Contributions to a Knowledge of the Morphology and Ecology of the Cactaceae:
II¹. The Comparative Morphology of the Embryos and Seedlings.

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With Plate XXVI.

THE present paper comprises the results of an examination into the comparative morphological development of representatives of the genera of Cactaceae. In this investigation I have had four objects in view:—

1. To discover whether the conclusions reached by a study of the comparative anatomy and development at the growing-point of the adults in this family are sustained by a study of their ontogeny; and in how far the very peculiar morphological features of the adults are present in the embryos, and at what stages they develop.

2. To determine whether the form-conditions of the seedlings answer or not to the form-conditions of the adults;

¹ I. Die Morphologie und Biologie der vegetativen Theile. Flora, 1894, Ergänzungsband, pp. 49–86.

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and, if so, whether these shapes are the result of adaptation to similar conditions, or are determined by the working back of adaptive characters of the adults, or are due to some other cause.

3. To find whether the young stages show features indicating anything as to the phylogeny of the genera.

4. To find whatever else of interest might come out of a minute study of the young stages of this highly specialized family.

HISTORICAL.

Although there are many references to the germination and the seedlings of Cactaceae in systematic works treating of that family, as well as in other works of a morphological or ecological character, nevertheless no comparative study of the young stages has yet been attempted. It is still nearly as true as it was in 1858, when Labouret wrote: 'Les faits relatifs à la germination sont incomplètement observés.' Doubtless there are two reasons why this family, of such unusual morphological and ecological interest, has been neglected in this respect: first, the great difficulty of obtaining authentic seeds, and the considerable difficulty of raising them; and second, the widely spread opinion, distinctly formulated by Pfeiffer, that the seedlings have no taxonomic value. Pfeiffer in 1837 wrote upon this subject as follows:—
'Diese Beobachtungen lieferten mir den Beweis, dass die Keimung bei allen Cacteen, welche keine wahren Blätter haben, sehr ähnlich ist, und dass die Gestalt ihrer Cotyledonen keinen Gattungscharakter abgeben kann. Denn:

(1) Ist dieselbe bei allen Mammillarien und Melocacten ganz gleich, wie ich bereits an einer grossen Menge von Arten beobachtet habe;

(2) Die Form derselben bei *Echin. ingens* unterscheidet sich auffallend von der der übrigen bekannten Echinocacten;

(3) Unter den jungen Pflänzchen von *Echin. robustus*, von welchen ich eine ziemlich beträchtliche Menge besass, war die grösste Verschiedenheit der Gestalt, weshalb ich auch drei

dieser Formen auf ziemlich gleicher Entwicklungsstufe abzeichnete.'

The evidence given in this paper shows that these deductions of Pfeiffer's are incorrect, but they have doubtless had weight with other systematists; and morphologists, for the other reason given, have hardly yet taken them up.

The first writer to describe and figure seedlings of this family was De Candolle, who in 1827 gave a drawing ('made in 1800') of a seedling of *Cactus Melocactus* (*Melocactus communis*), which unhappily contains a morphological error, as pointed out by Miquel in 1839. From that time on to the present, figures and descriptions have from time to time appeared, though in no great abundance, of which I need mention here only the more important, more especially since I have attempted to enumerate all these figures in the special part of this paper.

The earliest account of the process of germination in Cactaceae that I have found was given in 1836 by Zuccarini, who described it correctly in *Mamillaria* and *Echinocactus*. In the next year Pfeiffer figured and described several forms, and briefly discussed their germination in the passage I have quoted above, to which he added other remarks of less importance. Labouret, in 1858, devoted five and a half pages to the description of the germination of eleven species, but gave no figures. Klebs, in his work on Germination in 1885, gave a few observations upon this family. The various papers of George Engelmann figure many embryos as taken from the seed, but rarely figure the seedlings. Irmisch, in his paper on *Rhipsalis Cassytha*, has given the most satisfactory account of the germination of the seedlings of a species of this family which we possess. Goebel has given the fullest account of the seedlings which has yet appeared, including several of the best figures yet published, and a discussion of their ecologic and phylogenetic significance. Lubbock has described and figured several species. Schumann has said but little upon this phase of a subject on which he is such an authoritative writer. In a short paper by Mr. C. F. Maxwell

a few seedlings are described and sweeping conclusions drawn upon altogether too scanty evidence. There are of course other references, including those in inaugural dissertations by Kaufholz and Michaëlis, and in the 'Monatsschrift für Kakteenkunde,' but they are of minor importance. One characteristic of nearly all of the figures in the various works I have cited is this—they show the epicotyl very well developed, but not the form in its true embryo condition; and hence they are less instructive in the present study than would otherwise be the case.

MATERIALS.

The value of a study like the present depends very largely upon the authenticity of the seeds used; and the difficulties of obtaining and raising them are great. I have tried first of all to obtain seeds collected in the field by botanists who are known to be particularly well acquainted with their own flora, and for seeds collected under these conditions I am greatly indebted to Mr. S. B. Parish of San Bernardino and to Professor J. W. Toumey of the University of Arizona, both of whom have most liberally responded to my troublesome requests. Other materials have been sent me by Mr. C. R. Orcutt of San Diego, Mr. W. Fawcett of Hope Gardens, Jamaica, and by a few others, to all of whom I extend here my sincere thanks. Next to material from this source, I have valued that obtained from Botanic Gardens, particularly from those of Palermo and Florence, where the Cactaceae grow under conditions far more nearly natural than in the northern gardens, where indeed many kinds do not bloom at all, or only rarely and in single specimens. Finally, I have obtained some seeds from dealers, but in general I have only trusted the correctness of the naming of the seeds I have bought when they grew into seedlings recognizable as of that species, or when from two distinct sources I have obtained what are plainly the same seedlings; and indeed I have tried to apply this test also to those obtained from Botanic Gardens. One source of error in raising them must be guarded against—

an occasional mixing which happens through careless watering where several pots stand together; the water carrying seeds may splash from one pot into another. It is not impossible that some of the remarkable cases of seeming polymorphism in seedlings described by Pfeiffer and others may be due to a mixing of distinct kinds; and a wrong identification of a given seedling might thus readily come about. In obtaining the seeds I have tried especially to secure representatives of all the genera, of each of the marked divisions of a large genus, and of the morphologically remarkable species. Of the fresh seeds sent me by botanists there is hardly a case where they failed to germinate, though those which were bought often failed to come up. My experience is in marked contrast to that of Henslow, who comments upon the great difficulty of germinating seeds of desert-plants¹. After the embryos are well developed, however, it becomes increasingly difficult to grow them, though naturally there are the greatest differences between them in this respect. The transition from embryo to seedling, i.e. the formation of the epicotyl, is a crucial point which some cannot pass. They are very liable to rot at the root, or else to form there much corky tissue, which interferes with their proper nutrition and ultimately distorts and destroys them. Still with reasonable care, it is not difficult to raise most of the species.

A very important question here arises as to how far the seedlings raised in a northern greenhouse correspond to those growing naturally at home, and whether safe conclusions as to the latter may be drawn from the former. At least one author (Schumann) has stated that the seedlings vary too much under these conditions to be trusted. But within certain limits I believe there is but little difference between the domestic and the wild seedlings. First; upon *a priori* grounds we might suppose that in one generation, while there may be changes in those characters, such as length, thickness, colour, which are developed in irritable

¹ Journ. Linn. Soc. xxx. 222.

response to outside conditions of light, moisture, &c., in each generation, yet in those characters which are hereditary, i.e. the ground-form, relative positions of the parts, their order of appearance, &c., there can be no perceptible change in one generation. Secondly, the germination of the seeds at home in the desert must take place at the rainy season, for then only is the necessary water available. Now the conditions of the desert in the cloudy time of the rainy season are not so very different from those of our greenhouses. This similarity is in a manner confirmed by the fact that the young embryos will not grow well if exposed in our greenhouses to too bright light, showing that at home they must grow at first in shade. Thirdly, seeds of the same species have been grown by us under very different conditions of moisture and soil, even to such extremes as sand, peat, and sawdust, and despite this the seedlings vary extremely little from one another, except when 'drawn' through lack of light, or dwarfed through some kind of starvation. Some of these conditions must be as far removed from one another as desert from greenhouse. I think that so far at least as concerns the stages before the seedlings begin to depend upon new food-supply made by their own chlorophyll, they are much alike under all conditions. Fourthly, we have raised many of these seedlings into adult stages; and these, except for too great slenderness in some *Opuntias* and too little colour in some reddish kinds, are not distinguishable from the wild forms of the same species which we find at home in the desert. If the adult stages thus correspond under long-continued differences of conditions, much more must the young stages under very short periods of difference. I believe therefore that seedlings raised in greenhouses with all the light that is good for them, are safe examples of the seedlings of those species in a wild state, the differences being too small to be appreciable in such a study as the present. Nevertheless I freely admit that such studies as these would be much better carried on in the native homes of the plants, for which a properly equipped

desert-station is essential; and after the tropical gardens have been provided for, this may well next attract the attention of botanists.

