of numerous layers of cork-cells. Most of these have collapsed in a radial direction and can only be roughly counted (Pl. XXVI, Figs. 31, 32). The cork is about 10-20 layers deep at the most. The size of the cork-cells is very uniform. They are $70-80\mu$ long, and about $50-60\mu$ broad in the tangential direction of the whole root. Their radial diameter is often almost nil, owing to compression. It does not exceed 24μ (Pl. XXVI, Figs. 31, 32).

In the young root of about 1000μ in diameter just described the different tissues make up on the average the following proportions of any given radius:—Cork 40μ , cortex 100μ , bast 40μ , wood 270μ , the remaining tissues to the centre 60μ .

An older root higher up, just before it passes into the shoot, does not differ much from the thinner root just described. But certain structures are found, which we have not yet met with, at least in the root.

At the point where the root passes into the stem there occur in the wood-part of the bundle small masses of libriform cells, already mentioned as being found near the older and lower end of the vascular bundle of the stem. The presence of these libriform cells seems to be characteristic of the lower end of the stem and upper portion of the root. The roots showing these libriform cells seemed to be 1.5 to 2 mm. in thickness. Quite large quantities are found at these points in the stem and main root. In smaller adventitious roots I have never, however, seen them pass into the root-tissue except for a distance of $10-15\mu$, though they may be found plentifully in the continuation of the latter into the stem. In the larger main roots I

have seen them penetrate as far as 3 mm., but at this point they are much reduced in quantity. The libriform cells of the root agree in every way with those of the stem in structure and form.

We find that the tracheids of the root with their characteristic annular thickening are gradually replaced by the spiral tracheids of the stem. In some cases intermediate stages are found, giving the appearance of reticulate tracheids. Cork is extensively formed in this region. It lines, as already mentioned, the passages through the cortex made by the adventitious roots, and also covers the roots for a very long distance.

Root-hairs may occur in large quantities on the root, often obscuring very largely the growing-points of the young lateral roots. They very soon apparently lose their absorptive function and then may resemble fungal hyphae. But I was unable to detect the presence of any mycorrhiza at all.

In the older roots the proportion of wood to parenchyma in the metaxylem is different to what it is in the younger root. There is in the former more lignified tissue, and it is therefore harder and tougher.

In *Melocactus*, v. Breda de Haan notes that the protoxylem of the root consists of spiral vessels (4, pp. 9, 10) and the metaxylem of scalariform vessels (4, p. 12).

(c) *Anatomy of the Tubercle.*

The arrangement of the tissues in the tubercles or warts which form such a prominent feature of the Mamillariae is extremely characteristic and interesting. Each tubercle is roughly of the shape of a stunted cone, the blunt apex of the latter being crowned by a marginal ring of spines with one central one (Pl. XXV, Figs. 1, 2, 3).

We can distinguish first an epidermis, which covers the whole tubercle (Pl. XXV, Fig. 15, *e*). The cells are flattened and have wavy outlines. The cuticle is not very thick, namely about 1.5μ . The epidermis contains no chloroplastids. It is interrupted by fairly numerous stomata (Pl. XXVI, Figs. 9, 15). These are of the typical cactaceous type (28, p. 459). Several subsidiary cells are found running parallel to the guard-cells. In a transverse median section the guard-cells are seen to be at the same level as the other epidermal cells and are not depressed. A small ledge of cuticular wall projects in such a way as to produce a small antechamber which leads to the actual passage between the guard-cells. This leads to the internal air-chamber with which the whole very extensive system of intercellular air-spaces inside the tubercle communicates.

Disregarding the spines and the cushion on which they are inserted, the remaining tissues of the tubercle are ground-tissue and vascular tissue (Pl. XXVI, Fig. 15).

The cells of the ground-tissue are parenchymatous throughout. Immediately inside the epidermis is found an hypoderma (*d*), consisting of flat, short cells, which really differ only in form from the next inner cells. They usually contain a few chloroplastids. Except near the stomata, they leave no intercellular spaces between themselves and the epidermis.

These cells are succeeded by rows of palisade-cells, which run parallel to one another and make a definite angle with the epidermal layer; each row consists of 2-6 cells. Very extensive and continuous air-spaces are found in connexion with these rows of cells. They seem often to completely surround the palisade-cells, so that these appear to be like the assimilating filaments in *Marchantia*, namely, loose threads. This is, however, not actually the case. They represent the chief assimilating cells of the plant and contain therefore very many chloroplastids. These are round in form and measure 5-7 μ across. I have nearly always found the chloroplastids applied to the two walls which run parallel to the longitudinal axis of the filaments, at other times they closely surround the nucleus. Most of the remaining inner part of the ground-tissue consists of large roundish cells, with but few chloroplastids. Some of these cells, more particularly nearer the apex of the wart, contain large crystals of calcium oxalate. The ordinary round ground-tissue cells pass into the filamentous palisade-cells very abruptly.

A number of parenchymatous cells are enclosed in the cup-like ending of the vascular tissue. They are almost colourless, clear cells, and also frequently contain large quantities of calcium oxalate.

Of very great interest is the ending in the tubercle of the vascular system. This is a very highly developed structure, and it alone would show that *M. elongata* represents a very high degree of adaptation to external conditions.

The bundle-system of the tubercles is of course connected with that of the main stem. The arrangement met with is that described by Ganong for those *Mamillariae* which have no furrows on the upper side of the tubercles (10, p. 35, Fig. 14). From Ganong's observations and from my own it appears that one strand of vascular tissue leaves a bundle of the main stem for every tubercle (Pl. XXV, Fig. 3). This bundle is about 120-150 μ thick and it originates in the inner end of one of the stem-bundles. It consists in fact of part of the protoxylem and part of the metaxylem and the phloem. On leaving its parent bundle it passes between the two bundles to the cortex, rising slowly in a direction towards the tubercle. From this one lateral bundle are derived the bundles of the cortex of the main body of the plant, the bundles of the tubercle and those of the lateral bud, which is found in the axil of each tubercle. According to Ganong the bundles of the assimilating tubercle consist of a leaf and a cushion system of bundles fused. It is quite immaterial here what their morphological

nature is. It is important, however, to notice that the one branch from the main bundle divides, but that its branches in the tubercle and also in the cortex anastomose freely, and in the tubercle itself finally end in a large cup-like mass of big tracheids (Pl. XXV, Fig. 15).

On leaving the main bundle the lateral branch leading to the tubercle-system consists of extremely minute spiral tracheids. They are 12 to 16 μ in diameter. In the protoxylem the spiral bands are about 2 μ thick and as much as 8 μ apart. In the younger metaxylem the figures would be 2.5 and 3-4 μ respectively. I was unable to make out the length of the tracheids at this point in the bundles. But they are evidently fairly long, at any rate in proportion to their diameter. In this they differ very much from the spiral tracheids of the metaxylem of the main bundle. They are in fact more of the type of spiral vessel or tracheid met with in most protoxylems of the normal Angiosperm. Here and there we do, however, get one of the tracheids in the cortical bundles suddenly passing into a large spiral tracheid, measuring as much as 80 by 36 μ , which is of the typical cactaceous form. It will be found to be in contact with some two or three large parenchymatous cells of the cortex.

The bundles branch fairly frequently and anastomose again freely. A certain number of branches pass towards the growing-point, which is situated in the axil of the tubercle, but a greater number of bundles bend out and grow towards the outer end of the latter. Of these a certain number pass towards the rows of palisade-cells of the wart, and here they end blindly (Pl. XXV, Fig. 15).

All the bundles are accompanied by bast, the position of which, however, changes in such a way that finally it always lies outside the wood. The bundles passing to the tubercles therefore contain the following structures: bast, small and narrow tracheids with very close spirals, and larger tracheids with very loose spirals. This is what one might expect, but owing to the short distance between protoxylem and bast the contrast between the two forms of spiral tracheids is very marked (Pl. XXV, Fig. 19). The bast may extend to as great a depth as the wood when entering the tubercle, but later on it becomes very much reduced. The very last endings of the central mass of vascular tissue just underneath the cushion of spines are quite free of bast, being surrounded by parenchymatous cells only.

In a transverse section of a tubercle we would be able to notice, when cut half-way down, about 6-7 bundles which form an outer cortical ring (Pl. XXV, Fig. 10). These bundles end just inside the palisade-tissue. At the first point the cortical bundle would generally be about 70-90 μ deep in a radial direction, and about half that in a tangential direction with regard to the periphery of the whole tubercle (Pl. XXV, Fig. 7). In bulk the wood (*b* and *c*) is slightly in excess of the bast, although the

bast-cells (*a*), being smaller, exceed the wood-cells in number. The components of the wood are tracheids, which in the smaller cases are spiral, but in the larger ones are spiral to reticulate. The tracheids of the cortical bundles do not show any such remarkable development as we shall meet with in the case of the central bundles. But we may here and there get a large tracheid developed centripetally from the inner end of the wood-portion of the bundle (*c*). But these large tracheids, which may be 16μ in diameter, are large only as compared with the smaller ordinary tracheids of this bundle. These vary between 8 and 12μ in their largest diameter.

The last tracheids of a cortical bundle may be as much as 20μ in diameter, the thickening spiral being about 5μ deep (Pl. XXV, Fig. 8). They are unaccompanied by any bast-tissue.

The cortical bundles are closely surrounded by a number of large parenchymatous cells, which possess an internal cytoplasmic lining of $4-5\mu$ thickness in which are embedded the very numerous chloroplastids.

Of great interest is the structure of the central mass of vascular bundles.