GERMINATION.

The present study properly begins with the fully formed embryo in the ripe seeds. The development of the embryo, of the ovule, and of the fruit, is a distinct question on which I expect to make another communication later. The subject has already received some attention from Planchon¹, Payer², Guignard³, d'Hubert⁴, but the results are too fragmentary to be of use in this study. In general the seeds in the Cactaceae contain a curved embryo with but a slight quantity of albumen lying against its concave side.

In the germination of the seeds I have seen little that is especially remarkable. On absorption of water the seed-coat is either split open along a part of its length, as in *Opuntia*; or a piece is pushed off valve-like from the micropylar end, as in *Echinocactus*, *Cereus*, &c. In the latter cases, and no doubt in many others, this is effected by the great swelling of a ring of epidermal cells at the lower end of the hypocotyl, which form a distinct ridge or collar from which later the hair-collar develops. This swelling is common in other families, and no doubt forms the basis of the well-known 'wurzel-hals,' or 'haftscheibe.' Klebs has correctly described the nature of the germination in this family; it belongs distinctly to his fifth type, those with the main root growing little or not at all during germination, with a crown of long root-hairs on the swollen base of the hypocotyl, the hypocotyl lifting the cotyledons out of the seed to above ground. In the latter respect this account is not strictly accurate for this family, for the seed-coat is commonly carried up on one of the cotyledons, no doubt to allow of the absorption of the

¹ Ann. Sci. Nat., Bot., 1845, 275-311.

³ Bull. Soc. Bot. de France, XXXIII.

² Ann. Sci. Nat., Bot., 1872.

⁴ Ann. Sci. Nat., Bot., 1896.

last trace of the albumen in combination with an early spread of the cotyledons to the light.

As the lower end of the hypocotyl issues from the seed, its positive geotropism manifests itself, and it bends downwards; at the same time from the swollen collar there grows out at about 45° a great number of long slender straight hairs, which attach themselves to the soil or other substratum, forming a series of cords binding the young plant firmly to the soil (see Fig. 17 *c, d*). It seems to me that these hairs come out at a constant angle to the stem, and are not geotropic, in which case it is an interesting question how they are guided in assuming that direction. This method of binding the seedling to the soil is well known elsewhere (see Klebs), and is generally considered necessary to hold the seedling in position until its root becomes fixed. But it, like other methods of fastening young germinating embryos to the ground, may have rather the significance of providing a resistance for the root to work against in the mechanical work of forcing its way into the ground, as otherwise the embryo would simply be lifted, and there would be no leverage for the work. The root at first grows very slowly, but the hypocotyl, as it issues from the seed-coat, begins at once to swell at the base, and this swelling extends regularly upward as it issues from the seed. Finally, only the cotyledons, sometimes three in number, are left, and these are still very small; but now either these are disengaged and swell also, or else they remain, one or both, for a time in the seed; sometimes however they seem unable to withdraw themselves from the seed-coat, and they are held and cut by the seed-coat as they swell, though in their more vigorous growth at home in the deserts this probably does not happen. As soon as the hypocotyl is well out of the coat, its upper end manifests its apogeotropism and curves upwards. The embryo, on issuing from the seed, turns first pale green; but very soon, in many species, red colour appears. At first the cotyledons are tightly pressed against one another, but they separate later, and, as the epicotyl begins to grow,

they are forced apart until finally they stand out at right angles to the hypocotyl. Thus is germination completed.

A distinct and important feature of this process is the remarkable and rapid swelling of the hypocotyl, and consequent immediate assumption of a succulent habit. On examination, however, I have found this to be due, not to increase in number of cells through division, but chiefly to the great increase in size of the cells already laid down. In an embryo of *Cereus triangularis*, for example, lying in the seed, every cell is small and full of protoplasm and starch; while in that which is fully germinated the cells are many times larger, each one is rounded, and has a thin film of protoplasm around the wall, whilst their number is very nearly the same in the two cases¹. It is plain then that germination consists here simply of the absorption of large amounts of water, by which cells already laid down in the ungerminated embryo simply swell to full size, and no doubt with no material increase in dry weight. From this it follows also that up to the time when new substance is made by the chlorophyll in amount sufficient to enable new growth to begin, which period is roughly marked by the beginning of the growth of the epicotyl, there is no line to be drawn between embryo and seedling; in other words, we may best speak of the stage where the embryo is still lying in the seed as that of the ungerminated embryo, and that in which it has come out, turned green, spread its cotyledons, but before it shows the epicotyl, as that of the germinated embryo. It is this marked and important stage of the germinated embryo, with the epicotyl just beginning to show, that I have tried to represent in the drawings which accompany this paper. The stages after the epicotyl is developed may best be called the seedling. The shape of the seed makes the young embryo asymmetrical, but as it swells it becomes more and more symmetrical in form, though it does not, as a rule, become perfectly so.

There is naturally great variation in the rapidity of germina-

¹ The statistics upon this subject are to be given in a paper referred to on a later page.

tion of the different species, and on account of the condition of the seed, time of year, temperature, &c. In most forms, after the completion of germination, there is a pause, and some time elapses before the epicotyl appears: in many kinds which it is easy to germinate, it is very difficult to ensure development into the seedling-stage, which shows that the materials laid up in the seed make them to some extent independent of external conditions, but that when they must begin to rely upon the surroundings for further progress, they do not find these favourable. No doubt in the deserts, germination is more rapid than in our greenhouses, and one may suppose that the seedlings attain a considerable size before their first dry season arrives.

To show the rate of germination, the following facts are selected. On March 20, 1895, series of seeds were planted in a greenhouse under given favourable conditions; they appeared above ground as follows:—*Opuntia basilaris* var. *ramosa*, in five days; *O. serpentina*, nine days; *Echinocactus viridescens*, fifteen days; *O. echinocarpa*, nineteen days; *Mamillaria radiosa* var. *neo-mexicana*, twenty days; *O. tetracantha*, twenty-three days; *Echinocereus phoeniceus*, twenty-seven days; *E. pectinatus rigidissimus*, twenty-nine days; *M. Grahamei*, twenty-nine days; *O. phaeacantha*, fifty-two days. Some seeds of the above species did not germinate for a year (*O. echinocarpa* and *E. phoeniceus*), which is a phenomenon well known in other cases, and perhaps has an ecological meaning. None, however, came up in pots kept for a third year. I have made no observations upon the length of time Cactus-seeds retain their vitality. Pfeiffer¹, however, states that seeds of three species sown nine years after ripening came up in fourteen to eighteen days.

The seedling-growth is most rapid in *Opuntia*. In *O. echinocarpa* planted March 20, the epicotyl with leaves was 7 cm. long on June 13, and in May of the next year some were 15 cm. long and 3.3 cm. broad. The growth of *O. serpentina* planted at the same time was nearly as rapid.

¹ Neuere Erfahrungen, p. 122.