If we follow out the course of the more centrally placed or medullary bundles, we see that they are quite separate from the outer ones. The cortical bundles run just inside the cell-rows of the palisade-tissue, the medullary bundles are found further inside. At first they form a disconnected ring in transverse view, although they are actually anastomosing freely (Pl. XXV, Figs. 10, 11, 12 and 15). This refers to the lower end of the tubercle, as soon as the medullary and cortical bundles have become separate. The former appear gradually to move closer together, but as a matter of fact they are merely increasing in circumference at the expense of the surrounding ground-tissues. The diameter of the whole wart decreases, but the diameter of the bundle-ring may even increase slightly as we near the top of the tubercle.

Each medullary bundle consists primarily of a number of spiral tracheids, which are fairly narrow in diameter and have already been described. External to this xylem is the bast, which in the beginning may be in extent nearly equal to the wood-portion (Pl. XXV, Fig. 4). But gradually, as in the cortical bundles, large spiral tracheids are developed centripetally from the xylem of each bundle (Pl. XXV, Figs. 4, 5, *c*). These spiral tracheids soon extend from bundle to bundle, and may even completely surround all the wood of the original bundle (Pl. XXV, Fig. 6, *c*). But by this time the bast has practically disappeared. The completed ring of lignified cells consists finally then of groups of a few small spiral tracheids, which groups correspond in number to the original wood-bundles or branches of the latter (Pl. XXVI, Figs. 6 and 14). There may be as many as twelve such groups. Not unfrequently some of the bundles send branches into that part of the tissue enclosed by the cylinder of bundles

(Pl. XXVI, Figs. 13 and 14). These groups are joined together by the large tracheids.

The larger tracheids, which are formed here centripetally at first and later on all round, are very large indeed and show very well developed spiral or reticulate thickenings, which are usually very close together (Pl. XXV, Fig. 19). The tracheids may be as much as 60μ across in a transverse direction, and 160μ long. One particular tracheid measured 200 by 40μ , another 100 by 20μ . Next to these large cells we find the small, narrow spiral tracheids of the old bundles, measuring 10μ in diameter (Pl. XXV, Fig. 19).

The spiral thickenings of the larger spiral tracheids are very massive. Seen in surface view from the outside they are about 3 to 6μ broad, their actual point of attachment being about $\frac{1}{2}$ or $\frac{1}{3}$ this measurement in each case. They project into the cell-cavity a distance of 3– 6μ . The central point of the attachment of any spiral thickening at any given height is very generally about 10μ distant from the same point on the spiral above or below. The spirals do not in fact move further apart, they remain stationary, but the thickenings increase in size and so they appear to get nearer together. The form of these larger cells appears to be more or less barrel-shaped. The ends are slightly narrower than the middle. The difference, however, is less marked when the tracheids are long and narrow. The last tracheids at the top of the bundle-ending measure fairly regularly about 20– 30μ across and are 100 to 120μ long (Pl. XXV, Fig. 15).

The fusion of the medullary bundles and the formation of the large spiral tracheids results in the production of a cup-like ending to the vascular system just underneath the top of the tubercle. The cup consists of the small groups of smaller tracheids united laterally by the larger ones.

On the outside the tracheids are surrounded by large active parenchymatous cells, about two or three of which intervene between the tracheids and the palisade-cells. The cup is filled with parenchymatous cells likewise, which again are large and active. The tissue inside the cup and immediately outside it appears lighter in section than the palisade-cells because its cells contain very few chloroplastids. No air-spaces are found inside the cup.

The tissues mentioned so far as being found in the tubercles are not the only essential ones. The apex of the whole tubercle is occupied by a cushion of tissue in which are inserted a number of curiously complex spines, the lower ends of which are furthermore surrounded by a mass of hairs. There are on the average about twenty marginal spines in each set. In the centre is found a single spine, larger than the others. The marginal spines are 4 to 4.5 mm., the solitary central one 5 mm. long. The whole set of spines covers an area with a diameter of 7 to 8 mm. The distance from the centre of one set of spines to the centre of the nearest neigh-

bouring set is 4 to 5.5 mm. The various sets of spines therefore overlap considerably (Pl. XXV, Fig. 2).

I will now describe the full-grown spines and the cushion of tissue they are inserted on.

The cushion and its spines are quite definitely separated from the underlying tissue of the tubercle. The latter, although it includes the vascular tissue, may be considered the living and active part of the whole lateral organ; the former may be called the dead or passive portion (Pl. XXV, Fig. 15). These two parts are separated by a layer of cambium, which is continually adding to the cells of the outer dead tissues. It is not at all unlikely that a few cells of the living tissue of the tubercle are also derived from this cambial layer. The last few small cells of this tissue at least seem to run in regular rows, which end in one of the cambial cells (Pl. XXV, Fig. 15).

The cambial layer runs right across the whole tubercle, but it does not appear as a straight line in section. It is practically continuous with the epidermis of the tubercle, and it joins the latter just inside the small rim, with which the tissue of the tubercle surrounds the set of spines.

The cushion in which the lower ends of the spines are inserted is entirely made up of cork-tissue (*k*). The separate cells are arranged in the typical way, namely regular rows, the walls being often much contorted owing to unequal pressure. The cork-cells of the cushion at first show a clear cell-cavity, but as they get further away from the phellogen they become so much twisted about that it is almost impossible to recognize any cavity or even the thickness of the cell-wall. The whole cushion may reach a thickness of about 600–700 μ , being at the most about 800 μ broad. It is entirely cut off from the living cells of the tubercle, even portions of the epidermis giving rise to cork-cells (Pl. XXV, Fig. 15, *g*, *k*).

On the cushion are inserted the spines and a number of multicellular hairs. Inside the rim formed by the upper end of the tubercle, and growing from the corky tissue of the cushion, we meet with a ring of numerous dried hairs. These hairs may be no more than 4 μ thick, but about 20 to 40 μ broad (*i*). They have collapsed almost entirely in one plane and the transverse walls project like prominent ridges (Pl. XXV, Fig. 20, *i*). They are about 800–900 μ long, but often are much crumpled and twisted. These hairs consist almost entirely of cellulose, except a very thin outer wall of cuticle. This circle of hairs is followed by a ring of spines, then follows another circle of hairs, and finally a solitary central spine.

The spines are all of practically the same structure, but the solitary central one is larger than the others. It will, therefore, be sufficient to describe either one or the other (Pl. XXV, Figs. 15, 16).

In each spine three different tissues can be well distinguished, at least at the lower or basal end. At this point the core of the spine, whether it

be a central or a marginal one, is seen to consist of a conical mass of thick-walled fibres which are always filled with air (Pl. XXV, Fig. 15, 16, 17, *h*). The broad end of the cone somewhat abruptly passes into the corky layers of the cushion. It may become slightly narrower at its lower end. In a long central spine the mass of air-filled fibres would be about 700 to 800 μ long from the base to the top, and about 250 μ broad, the breadth of the spine being about 400 μ . For a shorter marginal spine the measurements would be about 700 μ , 160 μ , and 250 μ respectively. The separate fibres are not in the least crushed, but they have rather angular walls, not rounded off at the corners (Pl. XXVI, Fig. 28). Their length varies very much, but does not exceed 200 μ . They have tapering ends. In diameter they measure as much as 25 μ , and of this only about 2 μ all round must be taken as thickened wall. But, of course, smaller cavities are met with as the fibres taper off. The fibres form a compact mass at the lower end of the spine, but higher up they separate, and in transverse section appear to be quite separate (Pl. XXVI, Fig. 30, *h*), though they are not actually separated in a longitudinal direction. The last tapering ends may be no more than 3–4 μ in diameter, their walls, to a large extent at least, consisting of cellulose. In a spine which has not been sectioned, but which has been mounted whole, the conical mass of fibres with their cavities filled with air looks very striking. It is impossible to remove the air except by exposing the cavity of each single fibre, so firmly is it held.

These central fibres lie embedded in a mass of cortical fibres, which differ very much from the central ones (Pl. XXVI, Figs. 28 and 29, *t*). They appear round in transverse section, but it is almost impossible to make out their length, so closely do they fit together and so much reduced are their cavities. But they appear to have long tapering ends, and one I measured was 200 μ long. This was one of the inner ones closely surrounding the central mass of air-containing fibres. The inner cortical ones appear fairly round in transverse section, whereas the outer ones are rather flattened and also have more contents than the inner ones. The outer rather irregular fibres preponderate in the lower part of the spine, but higher up they are almost entirely replaced by the regular round ones, which low down are at first only found sparingly. But they gradually make their appearance between the central fibres, and finally they make up the bulk of the tissue of the spine. The outer and lower ones are compressed in a radial direction. They are about 12–15 μ in diameter, half of which may be wall-substance which seems to show no trace of any cellulose. The fibres higher up are generally isodiametrical and measure at the most about 20–25 μ , with a minute cell-cavity of generally about 1 μ diameter (Pl. XXVI, Fig. 29). These fibres are more rounded off than the lower central air-containing fibres. The thick walls show very clearly concentric striation.

It now remains to briefly describe the outer layer, which covers the whole spine and is a single plate of cells continuous with the epidermis of the tubercle. The cells are squarish and elongated in a direction parallel to the longitudinal axis of the spine. They are usually about 100μ long and in external view about 25μ broad. Their radial walls are $3-4\mu$ thick, but are not quite even.

At the lower end of the spine these cells are rather flattened radially, being then about 7μ deep, of which $3-4\mu$ form the outer wall, and 2μ the cell-cavity, which is filled with a brownish substance (Pl. XXVI, Fig. 28, *e*). Higher up they appear quite uncrushed, being sometimes as much as 15μ deep, 6μ of which fall to the outer wall, and a similar number to the cavity. The inner wall is very thin (Pl. XXVI, Fig. 29, *e*). The outer wall of these cells has peculiar projections into the cavity, which give the wall a transversely striated appearance in surface view. In the upper half of the spine, and even lower down, the epidermal cells are remarkable on account of a peculiar knob, which grows out from the upper end of each cell, and is an outgrowth of the wall only (Pl. XXV, Fig. 16). These knobs project as much as 25μ , and in diameter measure about 12μ . The thick walls of the epidermal cells consist almost entirely of cellulose, a fine cuticle only covering them on the outside.

Caspari briefly describes the structure of the spines in the Cactaceae generally. He finds, however, that the central portion of the spine consists of thick-walled sclerenchymatous cells, the outer portion of thin-walled cells (6, pp. 6, 7). This does certainly not agree with the observations on *Mamillaria elongata* just referred to above.

It has already been mentioned that the corky tissues of the cushion pass rather abruptly into the hard fibrous cells of the spines. The central spine ends square and is not very firmly secured in the tissue of the cushion. It therefore is very easily broken off. This we very frequently find to be the case. The marginal spines are much more rigidly connected with the underlying tissues. On their lower or inner side—nearest the living tissues of the wart—the central hard fibrous cells of the spine are continued some distance into the cushion. They are smaller here than higher up and are very much crushed and contorted (Pl. XXV, Fig. 20). They are here in very close contact with the corky cells of the cushion, which at this point, also very much contorted, dip down slightly. This internal projection from the spines into the cork-cushion is found just above, but outside the margin of the vascular cup (Pl. XXV, Fig. 15).

For the sake of completeness I must mention here that I have occasionally found fungal hyphae between the hairs on the cushion and also on the spines. These hyphae even penetrate into the spines, and some sections reveal the fact that the central air-filled fibres contain numerous fungal hyphae. I have not attempted to make pure cultures of these

Fungi, as I think they are in no way connected with the life of the plant. The parts which they infest are cut off completely from all cytoplasmic connexion with the living part of the plant. An investigation of their life-history would be of no interest except for mycologists. I therefore leave it to the latter to investigate the Fungus in question.

3. Homology of the Tubercle.

I have not considered it necessary or even important to investigate very fully the development of the different members and organs of our plant. But as I was not able to fully agree with some results obtained by other authors I did follow up the formation of the new organs at the growing-point of the shoot more in detail.

The actual growing-point of *Mamillaria elongata* can best be examined by cutting a series of microtome sections in directions parallel and transverse to the longitudinal axis of the plant. The vegetative point of the main axis, however, is often very difficult to cut except with the hand-razor, owing to the hardness of the spines and the impossibility of removing the air from the lower ends of the older and larger spines. But the small lateral detachable shoots can be embedded in paraffin *in toto*, and they give fairly satisfactory serial sections. Their spines are not yet very hard, and by prolonged lying in absolute alcohol the air can be almost entirely removed, but the older parenchymatous tissues shrink to a great extent. The cells near the apex, being full of protoplasm, seem to remain fairly well preserved.

The actual organic apex of the shoot is seen to be a very flat cone (Pl. XXV, Fig. 18; Pl. XXVI, Figs. 39 and 40). It is covered by a very distinct epidermis of fairly large cells. Further inside we get undifferentiated periblem, which is succeeded by a clear indication of the differentiation of the vascular strands of the plerome cylinder. A large-celled pith is soon marked off.

Laterally on the apical cone of the main apex smaller conical protuberances are being formed at very close intervals (*w*). They first appear as small outgrowths in the formation of which both dermatogen and periblem take an active part. We will follow out their development without discussing at present their homologies. Each of these new growing-points in its turn grows out, and at first slightly overgrows one of the next young growing-points. At this stage the most actively growing part of the outgrowth is on that side of the hump furthest from the central growing-point (Pl. XXVI, Fig. 40). The whole hump, which is simply a young tubercle, gradually becomes more differentiated (Pl. XXVI, Figs. 40-43). The body of the tubercle consists of fairly large cells which do not look as if they were very actively growing (Pl. XXVI, Fig. 45, *w*). The meristematically most active portion is the future cushion and its

spines. This part has gradually been carried up away from the growing-point (Pl. XXVI, Figs. 39-42, *v*). The active cushion is marked off by a rim which runs right round the upper end of the tubercle (Pl. XXVI, Fig. 43). Finally, the meristematic cushion-tissue is carried up to a position transverse to the longitudinal axis of the plant, through the inner side of the tubercle growing more rapidly than the outer one. The embryonic tissues of the cushion gradually show a number of well-developed conical projections, which represent the future spines (Pl. XXVI, Figs. 41-43, *v*). They are made up of dermatogen and periblem layers at first (Pl. XXVI, Fig. 45, *v*). In the centre of the tissue of the tubercle procambium-elements are visible, which branch and obviously lead to the embryonic spines (Pl. XXVI, Fig. 45, *v*). One of the small conical outgrowths of the tubercles may here be described more in detail. It is covered by an epidermis, which is continuous with the epidermis of the neighbouring embryonic spines and the epidermis of the whole tubercle (Pl. XXVI, Fig. 45, *e*). The tissue inside the young spine may be seen to be connected with the procambial strands forming lower down in the tubercle. From the epidermis which covers the tissues of the cushion lying between the spines, arise hairs, which form an important part of the spine-cushion in some of the later stages of its development (Pl. XXVI, Fig. 45, *i*). At this stage the outer cells of the sides of the cylindrical body of the tubercle are beginning to show the regular arrangement into palisade-rows. The depression immediately outside the spines now gradually becomes more accentuated by a ring-like outgrowth, which grows up all round the cushion and finally surrounds the spines so that the spines come to stand in a cuplike depression (Pl. XXVI, Fig. 43).

The spaces between the spines and between the younger tubercles in different stages of development are filled with hairs developed from the cushion of spines (Pl. XXVI, Fig. 39). Gradually the spines elongate, but they still at first stand erect on the tubercle and appear quite colourless. Later on they assume a reddish colour.

The procambium in the wart gradually becomes vascular tissue, but the lower cells of the spines, although they may for some time be connected with the procambial tissue, do not become vascular (Pl. XXVI, Fig. 44, *h*). Later on, the tissues at the lower end of the spine give rise to the hard, air-containing fibres. The epidermis of the spine is never thrown off, and the mature spine therefore remains covered with its original epidermis. The hairs found so plentifully between the mature spines also are epidermal structures.

The spines develop in such a way that in the earlier stages the larger ones are on that part of the cushion which is nearest the organic centre of the main axis. They may thus at one end be 0.4 mm. long and at the other end 1.2 mm. At a later stage they may be 1.5 mm. at one, and

3.5 mm. at the other. At this stage they would be red in colour for about $\frac{1}{2}$ or $\frac{2}{3}$ the way from their upper end downwards. The central spine may now be distinguished by being slightly broader and redder in colour than the others. A few small protuberances from the epidermis of the spines are to be noticed now. But these develop more later on. The spines are subsequently, through the activity of the cork cambium, unfolded in the typical spreading fashion. This change in position is accompanied by the appearance of air in the lower hard fibrous cells of the spines (Pl. XXV, Fig. 18).

The points of the spines still remain reddish brown for a time, but later this colour also disappears. The small outgrowths from the epidermis of the spines are found almost exclusively on the inner and middle portion of the marginal spines, but all round on the large central one. The whole set of spines remains permanently in a slight depression; at any rate the circular mound of tubercle tissue keeps pace with the growth of the whole spine-cushion (Pl. XXV, Fig. 15).

What then is to be said about the morphological nature of the tubercle and the spines?

The first small conical projections near the growing apex arise just in the way leaves would arise. To my mind there is no doubt that they represent leaves, that is leaf-primordia ('Blattanlagen'). The leaf-primordium grows, and at the top of it there appear a number of small protuberances, new actively growing portions (Pl. XXVI, Figs. 40, 41, 42 v). What do they represent? I have no doubt that the body of the primordium at this stage represents the leaf-base and the small protuberances represent the leaf-blade. The leaf-blade does not develop except to form the spines, and the leaf-stalk does not develop at all. The leaf-base develops most, but in the mature plant the tubercle may possibly represent in addition to the leaf-base, but to a limited extent, certain portions of the shoot which have become fused with it.

The leaf-nature of the tubercle-primordium becomes clearer still, when we notice how in its axil, a short distance behind the growing-point of the shoot, a small lateral bud is formed (Pl. XXVI, Fig. 46, y). This lateral bud, however, is formed more on the lowest portion of the base of the leaf-primordium than on the main shoot itself.

In *Mamillaria elongata*, at any rate, I can therefore see in the mature tubercle only the highly developed leaf-base. The spines together represent the leaf-blade, the leaf-stalk being absent. This view does not agree with that expressed by most other authors who have examined the morphology of the tubercle of the Cactaceae. Ganong briefly summarizes these views (10, p. 45). Kauffmann considers the spines to be leaves, Vöchting and Delbrouck look on them as emergences, in which point they agree with Schumann. Goebel makes out the whole tubercle at first

to be a leaf, and in its axil a lateral bud arises. Leaf and lateral bud grow up together and develop so as to form the cushion of tissue which gives rise to the spines or metamorphosed leaves. In the axil of a mature leaf-tubercle a lateral bud may be found. This, according to Goebel, is merely the result of a division into two of the original lateral growing-point which grew up with the leaf-base (12, pp. 77-84).

Quite recently Rudolph has published some observations on the spines of *Opuntia Missouriensis* (23, p. 103-109). He considers that in this species at any rate the spines are trichomes which have arisen in the axil of the leaf. He does not, however, wish to express any opinion concerning the other Cactaceae which he has not examined.