The development of the earliest stages of the epicotyl is much the same throughout the family. The cotyledons, however, behave differently in the different genera. In *Pereskia* they apparently fall off; in *Opuntia* and some of the broad-cotyledoned Cerei, and in *Phyllocactus*, they wither up without falling; in the other genera they are persistent, but in the further growth in diameter of the hypocotyl they broaden at the base and gradually become merged into the stem, a curious case of ontogenetic metamorphosis. In the development of the epicotyl, first of all two leaves appear from the growing-point at right angles to the cotyledons; then another pair nearly at right angles to these; then there comes either a fifth in position to begin a $\frac{2}{5}$ spiral, which later may become a $\frac{3}{8}$, as is common in *Opuntia* and *Mamillaria*; or else the second pair is at right angles to the first and the third pair over the first, thus forming four rows, the foundation for four ribs, as is common in the ribbed forms. These ribs may then diminish in number by dropping one or more, or may increase by the splitting of one or more. In the further development of the epicotyl, the peculiar characteristics of the adults appear at diverse stages, a subject which will be treated later in the special part of this paper.

The roots in both embryos and seedlings are very simple, slender, and sharply distinct from the hypocotyl. They rarely become succulent. In some species, as *Echinocactus Wislizeni*, the epicotyl develops very rapidly and the root very slowly, so that the seedling has a curious three-storied appearance—a swollen globular epicotyl above, a cylindrical smaller hypocotyl below that, and the very slender root below all.

CELLULAR ANATOMY.

The cellular anatomy of this entire family is of great interest and is still imperfectly known. I have naturally made some observations upon this subject in the embryos and seedlings, but shall not attempt to treat of it here, for the reason that it is being thoroughly studied by one of my students whose results will before very long appear, and whose paper on the

subject will be in a measure a supplement to the present one. I need only state that the chief characteristics of the cellular anatomy of the germinated embryos through the family are as follows:—epidermis, one layer of cells, thin, often papillate; cortex of very large round cells, sometimes visible to the naked eye, and forming the greater part of the hypocotyl, from four to six times the diameter of the central cylinder (Figs. 2 *d*, 5 *d*); central cylinder very simple, of two to six fibro-vascular bundles. The young root is characterized by a great development of cork, slight development of cortex, and a condensation of the central cylinder. Naturally this simple structure becomes much modified in the seedlings, and still more in the adults.

THE COLOUR-FACTORS OF THE EMBRYOS.

The germinated embryos in this family show a considerable range of colours, from a clear typical chlorophyll-green in some *Platopuntiae* and climbing *Cerei*, to a deep red in *Mamillariae* and others. As the embryos lie in the seeds they show no colour in any of the species I have observed, except the usual translucent white. On emerging from the seed, they turn at first pale green, which deepens upon some but in others is soon masked by the red, or, as in *Cylindropuntiae*, becomes olive or greyish green. In *Echinocactus viridescens*, for example, as it breaks out from the seed, the embryo turns at first pale green, but very soon a blush of clear red appears on the tips of the cotyledons, and spreads over all the upper part of the hypocotyl, and it appears vividly also on the first two leaves of the epicotyl. One of the most brilliantly red species I have noticed is *Mamillaria Nuttallii*. Here and there over these red embryos, one sees brighter greenish spots, which are areas under the stomata. Examination shows that the red colour is in the sap of the epidermal cells. Moreover its appearance is dependent upon light, for not only does it appear only on parts exposed directly to the light, even to the extent of forming only upon the upper side of a hypocotyl when this is lying upon its side, but in

E. ingens, which is normally very red, no colour at all appeared when I placed caps of tinfoil over the embryos as soon as germinated. The appearance of the colour, therefore, is a clear case of irritable response to the action of light as a stimulus. But there is another distribution of colour which is noticeable. In *Echinocactus Wislizeni*, *Opuntia Engelmanni occidentalis*, and some other species, the colour is not general, but is limited to a single bright red spot on the outside of the base of the cotyledons; and moreover the leaves of the epicotyl (particularly in *Cereus grandiflorus*) show the same feature. I think this is the result of the appearance of the colour only at the time when the leaves are very young and still folded with their faces against one another and their backs only exposed to the light. But it is not confined to the leaves, for the colour in some species only runs in streaks in the depressions between the ribs of the stem¹.

In seeking an explanation of the presence of the red colour, we must recall the fact already stated that it appears only in response to light as a stimulus; and it is most intense in the forms which live exposed to the greatest brightness. It does not appear at all in *Pereskia aculeata*, the climbing species of *Cereus*, *Phyllocactus*, *Rhipsalis*, and those *Platopuntiae* growing in the less extreme deserts, such as *Opuntia vulgaris* and *Rafinesquii*, and it is best developed in the most extreme desert-forms of *Mamillaria*, *Anhalonium*, and *Echinocactus*. In other words, the more mesophytic the habitat, the less the colour; the more xerophytic, the more the colour. There are two explanations of similar red colour elsewhere. First, according to Stahl, it may serve to absorb some of the light-rays, and convert them into heat which is of use in the processes of growth at a time when there is none too much heat available. Secondly, it may serve as a light-screen, cutting off the rays of the violet end of the spectrum, which act injuriously upon the living tissues. On the whole, in

¹ The spot of colour at the base of the leaf is not uncommon elsewhere. I have noticed it on the base of the petiole in *Lysimachia alnifolia*, in a species of Maple, and elsewhere; also in *Salicornia herbacea*.

view of its distribution, the latter seems far more probable than the former as an explanation of the colour in these embryos. It is true the colour is present in the wet season, when the weather is clouded, but it is not unlikely that even then there are periods of vivid sunshine. But in the absence of exact observations of the subject in their native homes, these theories, like many others relative to the ecology of desert-plants, are mere guesses.

THE SIZE-FACTORS OF THE EMBRYOS.

Comparing the germinated embryos throughout the family, we find a wide range of size, from *Pereskia* on the one hand to *Mamillaria* on the other (see figures; *Pereskia* and *Opuntia* are drawn natural size, all others magnified two and a half times). In seeking for the influences which determine the size in the different cases, we naturally turn first to ask whether size in the germinated embryo is related in any way to size of seed from which it comes. Excluding now certain cases presently to be considered, in some species of *Cereus*, *Phyllocactus*, and *Opuntia*, where there is a special growth of the cotyledons, it is plain that there is a relation between these two. It not only shows in a comparison of seed and embryo, but it follows also from the fact I have mentioned that the growth of the embryo to its fully germinated stage is little more than a swelling to full size of cells already laid down in the seed. The question then resolves itself into this—is it, in the main, the size of the seed which determines that of the germinated embryo, or is that of the embryo the more important factor, the seed being the size it is in order to accommodate it? If one compares the size of embryo or seed with the size of the adult plant throughout the family, it appears at first sight as though there were no constant connexion between these two. *Cereus giganteus*, for example, has a seed no larger than many of the smaller Cerei. But if, instead of particular species, we consider groups such as genera, we find that there is a relation between the average

or prevailing size of adults in the genus and that of the seeds and embryos. Thus *Pereskia*, including great shrubby climbers, has the largest embryos; next, *Opuntias* have the largest adults, seeds, and embryos; *Cereus* and *Echinocactus* are in all three respects much smaller, the latter more so than the former; *Mamillaria* and *Anhalonium* are in all respects smallest of all. Considering the natural relationships of these groups, we may say that the seeds in the Cactaceae have phylogenetically grown progressively smaller, just as the adult plants have done, taking the embryos with them. In general, though with some exceptions, this progressive diminution in size of the adults accompanies an increasing dryness of habitat. It is then probably true that the size of the embryos is reduced, not directly by the dryness, but that it accompanies the reduced size of the adults and seeds; for if the former were true we should find much greater variation in size of the embryos than we do. A marked and important exception to the reduction in size is found in the climbing *Cerei* and *Phyllocactus*, where the embryos are much larger than those of the desert *Cerei*, and have leaf-like cotyledons. But the forms possessing these larger embryos have abandoned the desert for a life in the woods, where the mesophytic conditions allow of a much larger spread of surface, and in this case it is plain that the embryos themselves respond to these conditions and increase in size, a point which will be discussed later.