It will be seen therefore that I do not quite agree with any views held by those who have examined the growing-points of Cactaceae. Referring to a figure by Goebel (12, p. 81, Fig. 41) which corresponds roughly to my Figs. 39 and 40 (Pl. XXVI), I can only say that what Goebel calls the growing-point of the axillary shoot is to my mind merely the embryonic apical part of the leaf-primordium. The axillary bud is formed much later, and at least in *Mamillaria elongata* has never been connected with the embryonic tissue which later on gives rise to the spines and which is supposed by Goebel to represent the axillary bud.

The tubercle as a whole, in *Mamillaria elongata* at least, represents mainly the leaf-base, although its lower end may be partly derived from the stem-portion of the shoot. The spines represent the modified leaf-blade.

Wetterwald's observations on the Euphorbieae and Cactaeae were interpreted by him in such a way as to confirm Goebel's results. In my opinion his figures of *Mamillaria coronaria* (Pl. XX, Figs. 33, 34) seem to agree quite well with my interpretation.

Caspari was unable to detect any vascular tissue in the spines, and therefore considers the spines to be anything but reduced leaves (6, p. 6). But an examination of the young spine-primordia does show that there is at first a rough indication of a continuity of the plerome of the tubercle with the inner tissue of the future spine, at least in *Mamillaria elongata* (Pl. XXVI, Figs. 44, 45). Ganong also figures a spine of *Opuntia coccinellifera* with a delicate spiral vessel at its lower end (10, p. 9, Fig. 3).

4. Physiology.

(a) *Introductory Remarks.*

As already mentioned in the introduction to this paper very little is known concerning the meteorological and other conditions under which the Cactaceae as a whole live.

Our plant *Mamillaria elongata* is mentioned by Schumann (26, p. 520) as occurring very extensively in the state of Hidalgo in Mexico. It has

been recorded from Limapan, and las Ajuntas on the river Moctezuma, near Ixmiquilpan, Mezquitlan, between Zucualtepan and the river Toliman and the Rio Grande. It is supposed to occur also in Chihuahua, but from this latter locality Schumann has not seen any authentic specimens. Hidalgo is a state or province of Mexico right in the centre of the high plateau on the top of the Mexican mountain range.

Schimper gives the following as the conditions obtaining in the Mexican plateau (24, p. 675). The climate generally is dry, though moister than that of the North American deserts. The annual rainfall appears never to be less than 50 cm., which is considerably above that of the typical desert climate. Even with a high temperature prevailing one would not expect to find a very poor vegetation except on soil very permeable to water.

Karsten gives us a very useful glimpse of the conditions prevailing in these localities (24, p. 678). In the summer the days are warm and sunny, little rain falls, and the nights are relatively very cold. In winter snow falls, but it very soon melts away.

It is difficult indeed from the data which are given in the literature of the subject to really get an accurate idea of the Mexican climate. It seems to be very hot during the day and cold during the night, in the summer. The rainfall, though low, is not a desert rainfall. But, as Schimper remarks, the height of the Mexican deserts makes them subject to many of the desiccating influences of an alpine climate. Edaphic influences, as yet not at all properly understood or even known, also probably are at work in determining the nature of the plant-forms. Volken's observations on the Arabian-Egyptian desert are very important, great stress being laid by him on the strength and clearness of the light (33, p. 15).

Walther briefly, but I think very well, summarizes the five conditions which in the desert are chiefly responsible for the poor development of the vegetation. They are the following (35, p. 79): (1) The scarcity of rain and dew; (2) the strength of the sun's rays; (3) the violence of the dry winds; (4) the looseness of the particles of soil; (5) the salinity of the soil.

Armed with these very few data I wish now to offer an explanation as far as possible of the structures met with in *Mamillaria elongata*. Of these some are not directly connected with the actual climatic conditions, but to make this paper more complete they will also be referred to.

The external and internal structure which a plant exhibits is mainly due to the way in which it has responded to the influence of external conditions. Ontogenetically or phylogenetically the form which a plant represents is an expression of those external conditions which in some way influence adversely or the reverse those functions which are carried out in the plant and which are of vital importance. Some structures met with in a plant may no longer be of use to the plant; they may in fact be merely

of morphological interest, indicating the persistent remains of an obsolete organ or member. The more adverse the conditions are, however, the more likely are we to find in a characteristic plant-form peculiar physiological structures which owe their presence to the adverse conditions directly, the less likely are we to find any useless members.

The conditions of the Mexican desert are very unfavourable, and we get there a very typical and characteristic plant-form, represented by almost the whole of the Cereoideae group of the Cactaceae. I think it very probable that the whole structure of these plants reflects almost in its entirety the influence of the prevailing adverse external conditions of the desert.

Of the vital processes which are being carried out in the plant, two, I think, may be considered as depending most on external conditions. The structure of the plant, as representing any particular plant-form, therefore, will be the more modified from what we can call the normal form, namely, a green land-plant with well-expanded foliage leaves, the more adversely external conditions affect the carrying out of these functions.

The first of these two functions includes all those processes which go to make up, or which take part in what is generally known as, the transpiration-stream: namely, the absorption of water with the raw material from the soil in solution, the carrying of the latter to the green leaves, their deposition in the green cells of the leaves, followed by the giving off of the greater part of the water thus brought up from the cell-surfaces in the intercellular spaces of the mesophyll. The second includes all the processes necessary for the carrying out of photosynthesis.

(b) *Physiology of Mamillaria elongata.*

Mamillaria elongata grows in dry and hot places and one might expect to find a fairly large root. Judging, however, from the plants I have been able to examine, the root is rather short and fat and but little branched (Pl. XXV, Fig. 3). It is impossible, however, for me to say what the root would be like if a plant were allowed to grow under natural conditions.

The root shows one very striking feature in the structure of the xylem. It consists of annular tracheids throughout, disregarding for the present the parenchymatous cells surrounding the wood tracheids. The spiral nature of the thickening in the protoxylem-elements of young plant-members of both root and stem has been thought to be of use in allowing the tracheids or vessels to elongate during the growth of the plant, without rupturing the whole tracheidal thickening (31, p. 469).

If this be the case, the annular tracheids of *Mamillaria* might be considered an adaptation to a possible and very likely shrinkage of the whole plant and especially the root during the dry season, and a subsequent swelling up again and elongation during the moist season. A shrinkage of

the root during the former would tend to fix the plant more firmly in the soil, as the lower tips of the roots would of course be firmly attached to the particles of soil by the root-hairs.

This fixing of the plant to the soil has been described by Michaelis for *Anhalonium fissuratum*, Lem. In this case, the whole plant during the dry season is bodily drawn into the soil (19, p. 22, Pl. III, Fig. 12). This plant appears also to exhibit annular thickening in the wood-portion of the root (19, pp. 17, 18).

It is not surprising that in the case of the root of *Mamillaria* we find not only the metaxylem but also the protoxylem developing annular to the complete exclusion of spiral elements (Pl. XXVI, Fig. 32). The annular tracheids can probably also store water.

As we ascend into the stem we find the annular tracheids of the root-metaxylem giving way to beautifully developed spiral tracheids. These are short and broad, and are not in any way of the type to which the protoxylem-tracheids of stem and root in other normal plants belong. In the large spiral tracheids of the succulent stem of our plant, I see as much water-storing as water-conducting organs. The spiral, again, is a structure which allows of an elongation of the cell to which it belongs, but probably not of a great subsequent contraction. The continuity of the lignified thickening is, as we can see by comparing the wood of the root and shoot, not necessary for the conduction of water. But of course the method by which the water passes along in the root may possibly differ from that by which it passes along in the shoot.

The libriform cells met with at the point of attachment of root to shoot may safely be put down as representing mechanical elements to strengthen the firmness of the plant at the point where it is fixed in the soil. For this reason we find these cells developed in the later-formed wood-portions of the bundle.

The large parenchymatous cells of the cortex of the main plant-body are no doubt cells which store water. I do not think, however, that they will exert a very strong osmotic pull on the wood-elements.

The ground-tissue cells immediately surrounding the bundles are flattened (Pl. XXVI, Fig. 21, s) and would possess a comparatively small vacuole. It is therefore probable that the transpiration stream is drawn osmotically to other parts of the plant where the water and its solutes are primarily more urgently needed, namely to the tubercles.

The large central vascular bundles send off branches, which consist, in their wood, almost entirely of spiral tracheids, narrow and apparently very long.

These spiral elements lead to the tubercles, and here they separate into two systems, namely a cortical and a medullary system—if I may use the terms cortical and medullary in this sense.

The cortical bundles pass along just inside the palisade-cells of the tubercle and then end blindly, before the tip of the latter is reached, without changing very much in structure with the exception of the bast, which is absent from the endings of the cortical bundles (Pl. XXV, Figs. 7, 8, 15).

The medullary bundles at first anastomose freely, and finally form a cup-like mass of wood-elements just beneath the tip of the tubercle (Pl. XXV, Figs. 10 to 15). At this point the bast again is seen to be absent, although it was present in the bundles lower down (Pl. XXV, Figs. 4 to 6). The wood-elements also have undergone a remarkable change. The long, thin spiral tracheids have gradually given way almost entirely to a mass of large, broad and stout cells with spiral and reticulate to annular thickening. The cup-like ending of the medullary bundle-system consists almost entirely of these cells, especially towards its outer margin, where it ends blindly (Pl. XXV, Figs. 15, 19, 20). These cells are surrounded immediately by large and clear cells, which by means of their large vacuole, no doubt, exert a strong osmotic suction on the water contained in the neighbouring tracheidal elements.

Not only are the surrounding parenchymatous cells large and more or less round in form, but the separate wood-cells also offer more than one flat surface to be acted upon by these cells. I have no doubt that the large wood-cells act also as storage-tracheids.

The water, with its solutes of raw food material, is drawn into the surrounding parenchymatous cells. In due time the water in the form of vapour passes out of those cells which are bordered by extensive inter-cellular spaces, into the latter, and finally makes good its escape through the stomata, by which the epidermis of the tubercle is interrupted.

We have thus far followed out the path of the transpiration-stream.

It might be of interest just to recall in a tabular form the measurements of the tracheids in the different parts of the plant, with reference to their varying function.

		Nature of thickening.	Breadth.	Length.
Root	protoxylem	Annular	10-15 μ	
	metaxylem	Annular	10-26 μ	200 μ
Stem	protoxylem	Spiral	10-20 μ	100 μ
	metaxylem	,,	30-40 μ	100 μ
Bundles leading to tubercles		,,	12-16 μ	
Tubercles	Medullary	,,	8-12 μ	
	Endings			
	Cortical	,,	16-20 μ	
	Medullary	,,	20-60 μ	100-200 μ

The narrow tracheids in the root and stem, and those leading into the tubercles, are primarily conducting elements; all the other larger ones, besides conducting, will also store. This view held by Strasburger seems to fit in well here (31, p. 469). The tracheids in the tubercle are also giving off water. Water is being taken from them by the osmotic action of the surrounding cells. The cells surrounding the large tracheids of the stem, however, probably have no such function. Their cavities, as already pointed out, are small (Pl. XXVI, Fig. 21).

From the figures given above, the goal of the upward current of water is always a large tracheidal cell. Strasburger mentions that the current of water is always towards the smaller cavity (31, p. 873), an observation which does not accord with my observations on *Mamillaria elongata* recorded here.

Mamillaria elongata growing in a dry desert region would naturally show a number of xerophil structures. Before however referring to these, it will be necessary to describe the arrangements for carrying out photosynthesis.

We have a very well-developed palisade-tissue on all sides of the tubercle (Pl. XXV, Fig. 15). The cells of this are supplied with raw material from the soil directly by the cortical bundles, and, more indirectly, by the medullary bundles. It may at first sight appear remarkable that the rows of palisade-cells should run at such a definite oblique angle with the epidermal layer of cells. The strongest light that falls on the palisade-tissue very probably impinges on the plant at this same angle. Light coming vertically down from the sun would not reach the tubercles low down on the plant (Pl. XXV, Fig. 3), but would be caught by those higher up, which are nearer the growing-point. But these tubercles are placed at a slightly different angle, with regard to the axis of the plant, than the lower ones. Their palisade-tissue also has its cell-rows at a different and again probably correct angle, in order again to catch the rays end on (Pl. XXV, Fig. 18). The same explanation serves to make clear the meaning of the rows of palisade-cells on the underside of the tubercles. They catch the also very strong light which is reflected from the surface of the soil. Whether this is glistening sand or not I cannot say, but it very likely frequently is in the natural habitat of our plant. This certainly appears to be the case with *Cereus peruvianus* and other Cactaceae as depicted by Karsten and Schenck (16, Pls. XXXIX to XLVIII).

The plastids are generally found on the radial walls of the palisade-cells, except on occasions when they congregate around the nucleus, an occurrence noted and figured already by Schleiden (25, p. 6, Pl. VII, Fig. 3). To the inside of the cortical bundles the large parenchymatous cells are arranged more like the ordinary cortical tissue of the main body of the plant (Pl. XXV, Fig. 15).

The arrangement of the rows of palisade-cells offers a strong confirmation of the view held by Stahl, that the characteristic development of this tissue is influenced by the strength of the light (30, pp. 36-38).

Haberlandt sees in the cell-rows of the palisade-tissue an arrangement for rapidly conducting away the elaborated organic products of photosynthetic activity. Their position and direction is in no way influenced by the light directly (13, p. 250). Eberdt puts down the varying development, but not the presence of palisade-tissue, as an adaptation to give transpiration and photosynthesis equal rights (19, pp. 373, 374). It is in fact a compromise between the two. Personally I should consider the elongation of the cells to be a concession only to photosynthesis, but the reduction in depth of the air-spaces accompanying the palisade-tissue as a concession to transpiration.

Nordhausen has recently published some very interesting observations, which in one particular are, however, not yet quite complete. He shows that the buds of Beech shoots, which have been grown in the shade, give rise to shade-leaves even when grown exposed to the full light (21, pp. 30 to 45). The bud in fact takes on the character of the leaf, in the axil of which it is formed. The chances generally are of course that it will grow up surrounded by the same conditions as that leaf. This is an interesting fact. But, as Nordhausen himself points out, it is desirable that further experiments should be carried out. A bud is developed in the axil of the leaf, which though itself exposed to strong sunlight is derived from the bud of a shade-leaf, and shows shade-leaf characters. Does this last bud produce shade-leaves or sun-leaves at once, or only after one or two years? The removal of the branch with its leaves from shade to light before the leaves in the bud are quite differentiated might lead to interesting results, and show how direct the influence of shadow and light is.

Areschoug (1, pp. 1-18, 38-43) lays greatest stress on the influence which the external conditions exert on the plant in its desire to keep the transpiration-stream under control. The reduction of air-spaces causes a reduction in the rate of transpiration. Therefore the palisade-tissue with its not very extensive air-spaces is an adaptation to reduce transpiration. In the case of *Mamillaria elongata* and those Cactaceae which show similarly equipped tubercles the palisade-tissue is clearly in my opinion a protection against the influence of the strong light on the green plastids, and not against undue transpiration, for if the latter were the case the inner cells would also show a similar arrangement (Pl. XXV, Fig. 14). The air-spaces in the inner tissue of the tubercle are slightly bigger than those in the palisade-tissue, but the cells are also less exposed to strong sunlight.

The extensive air-spaces by which almost every one of the carbon-dioxide absorbing cells is bordered to a smaller or larger extent do not separate the cell-walls very much. They are, that is to say, long but

shallow. I need only refer to the work of Brown and Escombe (5) as showing that the small diameter of the air-spaces is rather favourable to the rapid introduction of the carbon dioxide of the air into the air-spaces of the green tissues than otherwise.

The shallow air-spaces, however, serve a double purpose. The water brought up from the soil is evaporating into them, and the narrow diameter of the air-spaces has the important effect of reducing the rate of transpiration. Plants in dry regions reduce the lateral diameter of their air-spaces, although they cannot reduce their length, without interfering with the photosynthetical functions of the green cells.

This then is the first instance, in our plant, of an adaptation to the dry locality, where the two vital processes, photosynthesis and transpiration, come into conflict. To suit the former they must be retained and must extend to as many cells as possible, to enable the actual absorption of the carbon-dioxide gas, which is always slow, to be carried out. To suit the latter they are reduced as much as possible in depth.

The hypoderma, with its very few chloroplastids, no doubt serves as an additional protection, together with the epidermis, for the chlorophyll of the palisade-cells (Pl. XXV, Fig. 15).

There are not many stomata. These, furthermore, show none of the many well-known xerophil characters (Pl. XXV, Fig. 9). The stomata are on a level with the epidermis. The latter has not developed a very thick cuticle, and the outer cell-wall of the guard-cells is only a little thicker than that of the ordinary epidermal cells.

In what way then does the plant protect itself against the strong and clear light, which forms such a feature of the Mexican desert? Its harmful effect lies in its destructive action on the chlorophyll, and in the fact that strong light increases very rapidly the rate of transpiration.

The whole cylindrical form of the plant is beautifully adapted to exposure to strong light. The sides of the tubercle get very little of the strongest light during the day. Their sides very rarely get the light falling directly at right angles on their surface (Pl. XXV, Figs. 2, 3). This is owing to the surface of the plant being elevated into tubercles. Strong light falls on to the plant generally at some angle, which will probably correspond on the average to the direction in which the rows of palisade-cells run. The light which falls on to the plant and actually reaches the body is therefore undoubtedly partly reflected in such a way as to be fairly evenly distributed over the whole surface. The result is important both from the point of view of the transpiration-stream and from that of photosynthesis.

I have not, however, referred to the most characteristic external feature of our plant, namely the spines, which crown every tubercle.

The rate at which transpiration goes on depends to a great extent on the rate at which the air in the air-spaces is renewed. The flat and narrow

air-spaces do not favour a very rapid movement of the air in the plant. But the air immediately outside the fleshy part of the plant is kept more or less stagnant by the passive action of the spines. The whole set of marginal spines are spread out and the spines of one tubercle overlap those of the next (Pl. XXV, Figs. 2, 3). The spines in fact form a fairly complete screen, separating the air which immediately surrounds the plant from the air outside. The former is to a certain extent stagnating.

I have been unable to make any experiments to show that this is the case with *Mamillaria elongata*, but I have done so with *Echinocactus cylindraceus*, Eng. Placing a plant in the sunlight the temperature inside the spines and outside was measured. The temperature inside at three different times was 23° C., 28° C. and 28.5° C. The temperature outside was 17.75° C., 18.75° C. and 19.75° C. respectively. This proves to me that the air inside was stagnating. It was close, and hotter than outside. The air inside the spaces will therefore not be rapidly renewed. The spines consequently have a very important function to perform: they reduce the rate of transpiration. Further observations were made, at the risk of losing a valuable specimen, in order to determine the temperature right inside the plant body. *Echinocactus cylindraceus* was again used, a thermometer being forced into a hole bored into the body of the plant. When the sunlight was falling directly on to the plant, the temperature inside the plant body was 15° C., in the space between the plant body and the screen of spines 19° C., and that of the air outside 16° C. The three thermometers had been in position 1½ hours, the temperature outside the greenhouse in which the particular specimen of *Echinocactus* was growing being very low at the time.