Another and important incidental feature of size in the embryo is its increase when the epicotyl is not allowed to develop. In my plants, sometimes by accident and sometimes by design, the epicotyl and axillary buds of the cotyledons became removed; in such a case no new buds formed, but the embryo continued to increase in size until it became double that of the normal (Fig. 2 *e*). What this must mean is, that a certain amount of food-substance which would normally have gone into the building of the epicotyl, is here diverted into making larger the cells of the embryo (cotyledons and hypocotyl). This growth of the embryo under such conditions would be difficult to explain on the

supposition of a specific 'bildungs-stoff' for the epicotyl, but speaks rather for a large power of individual adjustment in the protoplasm of the embryo. The phenomenon is, of course, well known in other cases¹, and is, I suppose, comparable with the effects of castration in animals.

THE FORM-FACTORS OF THE EMBRYOS.

If we view now the forms or shapes of the embryos at the stage when germination is completed, and the epicotyl is about to appear, we find an immense range of form from the very un-Cactus-like *Pereskia* (Fig. 1) on the one hand to the nearly globular, almost cotyledonless *Mamillaria* (Fig. 47) on the other. As this subject constitutes the most important part of our present inquiry, I must here treat it in some detail, and shall take up the genera in succession. At the same time I shall describe the development of the epicotyl when it is noteworthy, and add remarks upon other features of importance. In addition to references to figures accompanying this paper, I shall mention all other figures of germinated embryos known to me, excepting a very few which are worthless, so that in this respect I mean this work to be monographic. Finally, I shall add a summary of what may be deduced as to form-factors.

1. Genus *Pereskia*.

P. aculeata, Mill. Figure 1.

P. Pititache, Karw. Figure 9, Pl. II, in Zuccarini.

P. Bleo, DC. Figure (embryo in seed), Pl. LXIII in Schumann, Flora brasiliensis.

This genus consists of climbing woody forms with perfectly developed leaves, merging over to upright succulent species, approaching and perhaps merging with *Cylindropuntiae*. The embryo (Fig. 1) of *P. aculeata* has thin, very leafy cotyledons, showing distinct netted veins; their asymmetry is due to their position in the seeds, which are very flat. As they grow they become jointed at the base, precisely as are

¹ Jost, Prings. Jahrb. 1895; also very easy to produce in young Bean-plants.

the later leaves, and probably like them they are shed at the dry season. The plumule shows first a leaf like the later ones, then another, and so on alternately. As the cotyledons lie in the seed they are flat, and hence very different from those of *P. Bleo* as figured by Schumann. There is no doubt of the identity of my seeds, for one of them grew into a seedling of this species. *P. Pititache*, as figured by Zuccarini, has an embryo resembling more nearly *Opuntia*, though the adult is described as woody. Probably the embryos of some of the succulent species, as *P. spathulata*, will be much like those of *Opuntia*. This mesophytic type of germinated embryo in *P. aculeata* is of course correlated with its growth under mesophytic conditions. No spines are produced in the young seedling, though the axillary buds produce the multicellular hair-like structures which are probably homologous with them.

2. Genus *Opuntia*.

- O. bernardina*, Engelm. Figure 2.
O. echinocarpa, Engelm. and Bigel. Figure 3. Also in Engelmann, Pl. XXIV.
O. Whipplei, Engelm. and Bigel. Figures 9, 10, Pl. XXIV, in Engelmann.
O. vulgaris, Mill. Figure 5. Also Fig. 57 G in Schumann (Engler and Prantl). Also Ganong in Botanical Gazette, XXV, Pl. XVI.
O. Rafinesquii, Engelm. Figure 7, Pl. XXIII, in Engelmann.
O. missouriensis, DC. Figure 17, Pl. XXIII, in Engelmann.
O. tortispina, Engelm. and Bigel. Figure 5, Pl. XXIII, in Engelmann.
O. basilaris, Engelm. and Bigel. Figure 398 in Lubbock, II, 11.
O. basilaris ramosa. Figure 4.
O. Engelmanni occidentalis, Salm-Dyck. Figure 7. Figure 400 in Lubbock, II, 12.
O. Ficus-indica, Mill. Figure 6. Also in Schacht, Lehrbuch der Anat. u. Phys. der Pflanzen, Fig. 472, Pl. II (not seen).
O. sp. ? Figure in Zuccarini, 8, Pl. II.

Very numerous beautiful figures of ungerminated embryos of species of *Opuntia* are given in Engelmann's works.

This genus, nearly related to *Pereskia*, consists of shrubby, branching, jointed forms, falling into two groups:—the *Cylindropuntiae*, living in dry deserts, with cylindrical joints and usually subulate leaves which may be up to an inch in length; and the *Platopuntiae*, with flattened joints becoming true phyllocladia, smaller leaves, and as a rule occupying less

extreme desert situations than the *Cylindropuntiae*, some of them growing even in woods. Many lines of evidence show that the *Cylindropuntiae* are the stem-group from which the *Platopuntiae* are an offshoot.

Turning to the embryos, we find that all have a slender, non-succulent hypocotyl, and well-developed, though fleshy, cotyledons approximately the length of the hypocotyl. With respect to the exact form of the cotyledons, however, two types are distinguishable;—some, such as *O. bernardina*, *echinocarpa*, *serpentina*, and *tetracantha*, have equal tapering cotyledons, triangular-cylindrical in section (Fig. 2 c), becoming flatter with age, shorter than the hypocotyl; while others, *O. vulgaris*, *missouriensis*, *Ficus-indica*, *tortispina*, *Rafinesquii*, *Engelmanni occidentalis*, *phaeacantha*, and other *Platopuntiae*, have them flatter and more leaf-like (Fig. 5 c), unequal, and usually longer than the hypocotyl¹. This distinction of the thick leaves for the *Cylindropuntiae*, and the thinner for the *Platopuntiae*, holds in all species that I know of, with the following exceptions:—as figured in Engelmann *O. Whipplei* seems to have flat cotyledons, but as the plumule is shown developed, and since even in *Cylindropuntiae* they flatten with age, this may not be a real exception; *Opuntia basilaris* is, however, a real and marked exception, for in Lubbock's figures and my own, the cotyledons are distinctly of the *Cylindropuntiae* type, though this species belongs to the *Platopuntiae*². As however *O. basilaris* is an extreme desert-species, it suggests that the form of the cotyledons is determined chiefly by the direct environment, the more condensed form occurring in the more extreme deserts, and the flatter and more leaf-like in moister climates, where the natural tendency of the plant to spread as much leaf-surface as possible is allowed more freedom to produce larger and flatter leaves. This can be tested by observing on the one

¹ The extreme of this flattening is probably reached in *O. brasiliensis*, as shown by Schumann's figure on Pl. 61, *Flora brasiliensis*.

² *O. basilaris* is in several respects a remarkable form; particularly noteworthy is its profuse branching from near the base. My seedlings of 2 cm. length (in the var. *ramosa*) showed no trace of it, though a larger one showed one branch.

hand *Cylindropuntiae* which grow in the moister climates, and on the other, *Platopuntiae* which grow in the extreme deserts, but at present I have not material for this comparison. In any case there can be no doubt that the relatively larger and flatter cotyledons of the *Platopuntiae* do not indicate that they are more nearly related to *Pereskia* than are the *Cylindropuntiae*, for all evidence is against such a possibility, but they are the result of a re-enlargement allowed by the moister climate in which they grow. Another explanation for the cotyledons of *O. basilaris* is that this form has come off from the *Cylindropuntiae* entirely independently of the other *Platopuntiae*, and has retained the primitive leaves.

The differences between the two divisions of *Opuntia* are shown clearly also in the cellular anatomy, but I shall here cite but one phase of this. The *Cylindropuntiae* have a six-bundled central cylinder, as shown in Fig. 2 *d*, while the *Platopuntiae* have a two- or four-bundled cylinder arranged as shown in Fig. 5 *d*.

The cotyledons, normally two, are sometimes one, often three; and sometimes, as in *O. vulgaris*, elsewhere described, which is polyembryonic, there may be more, with some imperfect. In *Platopuntiae* they are unequal in size, and it is easy to see that the longer is on the convex side in the seed, and the shorter on the concave. No doubt this inequality of the cotyledons is not in the least to be traced to adaptation, but is a simple result of position in the seed, which gives less room to one than to the other, hence allowing it to make fewer cells; and as germination is little more than the swelling of cells already laid down, the cotyledons must be unequal. Many *Platopuntiae* have the cotyledons placed incumbently in the seed, while some *Cylindropuntiae* have them accumbently, and one at first attributes the flat cotyledons of the former and the nearly half-cylindrical form of the latter to this position: but an inspection of the many fine figures of embryos and seeds given by Engelmann disproves such a connexion.

The cotyledons have axillary buds, which I have made to

develop by removing the epicotyl in *O. bernardina* and one or two other species. A remarkable feature occurred in one seedling of *O. echinocarpa* (Fig. 3 *c*). One of the cotyledons, possibly in reality two congenitally united, was forked near its tip, and in the fork bore a bud producing hairs and spines of an altogether normal sort, which persisted long after the epicotyl developed. Such a case is difficult to explain on the basis of a formal morphology, for leaves, which the cotyledons undoubtedly are, do not produce buds normally in this family.

The development of the epicotyl is simple, and is as described earlier for the family in general. From the first, the general mode of formation of leaves and axillary buds agrees with what is found in the adults, except that the characteristic bristles (Borsten), the remarkable hair-sheath of the spines in *Cylindropuntiae*, and the nectar-glands formed of metamorphosed spines are all absent from the earliest clusters and appear later, though I have not determined exactly when nor how.

The epicotyl in all species of this genus is at first cylindrical. In *O. vulgaris* and other *Platopuntiae* it is only when the epicotyl is at least a centimetre long that it begins to flatten, and then it is parallel to the faces of the cotyledons. It would be of much interest to determine whether in the seedlings, as in the young shoots described by Goebel¹, the flattening is dependent upon the presence of light, and hence is a phenomenon of irritable response in which the growth-effect has not yet become hereditary.

The epicotyl in its development forces apart the cotyledons, which however retain a connexion with one another at their bases, so that the epicotyl seems to rise from a sort of sheath. When the epicotyl and the axillary buds of the cotyledons are removed, the hypocotyl grows far above the normal size, but the cotyledons wither as they do under normal conditions (Fig. 2 *e*).

¹ *Flora*, lxxx, 98.

3. Genus *Cereus*.

- C. Thurberi*, Engelm. Figure 8.
C. giganteus, Engelm. Figure 9.
C. peruvianus, Mill. Figure 10.
C. Hystrix, Sweet. Figure 11.
C. Bonplandi, Parm. Figure 12.
C. Martianus, Zucc. Figure 13.
C. grandiflorus, Mill. Figure 14; also Fig. 5, Pl. II, Goebel, *Schilderungen*, I.
C. nycticaulis, Link. Figure 15.
C. spinulosus, DC. Figure 16.
C. triangularis, Mill. Figure 17.
C. subrepandus, Haw. Figure 10, Pl. XVI, in Pfeiffer.
C. eriophorus, Hort. Figures 4, 5, 6, 7, Pl. II, in Zuccarini.
C. Gregii, Engelm. Figure, Pl. LXIII, in Engelmann.
C. Emoryi, Engelm. Figure, in Lubbock, II, 9.

This genus consists of stout columnar to short almost globular, or else deflexed or creeping or slender climbing forms, rarely jointed, always (excluding *Phyllocactus*) radial, generally ribbed. We recognize, with Schumann in his latest monograph, four main divisions:—*A*, those with erect columnar stems; *B*, those with stems at first upright, but at length declined on the ground; *C*, those at first upright, later leaning upon supports, and thus climbing or hanging but lacking aerial roots; *D*, those climbing and possessing aerial roots. This apparently very artificial division is much more natural than it seems, but is far from satisfactory. It is, however, the best we have. In this family, as Schumann has pointed out, the vegetative characters are more important in classification than those taken from the flowers, which in the large genera are singularly uniform.

Taking *Cereus* as a whole, we find throughout a succulent hypocotyl, with distinct cotyledons, usually broad at the base and set a little apart, with bases parallel. In the relatively large size of the cotyledons they approach *Opuntia*. But in the different divisions there are differences which are fairly constant and which usually distinguish them. Of the important columnar group, good types are *C. Thurberi* and *giganteus* (Figs. 8 and 9). In these two very similar and closely related

forms the cotyledons are as broad as the hypocotyl and about as long, pointed, triangular in section, with the inner line of their bases parallel. In all of these characters they show resemblance and doubtless relationship with the *Opuntiae*, particularly the *Cylindropuntiae*, and stand nearer to that group than do any other *Cactaceae* I have studied. As compared with *Cylindropuntiae*, these germinated embryos are of smaller size and much more succulent, as is to be expected in a group which upon the whole is more xerophilous in habit. The resemblance is further increased by the common occurrence of axillary buds to the cotyledons in *Cereus*. The epicotyl at first bears the leaves and axillary clusters only upon the $\frac{2}{5}$ system, and the development of ribs comes later, one of the cases numerous in this family in which phylogeny is repeated in ontogeny. The transition to ribs is easy, for these at first are five in number, representing of course the vertical orthostichies of the $\frac{2}{5}$ phyllotaxy.

Another division of columnar *Cerei* is that including *C. peruvianus* and *C. Hystrix* (Figs. 10 and 11). In both of these the cotyledons are much shorter and somewhat narrower than the hypocotyl, and the hypocotyls themselves are comparatively slender. I cannot explain their great deviation from the *giganteus* type except by supposing that the relationship of these two groups is not so close as has been thought. In *C. peruvianus* the axillary clusters fall into lines, and the ribs, usually five, form at once. In the variety *monstrosus*, which reproduces through seeds, the fasciation did not appear in seedlings under 2 cm. in height.

In division *B* I have had no material, though the *C. Emoryi*, figured by Lubbock, belongs here.

To division *C* belongs *C. Bonplandi* (Fig. 12), in which the form of the embryo, though not of the adult, suggests relationship with *C. peruvianus* and *Hystrix*. This species shows a peculiar feature of the cotyledons, in that one of them is always cleft at the tip, and this is rarely the case with both. This feature occurs rarely in other species, but this is the

only one in which I have found it regular. One supposes at first that it is due to the splitting of the tip of the convex cotyledon against the tip of the concave one in the seed, but careful examination has not certainly confirmed this. Another peculiarity in this species, also unique in my observation, is the intercalary basal growth of the cotyledons after development of the epicotyl, thus carrying the axillary buds away from the latter (Fig. 12 *c*). This suggests the similar basal growth of the tubercles in *Mamillaria*, *Leuchtenbergia*, &c., so important in producing the configuration of those genera. I have made one of these buds develop by removing the epicotyl. On the epicotyl at first four ribs develop, which often become eight, later dropping back to five.

In division *D* occur several forms of much importance. First is *C. Martianus*, which differs so much from others in this division as to raise the suspicion either that my material is wrongly named, or else that the species does not belong to this division. The germinated embryos (Fig. 13) appear to stand about intermediate between the columnar *giganteus*-like forms and the climbing species now to be described.

In *C. grandiflorus* and *nycticaulis* we have two climbing species very closely related, and very much alike both in adults and embryos (Figs. 14 and 15). In both of these, and also in *C. spinulosus* and *triangularis* (Figs. 16 and 17), two other climbing and not-distantly related forms, the cotyledons are unequal, flat and broader than the hypocotyl, though they are not broadest at base as are most other *Cerei*, but a little above it. One notices in these cotyledons a resemblance to those of the *Platopuntiae*, but only a little reflection is needed to show that this resemblance is not genetic, but ecological. These climbing *Cerei* live under conditions more mesophytic than xerophytic; and as all evidence shows that they have been derived from forms more like the columnar species, this larger size of the cotyledons cannot be primitive, but must have been re-acquired in response to conditions which permit of that increase of surface towards which green parts are continually tending. They are of

a clear green in all of these species, and large enough to do no inconsiderable amount of leaf-work, and wither with age instead of merging with the stem. They have good buds in their axils. Another feature which the embryos of these species have in common, and which may be correlated with their habitat, is the rapid growth of the hypocotyl and the relatively slower development of the cotyledons. In *C. nycticaulis* and *triangularis* the epicotyl forms first two leaves at right angles to the cotyledons, then two at right angles to these, thus forming four rows giving origin to four ribs. In *C. nycticaulis* one of these ribs soon splits into two, and the five then distribute themselves over the entire circle. This formation of new ribs by the forking or splitting of old ones is common in this family, indeed is the common method of forming the new ribs, and it shows how the rib once formed becomes, as it were, a true morphological element. In *C. triangularis*, on the other hand, one of the ribs soon stops abruptly; the one opposite to it keeps on its course, while the two intermediates turn spirally until they evenly occupy the circumference, after which the three persist through the life of the plant. In this early and temporary presence of four or five ribs in a characteristically three-ribbed species, we have another good case of repetition of phylogeny in ontogeny, a principle not very frequently illustrated by plants.