The air in the air-spaces is therefore evidently lower than that immediately outside the plant body, and we will clearly not get a rapid current of air outwards. The low temperature is clearly of use in reducing the rate of transpiration.

Peirce makes the statement that the rate and volume of transpiration is reduced, in plants like the Cactaceae, by the body temperature of the plant being lower than that of the air when the air could otherwise take up most moisture (22, pp. 137, 138). He refers for support of this view to Goebel, Schimper and Volkens. In the books of the two first authors mentioned I find reference made to a paper by Askenasy (12, p. 34, and 24, p. 49). Askenasy gives a higher temperature for the inside of the plant than for the outside. This author enumerates a large number of plants where this is the case (2, p. 441). Volkens records an observation on the body temperature of *Mesembryanthemum Forskalii*. During the hottest part of the day the temperature of the leaf is 5 to 8° C. above that of the air (33, p. 40). It is a question about which a large number of readings need to be taken—for the Cactaceae at least—in the desert.

Being not very closely set, the spines do not interfere with the light which the plant needs to be supplied with for the photosynthetical functions. But they will probably act as a useful sunshade also in this direction.

The whole set of spines again serves as a protection for the main ending of the medullary bundles in the tubercle. These with their storage-water are protected from the strong light by the broad lower ends of the spines, glistening with the imprisoned air. A mass of white glistening hairs between the bases of the spines helps in the same way. No water can escape by evaporation at this end, because a broad plate of corky tissue underlies the set of spines, and almost overlies the mass of storage tracheids. How effectually the spines do keep off the light may be seen from the light colour of the cells which lie inside the storage-tracheids. They contain hardly any chlorophyll.

The single central spine acts in the same way as the other spines, but is most effective when the sun shines directly on to the tip of the tubercle.

It may be mentioned here that the apical and more delicate portion of the whole plant is extremely well protected against the strong light by the spines and hairs arising from the young developing tubercles (Pl. XXV, Fig. 18). These are at first very closely set, and completely obscure the growing apex. The function which the whole set of spines performs for the benefit of the plant is, therefore, to sum up, that of a screen or sunshade.

I consider this function so important that I have thought it worth while calling such an organ as the whole set of spines represents a *paraheliode*.

Attention was already called in 1876 by Wiesner to the possibility of hairs being of use to the plant in acting as a protective screen between the strong sunlight and the chlorophyll of young developing and therefore rather delicate organs of the plant. Wiesner instances the case of *Tussilago Farfara*. The coat of white hairs on the upper surface remains on the leaf as long as the green colour has not fully developed. It is then thrown off. If removed prematurely the formation of the chlorophyll seems to be impeded (39, pp. 24, 42).

Warming also refers to this function of hairs, as damping the effect of the sun's rays (36, p. 18).

I do not intend in this paper to refer to the question of the function or meaning of the deposits of calcium oxalate, nor to the well-known strong acidity of the cactaceous cell-sap (vide 3 and 34, &c.).

(c) *Comparison with other plants.*

As already mentioned, the similarity in appearance of certain species of *Mamillaria* and certain species of *Mesembryanthemum* is very striking.

I have been able to examine the structure only of *Mesembryanthemum stellatum*, but there are quite a number of species which have the same external appearance.

The conditions under which *M. stellatum* lives are probably very much the same as those under which our *Mamillaria elongata* flourishes. An examination of its structure is therefore of particular interest.

Mesembryanthemum stellatum has fleshy leaves, which are roughly triangular in transverse section, but more or less cylindrical in longitudinal view.

The leaves are here the chief assimilating organs, and in their function and structure they correspond exactly to the tubercles described for *Mamillaria elongata*.

We can follow up the vascular bundles coming from the stem and see them branching and anastomosing freely in the leaf. They become closer and closer towards the tip of the leaf, where they end blindly, in a number of fairly large tracheids. Just underneath the apex of the leaf we get the largest mass of tracheidal tissue, the component cells of the latter being large reticulate storage-tracheids.

The assimilating tissue forming the outer layers of the leaf-organ consists of cells arranged in regular rows, and represents roughly the same type of palisade-tissue as that met with in *Mamillaria*. It makes roughly the same angle with the epidermis as we found in *Mamillaria elongata*.

The assimilating tissue of the leaf is traversed extensively by long but shallow air-spaces, which communicate with the outside air through the stomata.

The leaves of *M. stellatum* are protected against the effects of the strong sunlight, to which the plant is exposed in its native localities, by two means. The whole leaf is covered by large cells, which grow out from the epidermis and expand so as to screen the epidermis and the underlying tissue very effectively from too strong light.

These large cells possess a very thin lining of cytoplasm and a very large vacuole. The cell-wall is very thick and hard, and it seems to glisten in the sun, a sign that light is being reflected. In this way transpiration is reduced.

Volkens refers to the large epidermal cells of *Mesembryanthemum crystallinum* as water-storers (33, p. 123, Pl. XIII, Figs. 4, 5). I would not however like to call them water-storing cells, although they may possibly retain water for a long time. Generally we find water stored inside the plant and away from its chief enemy the sun. Rather should

we primarily look at these large cells as an arrangement for the reduction of transpiration. Before however any opinion could be expressed on this question, it would be necessary to determine more carefully the histology of these epidermal cells, and the exact nature, chemical composition and degrees of concentration of their contents. It might then be possible to explain their relation to transpiration more fully. As it is now, I consider that they represent paraheliode structures. The rate of transpiration is reduced by the large epidermal cells keeping down the circulation of air around the stomata, a fact which was proved experimentally by Hagen some thirty years ago (14, p. 24). The stomata are placed in between these peculiar cells and do not lie exposed to the air directly.

Each leaf is crowned by a set of hairs. Each hair is derived from a single epidermal cell. But despite its unicellular nature, it very much resembles in structure one of the multicellular spines of *Mamillaria elongata*. It has a pointed upper end, but its lower end is much swollen and contains a glistening mass of air. The swollen part is also coloured brick-red, and will absorb rays from the sun. These hairs are very soft and almost papery in texture, but I have no doubt that here, as in *Mamillaria elongata*, they form a useful sunscreen or paraheliode for the protection of the underlying leaf-structures, the endings of the vascular tissue being found most abundantly here.

Mesembryanthemum stellatum forms, I think, a very strong parallel case in support of my views on the function of the spines, as, though being a member of a natural order quite different to the Cactaceae, it has nevertheless developed the same plant-form as these.

A very great number of Cactaceae belong to the same plant-form as *Mamillaria elongata*. Schumann has pictured many of these in his *Iconographia Cactacearum*. His representation of *Echinocereus subinermis*, Salm-Dyck (27, Vol. I, Pl. III), is very interesting on account of the fact that the young flower-shoots are well protected by spiny paraheliodes, but in the older portions these almost disappear (26, p. 250). The tubercles, with the apical set of spines, gradually pass into the outer leaves of the flower. These leaves are foliaceous in form, and they also at first bear an apical set of spines. This confirms my view on the homology of the spines in *Mamillaria elongata*.

Paraheliode structures of the nature and kind described for *Mamillaria elongata* are not, however, met with in all Cactaceae. It would be very interesting and most instructive to examine a large number of species of this natural order, and determine the relation existing between the external conditions on the one hand and the development of the paraheliodes on the other. It would be of great interest to determine whether, when the paraheliode spines are smaller and evidently less efficient as

sunshades, some other structure in the plant takes on the paraheliode function.

I have been able to examine only a few species from this last point of view. The results obtained are not satisfactory, as long as it is impossible to take into very careful consideration the details of the natural conditions which surround the plants in their native habitat.

I am therefore simply quoting a few of the plants examined, in order to show on what lines such an inquiry could, I think, be carried out with advantage.

	Paraheliode effect of spines.	Depth at which chlorophyll begins.	Total wall- thickness in this depth.	Cuticle.
<i>Leuchtenbergia principis</i>	Very small	208.5 μ	75 μ	3.5 μ
<i>Echinocactus cylindraceus</i>	Very strong	185.5 μ	127 μ	17.5 μ
<i>Anhalonium Williamsonii</i>	Absent	141.2 μ	—	7 μ
<i>Echinopsis Mülleri</i>	Strong	122.5 μ	31.5 μ	2 μ
<i>Echinocactus cornigerus</i>	Weak	105 μ	70 μ	3.5 μ
„ <i>gibbosus</i>	Weak	101 μ	16 μ	2.5 μ
<i>Cereus Baumannii</i>	Weak	76.5 μ	10.5 μ	2 μ
<i>Mamillaria Bocasana</i>	Very strong	24.5 μ	2.5 μ	1.5 μ
„ <i>pusilla</i>	Very strong	21.5 μ	3.5 μ	1.5 μ
„ <i>elongata</i>	Very strong	19 μ	7.0 μ	1.5 μ

From this table, which refers only to very few species, we can see the degree to which the depth varies at which the chlorophyll begins. The cuticle is generally found to be thin. I have not been able to detect the relation which may exist between the spines and the layers overlying the chlorophyll. It is, I think, more likely that the paraheliode effect of the spines should be added to that due to the white protective layers of epidermis and hypoderma, and these two features together should be brought into relation with the surrounding conditions.

Michaelis refers to the thick cuticle of *Echinocactus* and the thin cuticle of *Mamillaria*, but he mentions the hypoderma of the latter as consisting of tall, slightly thickened cells (19, p. 26). In the few plants of this genus which I have examined they appear flat (Pl. XXV, Fig. 15).

The Cactaceae and the species of *Mesembryanthemum* are, of course, not the only plants which have paraheliode structures. Very few green land-plants are entirely devoid of such. A beautiful example of a plant living in dark caves, and therefore not provided with any paraheliode structure but rather with a light-collecting arrangement, is met with in the case of the protonema of *Schistostega osmundacea*. This plant is figured and described by Noll (20 and 24, p. 70).