In *Cereus* the morphological composition of the adults is extremely simple. The same axillary points produce first a cluster of spines and later a branch or flower. Hence nothing of special importance is to be expected in the seedlings, for this is practically the kind of axillary bud which the seedlings produce throughout the family.

4. Genus *Phyllocactus*.

P. Ackermanni, Walp. Figure 18.

P. anguliger, Lem Figure 19.

P. phyllanthoides, Link, *grandiflorus*. Figure 20.

P. Phyllanthus, Link. Figure 21.

P. stenopetalus, Salm-Dyck. Figure in Goebel, 104; also Lubbock, II, 9.

P. latifrons, Walp. Figure 6, Pl. II, in Goebel.

P. Phyllanthus × *C. flagelliformis*. Figure in Pfeiffer, XI, Pl. XVI.

This genus, which merges with *Cereus* through the climbing triangular species (like *C. triangularis*), contains mostly epiphytic forms in which the ribs are reduced to two, resulting in flat phyllocladia (with axillary buds only upon the margins), which finally become thin and leaf-like upon cylindrical stems. These phyllocladia are set vertically, which probably comes about through suppression of the lateral ribs. Goebel has given a full account of the form-conditions in this genus.

The germinated embryos show a close resemblance to those of the climbing Cerei. In *P. anguliger* and *P. Ackermanni* (Figs. 18, 19), however, the cotyledons are somewhat less leaf-like than in *P. phyllanthoides grandiflorus* and *P. Phyllanthus* (Figs. 20, 21). In the latter the cotyledons are even more leaf-like than in any of the climbing Cerei, and show distinctly a yet greater departure from the triangular towards a rounded outline. This enlargement and rounding is, of course, in adaptation to the more mesophytic conditions which surround them. They are all of a clear green colour.

The epicotyls of the different species I have studied show considerable differences. Thus in *P. anguliger* four or five ribs form nearly at once, showing clearly enough the nearness of this species to *Cereus*; indeed the early stages of the seedlings are very *Cereus*-like. The same is true of *P. phyllanthoides grandiflorus*, and, according to Goebel's figure (Plate II, Fig. 6), of *P. latifrons*. But I think Goebel's figure does not represent this species, but some *Cereus*. *P. latifrons* has very flat broad phyllocladia and belongs near *stenopetalus*; indeed Schumann considers it probable that *latifrons* and *stenopetalus* are identical. But Goebel's own figure for *stenopetalus* (p. 104) is entirely different, and exactly what is to be expected for both *stenopetalus* and *latifrons*. *P. Phyllanthus*, which has the most leaf-like cotyledons of all, has an epicotyl of special interest (Fig. 21). The two first leaves form at right angles to the cotyledons, and the next two over the cotyledons; but the fifth comes over the third or fourth, not over the first or second, so that the epicotyl becomes at once two-ribbed and flat, and this flattening is in the plane

of the cotyledons, at right angles to their faces, and not in the plane of the faces as one would expect, and as is the case with the flattening in the *Platopuntiae*. The epicotyl is thus formed also in *P. stenopetalus*, as shown by the figures given by Goebel and by Lubbock. In comparing the species showing this early flattening of the epicotyl with those which have the latter ribbed, it is plain that the flat epicotyl accompanies the flattest and most leaf-like phyllocladia, and the ribbed epicotyl accompanies those less leaf-like and which oftenest show reversions towards *Cereus* in the production of joints possessing three or more ribs. The direction of the flattening in the epicotyl implies that the flattening has worked back from the adult stages, and not up from the embryonic stages, for in the latter case it would have come about in the plane of least resistance, i. e. in the plane of the faces of the cotyledons. Probably the direction is connected with the vertical position of the phyllocladia of the adults; as they are there flattened in the plane of the subtending leaf and the stem, so the flattening has worked back to stand in the plane of the two subtending cotyledons. In *P. Phyllanthus* the flattening has gone so far that the only trace of other ribs are the first and second axillary clusters. In the different species of this genus, then, we have another good illustration of the working of the principle of repetition of phylogeny in ontogeny, and a particularly good illustration of its real meaning, i. e. that a new character is acquired by adaptation in the later or adult stages of the plant, and then, in successive generations, appears earlier and earlier, until finally it has worked back to the earliest stages of the seedling, thus replacing the ancestral characters which finally cease to be repeated.

5. Genus **Epiphyllum**.

E. truncatum, Haw. Figure 55, p. 103, in Goebel; also (under name *E. Altensteinii*) in Pfeiffer and Otto, Figs. 2-5, Pl. XXVIII.

This genus, according to Schumann's monograph, contains properly but one species, the others often placed in it

belonging to *Phyllocactus*. It merges with the latter genus through such jointed forms as *P. Russellianus* and *Gärtneri*. *E. truncatum* is an epiphytic, hanging, much-jointed form, too well known to need description.

None of my many seeds of *Epiphyllum* have germinated, and hence I have no data as to the embryos and seedlings except the two figures cited above. Both figures show a rather stout embryo with the hypocotyl angular, or quadrangular, in section, and with short, tapering, pointed cotyledons. This is not at all the type of embryo which one would expect theoretically in this genus. Considering the marked mesophytic character of the adults reached through the increasingly mesophytic climbing *Cerei* and *Phyllocacti*, one would expect a still further development of surface in the most mesophytic *Epiphyllum*. That this is not the case remains to be explained. Possibly we are in error as to the affinities of this genus; there is something about the cotyledons, as shown in the figures, which suggests *Rhipsalis*. But it is more likely that the extremely epiphytic habit of the species has something to do with it. The epiphytic habit always requires some xerophytic characters, and of these one of the first is reduction in size of leaf-surfaces. In this connexion the embryos of *P. Russellianus* and *Gärtneri* would be of great interest.

The epicotyl in *E. truncatum*, as described by Goebel, is flat. It forms at first four polsters as the beginning of four ribs, but two of these fail to develop farther, so that the other two form a flat structure precisely as has been described and figured above for *Phyllocactus Phyllanthus*. This form of epicotyl is precisely that which we would theoretically expect.

6. Genus *Pilocereus*.

P. Houlettii, Lem. Figure 22.

This genus merges with the large columnar *Cerei*, from which it is distinguished by very minor characters.

The germinated embryos of *P. Houlettii* (Fig. 22) resemble

the columnar *Cerei* in their broad cotyledons, though these are less broad than in the *Cerei*, and in the very succulent hypocotyl, which is somewhat more elongated in this form. The epicotyl has eight ribs from the start, showing how old is the rib-forming habit.

7. Genus *Cephalocereus*.

C. senilis, Pfeiff. Figure 23.

This genus merges with the last and with the columnar *Cerei*. In *C. senilis* (Fig. 23) the cotyledons are narrower than in the columnar *Cerei*, and the hypocotyl is relatively more succulent. The large size of the embryos is noticeable.

8. Genus *Echinocereus*.

E. caespitosus, Engelm. Figure 11 g in Engelmann, Pl. XLIV.

E. pectinatus rigidissimus, Engelm. Figure 24.

E. phoeniceus, Lem. Figure 25.

E. Engelmanni, Lem. Figure 26.

E. procumbens, Lem. Figure 27.

E. tuberosus, Poselger. Figure 28.

This genus is very closely related to *Cereus*, though Schumann now considers it as well marked. It belongs nearest to the columnar *Cerei*, but to a division of the latter containing small forms. All forms in this genus are small and weakly armed. According to Schumann there are four subgroups. One of these, including the erect forms and nearest to *Cereus*, includes *E. pectinatus rigidissimus*, *phoeniceus*, and *Engelmanni* (Figs. 24, 25, 26), which I have studied. The very broad cotyledons of *C. pectinatus rigidissimus* show the closest resemblance to the columnar *Cerei*, though the embryos are of much smaller size than in the *giganteus* section. Of much larger size, and with the cotyledons somewhat less broad, is *E. phoeniceus* (Fig. 25), but it has the distinctive parallelism as to their bases so characteristic of *Cereus*. *E. Engelmanni* (Fig. 26) has the cotyledons much reduced and resembles more nearly some of the *Echinocacti*, and there is possibly some error in my materials. A second division of this genus

includes the prostrate forms of which *E. procumbens* is a good type. The embryos of this species (Fig. 27) show a reduction in the cotyledons and in size, though they still appear *Cereus*-like. Of the third division I have no material: but in the fourth, slender creeping forms, *E. tuberosus* is the type, but its embryos resemble very closely those of the last-mentioned species.

The development of the epicotyl in the few species in which I have followed it shows nothing remarkable, for the adults in this genus share the morphological simplicity of *Cereus*. The leaves at first show a tendency to fall into spirals, and the ribs appear relatively late.

9. Genus **Echinopsis**.

E. Zuccariniana, Pfeiff. and Otto. Figure 29.

E. Eyriesii, Pfeiff. Figure 30.

E. multiplex, Pfeiff. and Otto. Figure in Pfeiffer and Otto, IV.

This genus is very close to the columnar *Cerei*, and really represents very short, many-ribbed forms of that genus. The germinated embryos as shown in *E. Zuccariniana* (Fig. 29) and *E. Eyriesii* (Fig. 30) possess remarkably slender cotyledons and an almost globular hypocotyl. The former character suggests some relationship with *Echinocactus*; and indeed Schumann in his recent monograph says, 'Die Gattung steht in der Mitte zwischen *Cereus* und *Echinocactus*.' The adult forms, however, certainly resemble the former much more closely than the latter genus, and it is probable that the connexion with *Echinocactus* is not closer than would result from a separation of *Echinopsis* from *Cereus* near where *Echinocactus* comes off from *Cereus*. In this connexion the embryos of *E. cinnabarina*, which Schumann considers as much *Echinocactus* as *Echinopsis*, would be of great interest.

The epicotyl, as is common in the *Cereus*-like forms, shows nothing of especial interest. In *E. multiplex* eight ribs form at once without any stage with spirally arranged axillary clusters, showing how old and thoroughly fixed is the rib-producing character in this genus.

10. Genus *Rhipsalis*.

R. Cassytha, Gaertn. Figure 31; also in Irmisch, *Botanische Zeitung*, 1876; also Pfeiffer, Fig. 13, Pl. XV.

R. (Lepismium) commune, Pfeiff. Figure in Goebel, Pl. II, Figs. 3 and 4 (misnamed *L. radicans* in explanations; see p. 102 of text); also Pfeiffer, Pl. XVI, Fig. 12.

This very important genus has been fully discussed in a well-known memoir by Vöchting¹ (which curiously neglects the early stages), and more briefly by Goebel. All of the species are small and epiphytic, with joints sometimes ribbed, sometimes cylindrical, sometimes flat. They are, without doubt, derived from slender climbing Cerei. I have been able to study embryos only of the well-known *R. Cassytha*, and figures of no others are in the books, but Goebel has given a very satisfactory account of five other species which he has studied (pp. 102, 103). *R. Cassytha* in its embryo and seedling stages has been exhaustively described and figured by Irmisch in his 'Ueber die Keimpflanzen von *Rhipsalis Cassytha*.'

In *R. Cassytha* the cotyledons are as broad as the hypocotyl, thus recalling *Cereus*, but they are stouter than in that genus and more nearly round than flat in section, and merge more evenly into the hypocotyl. The latter is also proportionally longer than in *Cereus* (Fig. 31). They are clear green in colour. From the epiphytic, and therefore to some extent mesophytic, habit of this genus, one would expect more leafy cotyledons; but perhaps, as suggested for *Epiphyllum*, the xerophytic outweigh the mesophytic influences in the epiphytic life. The figure given by Pfeiffer suggests very much more leaf-like cotyledons than do Goebel's figures, and it is difficult to believe they represent the same species.

In *R. Cassytha* the epicotyl contains at first four distinct ribs, which merge above into the spirally-placed clusters characteristic of this species. In this we have another good illustration of biogenesis; the ribs are no doubt an inheritance

¹ In Pringsheim's *Jahrbücher*, IX.

from *Cereus*, while the spiral arrangement in the adults is a re-development of what is really a primitive character in the family Cactaceae. Goebel shows that several other species of this genus form the beginnings of four ribs: some continue to form them for a time, but *R. commune*, which when adult is triangular, immediately drops one and becomes triangular; while in *R. rhombea* and *R. pachyptera*, which in the adults have very flat, thin phyllocladia, two of the ribs are represented by single polsters only, and the epicotyl from the first is flat in the plane of the cotyledons in precisely the same way as has been described and figured above for *Phyllocactus Phyllanthus*. The exactly parallel character of the mode of formation of the epicotyl in *Phyllocactus* and *Rhipsalis* accompanies a parallelism in the adults in these two genera. This does not in the least mean that these groups have had any direct genetic connexion; probably both have come off from climbing Cerei but quite independently, *Phyllocactus* from *triangularis*-like, but *Rhipsalis* from very slender *flagelliformis*-like forms. The parallelism, then, has come about through modifications due to similar habit working upon a similar morphological basis. In both genera the ribbed character is primitive, and the flattened condition newly acquired, and the working back of the latter into the seedling until finally it quite obliterates the ribbed condition affords some of the best examples and illustrations of the true meaning of repetition of phylogeny in ontogeny yet adduced among plants.

11. Genus *Hariota*.

I have no data, nor does the literature contain any, upon the embryology of this group.

12. Genus *Pfeiffera*.

P. cereiformis, Salm-Dyck. Figure, Pl. IX of Pfeiffer and Otto; also in Goebel, p. 86.

I have not myself studied this genus. The figure given by Goebel shows a short stout epicotyl with stout pointed

cotyledons, in which one can imagine a resemblance to those of *R. Cassytha*, and which also recall *Cereus*. The remarkable figure given by Pfeiffer I do not understand, and think it must represent something abnormal, for the epicotyl as he figures it is like nothing I have seen in this family. Probably the embryos and seedlings would show whether this genus belongs more nearly with *Rhipsalis* or with *Cereus*. Vöchting, reasoning from anatomy, considered that *Pfeiffera* is the nearest living representative of the connecting forms between *Cereus* and *Rhipsalis*.

13. Genus **Echinocactus**.

- E. robustus*, Otto. Figure 6 in Pfeiffer, Pl. XVI.
E. Wislizeni, Engelm. Figure 32.
E. viridescens, Nutt. Figure 33; also in Lubbock, II, p. 8.
E. texensis, Hopf. Figure 34.
E. cornigerus, DC. Figure 36; also in De Candolle (Mémoire), Pl. X, Figs. 5-7.
E. longihamatus, Gal. Figure 35.
E. setispinus, Engelm. and Gray. Figure in Maxwell, p. 29.
E. recurvus, Link and Otto. Figure in Pfeiffer (as *E. spiralis*), Pl. XVI, Fig. 7.
E. ingens, Zucc. Figure 37; also in Pfeiffer, Pl. XVI, Fig. 5; also in Goebel (as *E. aulacogonus*), p. 86.
E. horizontalonius, Lem. Figure 38.
E. phyllacanthus, Mart. Figure in Zuccarini, Pl. II, Fig. 3 (seedling).
E. Williamsii, Lem. Figure 39.
E. myriostigma, Salm-Dyck. Figure 40.
E. capricornis, A. Dietr. Figure 41.
E. lophothele, Salm-Dyck. Figure 42.
E. Scheerii, Salm-Dyck. Figure 43.
E. Simsoni, Engelm. Figure in Engelmann, Simson's Expedition, Pl. II, Fig. 16.
E. corynodes, Otto. Figure in Zuccarini, Pl. I, Fig. III, 3, 4; also Pl. II, 2.