The epidermis which covers the upper and under surface of most leaves of our zone can, I think, be taken as having a paraheliode function.

This function is accentuated by the presence of a colourless hypoderma in a plant like *Ilex aquifolium*. Paraheliode structures may have two or one of two functions. They may damp the strong light in order to protect the chlorophyll, or they may do so for the purpose of keeping down the rate of transpiration. In the latter case only would they be xerophil structures.

Examples of paraheliode structures could be added to in large numbers. I would like, however, without citing too many examples, only just to quote a few, in order to make it clear in which way the word paraheliode should be used, if it is adopted.

A paraheliode is an organ for damping the effect of the strong sunlight. It thus acts like a parasol or sunshade. A layer of cells, like the hypoderma, can well be called a paraheliode. The whole set of spines crowning the tubercles in *Mamillaria* form a paraheliode. I can well imagine that the masses of hard white bast-plates, which we so frequently meet with in many plants of dry and light regions, are really, in part at least, paraheliodes to protect the underlying tissues. But I am in this case merely making a suggestion as to a possible explanation. I am thinking here of some of the leaves, sections of which are figured by Volken in his splendid book on the Egyptian desert-flora (33, Pls. XVI, XVII, XVIII). The green tissues not unfrequently have interposed between them and the direct sunlight thick plates of strong mechanical tissue, which absorb a very large amount of light. This tissue is no doubt of most importance when these plants are in a dry condition. The leaves then roll up, and the green cells would thus be in almost complete darkness. The leaves of *Aristida ciliata* would seem to be of this nature (33, Pl. XVI, Fig. 4). From the description by Volken they appear to be permanently rolled up longitudinally (33, p. 150).

The red colour clearly offers in many cases a protection to the underlying chlorophyll or protoplasm against the undue strength of the sunlight (36, p. 18).

C. CONCLUDING REMARKS.

Before putting together in an abbreviated form the results of this investigation, I would like to make some general concluding remarks.

I have not so far referred to the function which is very generally assigned to many of the spines, thorns, and prickles of many plants.

Large and strong prickly structures are generally credited with being defensive organs for keeping off animals, which might otherwise graze on the plants concerned, and thus destroy or at least injure them.

With regard to the spines of the Cactaceae this is the view held by Goebel (12, p. 35), and, I think I may say, by botanists generally. Ganong

(11, p. 129), Kuntze (17, p. 30), and many others agree with Goebel in this particular.

The evidence in support of this view is not, I think, of a very satisfactory kind. We have no general direct evidence that these spines do even really keep off animals, which otherwise to a large extent might feed upon the plants in question with fatal results for the plant. Experiments will have to be made on an extensive scale on the Cactaceae in their native haunts before the question can be taken as settled.

Let us for a moment turn to the Hawthorn, *Crataegus*, which develops thorns. Delbrouck, in 1873, suggested that this plant through its thorns offered protection to certain birds which feed, or the young of which feed, on insects frequently found on buds and young twigs, thus proving injurious to these. This he finds to be the case with *Silvia curruca* and *cinerea*, which he calls 'Dornvögel.' The plant has developed thorns, which protect the birds and their nests against beasts of prey, and the birds by feeding on injurious insects protect the buds of the plant. Grain-feeding birds, or birds which feed on insects on the wing, or feed on grubs and caterpillars, are never 'Dornvögel,' but secure their nests by hiding them in the bushes (7, pp. 38 to 43). Delbrouck therefore imagines that these thorns have been developed, I presume, by natural selection as a protection against the raids of injurious insects. His views may rest on facts correctly observed, but even in that case his explanation is unsatisfactory. I do not think, for one thing, that the advantage and therefore importance of the thorns to the plant will be very great. This theory again does not account for the varying degree of development of the thorns in different localities and on different parts of the same plant.

Henslow is of opinion both from his own observations and those of other naturalists that the 'spinescent features of so many desert plants are simply the immediate results of the effect of the comparative waterless character of the environment' (15 *a*, p. 226).

Wiesner puts down the transformation of shoots into thorns to the light being either too intense or too weak (40, p. 87). This explanation at least rests on a physiological basis, the thorns being the expression of the effect and influence of the light on the growth of the plant-shoot.

Hansen mentions that the Cactaceae appear to him to be plants which are best protected against the drying influence of the wind (15, p. 84). But it does not appear from his remarks whether they owe their immunity from the evil effects of the wind to their internal structure or to the spines. The spines clearly prevent the too rapid renewal of the air inside and immediately around the plant-body, but inside the screen of spines, by the action of the wind.

I would like here to point out why I consider it unlikely on general

grounds, that plants develop in such a way as to offer armed resistance to animals, although they may as a matter of fact carry organs which may actually inflict injury and pain on animals.

Most green land-plants are during the vegetative phase of their development of sedentary habits. They are tied to the spot to which they have once affixed themselves. It is necessary therefore that under these conditions plants should possess the property of adapting themselves to a certain extent to external conditions. I am not referring here so much to ontogenetic as rather to phylogenetic adaptation. The former differs from the latter only in degree.

A race of plants incapable of adapting itself to altered climatic and edaphic conditions must succumb.

Only those external conditions influence the plant which in some way adversely or favourably affect the carrying out of the vital functions of the plant. Of these there are the two already referred to, through which the plant is most powerfully influenced by the external world, namely, transpiration and photosynthesis.

The green plant must carry out these two life-processes itself and under all conditions. It must provide its cytoplasm with organic food, representing matter and energy. It is dependent on its immediate neighbourhood for the supply of both. The main idea which therefore I consider underlies the adaptation of plants is that of building up organic food—that is, of carrying out at all costs the processes of transpiration and photosynthesis. The plant has inherited in an increasing degree this property of adapting itself in such a way as to carry out these functions most effectively. Thus we get the various plant-forms—which in each case represent the balance between the tendency of the plant to develop its organs of transpiration and photosynthesis, and the influence of the external conditions on the carrying out of these functions.

In every plant-form a struggle is going on between transpiration and photosynthesis, until a compromise is arrived at. In a very dry place the function of transpiration, influenced by the adverse external conditions, is withdrawing the plant away from exposure to light and air. Photosynthesis is drawing the organs to the light.

To put it briefly I might say that the main principle which underlies adaptation in plants has a physiological basis. It is on this basis mainly, if not entirely, that many of the remarkable, as yet little understood plant-forms will be explained. Schimper has thus rested his book on the geographical distribution of plants on a physiological basis. It will then be found, I think, that organs, which are considered as offering protection against attacks by animals, and therefore would not of course represent a physiological adaptation, are really very often, if not entirely, structures with a physiological meaning. This would not however prevent, in

individual cases, their being as a matter of fact of use in warding off the attacks of animals.

A green plant collects, elaborates, stores and assimilates its food without moving. How different the higher animals. The animal can collect its food on one spot, store it in another, and digest it in still another. The energy which I am now displaying in writing this paper may have been fixed by plants in New Zealand, being finally transferred by various indirect ways to my body. For their food-supply animals are in fact far more independent of their immediate neighbourhood than plants, and often entirely so.

The guiding principle which underlies the adaptation of the animal form is far more likely to be protection. Animals generally possess weapons of various kinds and degrees to protect what they have got and to protect their offspring, which they are able to do thanks to the intelligence which they possess.

The views put forward here are not mere speculation but are based on numerous observations. They certainly may help to explain many structures which otherwise it might be difficult to interpret.

Stahl has described in a classical paper how snails will not touch plants which contain certain substances. These substances, according to Stahl, have no physiological meaning, but are protective excretions (29, p. 126). I cannot agree with Stahl in this point. These excretions will, no doubt, be found to have some physiological meaning, even if they turn out to be nothing else but useless by-products of metabolism. At the same time I do not wish to imply that they do not as a matter of fact keep off snails.

In a chapter on the methods of defence which plants adopt in order to ward off the attacks of animals, Weismann enumerates a number of plants, which for various reasons are not liked by herbivorous animals and are therefore not touched by them. The question is this: are these structures, which keep off animals, primarily protective organs, or is their function primarily a physiological one? I consider their chief function to be the latter, and the former to be only of secondary importance. Weismann refers specially to the spiny Cactaceae (37, p. 141), pointing out that these plants are protected against drying up by a thick epidermis, the spines being developed solely for the purpose of animal protection. This statement is certainly not correct, many of the Cactaceae having remarkably thin epidermal layers.

I would like to refer here to two publications which I did not see till after the completion of this paper in December, 1903.

MacDougal, D. T.: Some aspects of Desert Vegetation. From 'The Plant World,' 1903, vol. vi, p. 249. The author puts a very significant question on p. 257: 'Are the spines, thorns, prickles and poisons of desert

plants really the results of efforts on the part of the plant for self-protection?'

Coville, F. V., and MacDougal, D. T.: Desert Botanical Laboratory of the Carnegie Institution, Washington, 1903. This first report of the Desert Laboratory is naturally of a preliminary character; but it contains some excellent photographs, a brief account of some valuable observations, and also a useful Bibliography.

The main results obtained during the preparation of this paper may be briefly summed up thus.

(1) The set of spines by which the tubercles of *Mamillaria elongata* are crowned, form a structure which acts as a screen, protecting the underlying tissues of the tubercle from the strong sunlight. Such an organ may be called a paraheliode.

The set of hairs found at the top of the leaf of *Mesembryanthemum stellatum* also form a paraheliode. The large cells of the epidermis of the same plant are also paraheliode structures.

(2) The development of palisade-tissue is governed by the influence of the light on the photosynthetical processes, the depth, but not the extension of the air-spaces, is dependent on the conditions favourable or otherwise to transpiration.

(3) The tubercle of *Mamillaria elongata* represents morphologically the leaf-basis, and possibly in addition a portion of the stem. The spines are modified portions of the leaf-blade. There is only one bud in connexion with each tubercle or leaf, and that is axillary to the leaf, i. e. the tubercle.

(4) The guiding principle which underlies the adaptation of plants, and the production of plant-forms, is physiological. There is no evidence to show that direct protection against attacks by animals influences the development of any plant-form.

The foregoing remarks on *Mamillaria elongata* may, as regards the physiological results, be made to include, though in a form varying with specific peculiarities, most of the other members of the natural order Cactaceae, the structure of which is remarkably uniform.

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DESCRIPTION OF PLATES XXV AND XXVI.

Illustrating Dr. Darbishire's paper on *Mamillaria*.

<i>a</i> = phloem.	<i>i</i> = hairs.	<i>r</i> = cambium.
<i>b</i> = spiral tracheid.	<i>k</i> = cork.	<i>s</i> = cortex.
<i>c</i> = storage tracheid.	<i>l</i> = protoxylem.	<i>t</i> = thick-walled fibres.
<i>d</i> = hypoderma.	<i>m</i> = metaxylem.	<i>u</i> = medullary ray.
<i>e</i> = epidermis.	<i>n</i> = wood-parenchyma.	<i>v</i> = spine-primordium.
<i>f</i> = palisade-tissue.	<i>o</i> = protophloem.	<i>w</i> = tubercle-primordium.
<i>g</i> = phellogen.	<i>p</i> = cambiform cells.	<i>x</i> = axillary bud.
<i>h</i> = air-containing fibres.	<i>q</i> = libriform cells.	<i>y</i> = cuticle.
		<i>z</i> = intercellular space.

PLATE XXV.

Fig. 1. Photograph of clump of *Mamillaria elongata*, taken in the succulent House, Royal Botanic Gardens, Kew. Slightly reduced.

Fig. 2. Transverse section across main axis of young plant. The vascular bundles are seen to be cut across in the centre. Near the margin are the projecting tubercles and the paraheliode consisting of spines. $\times 3$.

Fig. 3. A complete young plant in longitudinal section. The root and shoot are seen, and in the latter again the tubercles, spines, and vascular bundles. $\times 3$.

Fig. 4. Central bundle of a tubercle, cut across low down in the latter. To the inside of the bast (*a*) is the wood (*b*), to which four storage tracheids (*c*) have been added centripetally; air-spaces (*z*) are also seen. $\times 160$.

Fig. 5. Two central bundles cut across higher up. The bast (*a*) and the smaller wood-cells (*b*) are seen. To the latter numerous storage tracheids (*c*) have been added; air-spaces (*z*) are also seen. $\times 160$.

Fig. 6. Three central bundles just underneath the paraheliode set of spines. The last has disappeared; the spiral tracheids (*b*) of the old wood and the new storage tracheids (*c*) can be distinguished. $\times 160$.

Fig. 7. A cortical bundle cut transversely low down in the tubercle. The bast (*a*), the wood (*b*), and a large storage tracheid at the inner side. $\times 430$.

Fig. 8. The ending of a cortical bundle higher up. The bast has disappeared and two storage tracheids (*c*) alone are visible. $\times 430$.

Fig. 9. A stoma from the epidermis of the tubercle. Cuticle (*y*), epidermis (*e*) with the two guard-cells, hypoderma (*d*), and a few palisade-cells (*f*), with air-spaces (*z*) can be noticed $\times 430$.

Fig. 10. Transverse section of a tubercle low down. The radiating lines mark the rows of palisade-cells. Five small cortical and seven larger central bundles can be distinguished. $\times 5$.

Fig. 11. The same higher up. The inner central bundles are forming a circle. $\times 5$.

Fig. 12. The same higher up. The central bundles have closed in still more. Of the cortical ones only two are left. $\times 5$.

Fig. 13. The same higher up. The cortical bundles have come to an end. The central bundles have closed in still more, but fourteen bast-portions are still shown by dark dots in the bundle-ring. $\times 5$.

Fig. 14. The same higher up. The bast has disappeared; the small crosses mark the old wood-portions, as distinguished from the storage tracheids. $\times 5$.

Fig. 15. A tubercle in longitudinal and vertical section. The following structures can be made out: cuticle (*y*), epidermis (*e*) with stomata, hypoderma (*d*), palisade-cells (*f*), air-spaces (*z*), cortical bundles, central bundles ending in the storage tracheids (*c*), bast (*a*), the cork layer (*g* and *k*) separating off the spines with their core containing air (*h*), the hairs in between (*i*). $\times 30$.

Fig. 16. A marginal spine, with air-containing core (*h*) at the lower end. $\times 30$.

Fig. 17. Transverse section of a large central spine showing the air-containing core (*h*). $\times 30$.

Fig. 18. The growing apex of a young plant. The developing tubercles with spines and hairs are seen. The upright position of the tubercles at first can be noticed and their gradual bending outwards. The actual growing point is well protected by the paraheliodes formed by the spine and hairs. $\times 6$.

Fig. 19. A few spiral tracheids (*b*) and storage tracheids (*c*) of a central bundle of the tubercle seen in longitudinal view. $\times 160$.

Fig. 20. Apical portion of tubercle, in longitudinal section, showing the multicellular hairs (*i*), the air-containing fibres (*h*) of the spine, the cork (*k*) underlying the spine, the cork cambium (*g*), and the storage tracheid endings (*c*) of the central bundles of the tubercle. $\times 150$.

PLATE XXVI.

Fig. 21. Transverse section across a bundle of the main axis. Cortex (*s*), protophloem (*o*), bast-parenchyma (*p*), cambium (*r*), wood-parenchyma (*n*), annular tracheids of the metaxylem (*m*), and of the protoxylem (*l*) can be made out. $\times 60$.

Fig. 22. Portion of the same. $\times 130$.

Fig. 23. The wood-portion of a similar bundle in longitudinal section. Spiral tracheids (*m*) and wood-parenchyma can be made out. $\times 130$.

Fig. 24. Transverse section of a bundle low down in the whole plant: wood-parenchyma (*n*), spiral tracheids (*m*), libriform cells (*q*). $\times 130$.

Fig. 25. A similar portion in longitudinal section. $\times 130$.

Fig. 26. Two adjoining libriform cells in longitudinal section. $\times 360$.

Fig. 27. Portion of the cork layer low down on the plant: cork (*k*), cork cambium (*g*), cortex (*s*). $\times 130$.

Fig. 28. Transverse section of a spine low down: epidermis (*e*), thick-walled fibres (*t*), air-containing fibres in the centre (*h*). $\times 360$.

Fig. 29. The outer layers of a spine higher up: epidermis (*e*) and thick-walled fibres (*t*). $\times 360$.

Fig. 30. The same further in: thick-walled fibres (*t*), and air-containing fibres (*h*). $\times 360$.

Fig. 31. Transverse section across young root: cork (*k*), cortex (*s*), bast-parenchyma (*p*), protophloem (*o*), cambium (*r*), annular tracheids of metaxylem (*m*), wood-parenchyma (*n*), annular tracheids of protoxylem (*l*). $\times 130$.

Fig. 32. The same in longitudinal section. $\times 130$.

Fig. 33. Transverse section of young root: cork (*k*), bast (*a*), metaxylem (*m*), protoxylem (*l*), and medullary ray (*u*). $\times 15$.

Fig. 34. The same but older. $\times 15$.

Fig. 35. The same but older. $\times 15$.

Fig. 36. The outer layer of the transverse section of old root: cork (*k*), cortex (*s*), bast-parenchyma (*p*), protophloem (*o*), cambium (*r*), medullary ray (*u*). $\times 130$.

Fig. 37. The next inner layers of the same section: annular tracheids (*m*) and parenchyma (*n*) of the metaxylem, medullary ray (*u*). $\times 130$.

Fig. 38. Innermost portions of the same section: annular tracheids (*m*) and parenchyma (*n*) of the metaxylem, annular tracheids of the protoxylem (*l*). $\times 130$.

Fig. 39. Longitudinal (microtome) section of growing point of young plant. Several young tubercle-primordia (*w*) can be made out, in between which is a mass of hairs. The black object to the left near the top is a spine cut across. $\times 14$.

Fig. 40. Portion of the same more highly magnified. Immediately on the left of the organic apex is a young tubercle-primordium (*w*), to the left of which is a further tubercle-primordium with a spine-primordium on its top (*v*). $\times 42$.

Fig. 41. An older tubercle-primordium (*w*) to the right of the organic centre, with a number of spine-primordia (*v*). $\times 42$.

Fig. 42. An older tubercle-primordium (*w*), with spine-primordia (*v*) and hairs (*i*). The palisade-cells are showing (*f*). $\times 40$.

Fig. 43. An older tubercle-primordium (*w*) to the right of the organic centre. The palisade-cells (*f*) are marked off and the rim surrounding the spines (*v*) and hairs (*i*). $\times 40$.

Fig. 44. Insertion of young spine-primordium on to tubercle. The epidermis (*e*) is clear, and the inner cells also, which will later on form air-containing fibres (*h*). $\times 330$.

Fig. 45. Young spine-primordium (*v*), with its epidermis (*e*), surrounded by hairs (*i*), joined on to the provascular cells of the tubercle-primordium (*w*). $\times 330$.

Fig. 46. Section through the axil of tubercle (*w*), from which springs a hair (*i*). The bud (*y*) is in the axil of the tubercle on the right; the other tubercle therefore is the one nearest the growing point. $\times 330$.

DARBISHIRE - MAMILLARIA.

O.V.Darbshire del. ad nat.

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