This very large genus contains condensed globular (becoming very short cylindrical), strongly ribbed forms, with the ribs rarely broken to tubercles, giving a transition to *Mamillaria*, and all of true desert habitat. They doubtless have come off from the columnar Cerei low down on the stem, and near *Echinopsis*.

Of the various sub-genera, some of which have been considered in the past as distinct, the one which comes nearest to the Cerei is, no doubt, Schumann's *Euechinocactus*. In

this division I have had no seeds; but *E. robustus*, of which figures of embryos are given by Pfeiffer, belongs here¹. Though in these figures the breadth of the cotyledons cannot be seen, the whole aspect, particularly of his figure *c*, is very *Cereus*-like, thus confirming the primitive position of this sub-genus.

Most important, and typical of this genus, is Schumann's division of *Ancistrocactus*. In it I have studied embryos of *E. Wislizeni* (Fig. 32), *viridescens* (Fig. 33), *texensis* (Fig. 34), *longihamatus* (Fig. 35), *cornigerus* (Fig. 36), while a figure of *E. recurvus* is given by Pfeiffer, and of *setispinus* by Maxwell. It will be noted that all of these figures agree in showing a much swollen hypocotyl with thick, pointed, flat-faced cotyledons which are much less broad than the hypocotyl, and do not merge gradually into it all around, but on the sides and faces are separated by a sharp angle which is at times almost a slight constriction. The cotyledons are smallest in *E. cornigerus*. The form of cotyledons shown in this group seems to be as characteristic for the genus *Echinocactus* as the broad and flatter ones are for *Cereus*, and the constancy of form through this large sub-group implies marked constancy in this character, and hence reliability as a test for affinities. In this group I have followed the development of the epicotyl in *E. Wislizeni*, *texensis*, and a few others. The axillary clusters are at first distinct, but stand in lines, and very soon run together to form ribs. In *E. texensis* new ribs appear among the older ones, starting abruptly with a small piece of rib below a spine-cluster. This occurs also in other species, and shows that in these forms rib-formation has become so fixed that the rib is itself a morphological element. They, together with most

¹ Of this species he figures three very different forms, and draws conclusions therefrom that the form of embryos and seedlings in the same species is very variable. I have only to say that I have never seen in any one of the many species of Cactaceae I have studied any such variation as Pfeiffer figures and describes, aside of course from specimens injured in some way or drawn for want of light. Seeds are apt to mix in the pots, as I have pointed out, and some of his different forms may be different kinds.

other forms of this genus, show the earlier formed spines feathered with fine hairs, which are prolongations of epidermal cells of the spines. This feathering does not occur in *Opuntia*, and not commonly in *Cereus*, or in any of the groups closely related to them, though it occurs also in *Mamillaria* and its relatives. In *E. Beguin*, in the young seedlings, it is particularly well marked, and it is this character intensified which gives us the plumose spines of *Mamillaria Bocasana*. Possibly when well developed it has an ecological use, but otherwise I think it may represent one of those lines of spontaneous variation which have no regard to utility. The subsequent and adult development of the species in this genus is simple, and very closely like that of the columnar Cerei.

Schumann, in his monograph, has placed *E. Scheerii* in this division of *Ancistrocactus*, but its embryology places it with the division *Thelocactus*, under which I shall consider it, and where indeed Schumann, in his *Cactaceae* in Engler and Prantl, originally placed it.

Another division of much importance is Schumann's *Cephalocactus*, in which I have studied *E. ingens* (Fig. 37) and *horizontalonius* (Fig. 38). These two species show embryos very like one another, but very different from those of the division last studied. In both the hypocotyl is very stout and somewhat elongated, and in both it shows a slight flattening, which is perhaps the result of their position in the seed. But the chief peculiarity is in the cotyledons, which, so far from being pointed, are rounded and scarcely raised out of the hypocotyl, and this character is more extreme in *E. horizontalonius* than in *E. ingens*. In fact the latter species, except for its large size, suggests *Anhalonium*, presently to be considered. The early development of the epicotyl in *E. horizontalonius* is shown in Fig. 38 *d*, where the characteristic rounded tubercles are of very unusual form, and the early development of *E. ingens* is much like it, though the tubercles are less rounded and pass at once to ribs. An excellent figure of a young plant at a much later stage is given by Engelmann (Pl. XXXII).

Very closely related to *Cephalocactus* is *Lophophora*, sometimes made a distinct group. It contains the species *E. Williamsii*. The embryos (Fig. 39) are nearly globular, and have very small rounded cotyledons, in this character resembling those of *E. horizontalonius*. The epicotyl in *E. Williamsii* bears rounded tubercles like those figured (Fig. 38 d) for *E. horizontalonius*, though less prominent, and bears small feathered spines. The spines in the adults, though seeming to be absent, are really present in this species, as I have elsewhere shown¹, and the species really represents a form like a young *horizontalonius* (compare Engelmann's figure) without the large spines, and there can be no doubt that it is an *Echinocactus*, closely related to the division *Cephalocactus*.

Another division often given distinct generic rank is *Astrophytum*, of which I have studied embryos of *A. myriostigma* and *A. capricornis* (Figs. 40, 41). Embryos of these two are much alike, and very different from those of any others I have studied. The hypocotyl is swollen, but more on one side than the other, which is due to the position in the seed; and the root, for the same reason, is somewhat on one side. The cotyledons are rather narrow but pointed, though less so than in some other divisions. In the epicotyl the first clusters at right angles to the cotyledons are very prominent, marking the immediate beginning of the ribs, and making the plant, as seen from above, almost quadrangular. The ribs hence develop earlier in this species than in any other I have seen in the family. Two others form over the cotyledons, and these four form the starting-point for four strong ribs which, by the forking of one, soon become five, which distribute themselves over the circumference. In their later growth these two species become less alike. The clusters of characteristic remarkably pitted hairs occur upon young seedlings. The spines in the first-formed clusters are well-developed, but later clusters have them very small.

In the important division *Stenocactus* I have had no

¹ Flora, op. cit., p. 72.

material, nor do I understand the curious figure given for *E. phyllacanthus* by Zuccarini.

In *Malacocarpus* I know only the figure of *E. corynodes* given by Zuccarini. The embryo has very small cotyledons, which are, however, prominent and pointed, on a nearly globular hypocotyl.

In the important *Thelocactus* I have studied embryos of *E. lophothele* and *E. Scheerii* (Figs. 42, 43). Both have nearly globular hypocotyls, with very small rounded cotyledons, and in these respects approach very near to *Mamillaria*, which genus indeed these species, particularly *E. Scheerii*, approach very closely, as is shown by other considerations given in the systematic works. *E. brevihamatus* would be an interesting form to study in this connexion. It is well known that *E. Scheerii* shows clearly the furrow on the upper side of the tubercle which represents the drawing out of the vegetative point by intercalary growth of the tubercle in that region, and this feature becomes of great importance in *Mamillaria*. The earlier tubercles do not show it, but in the development of the epicotyl in *E. Scheerii* it is easy to see how this groove develops ontogenetically. The earlier tubercles show no trace of it, but after some twenty of them are formed, one appears with a tiny groove projecting slightly from the spine-cluster on the upper side of the tubercle; the next shows this a little longer, and the next yet longer, and so on until the groove is complete. But it is not until much older tubercles than these are formed that the flowers first appear.

The fine figure of *E. Simpsoni* given by Engelmann shows pointed and rather large cotyledons, and seems related more nearly to the *Ancistrocactus* group, though its replacement of ribs by tubercles would suggest that it belongs to the division *Thelocactus*. The melting away of ribs into tubercles, however, is a character which can readily reappear again and again, and need not indicate relationship; and the close relationship of this species, emphasized by Engelmann, to *E. intertextus*, a ribbed species, confirms this.

(Genus **Astrophytum**. Treated under *Echinocactus*.)

(Genus **Malacocarpus**. Treated under *Echinocactus*.)

14. Genus **Melocactus**.

M. communis, Link and Otto. Figure in De Candolle, *Revue*, Pl. VI. Also (as *Cactus melocactus*) in De Candolle, *Organographie*, Pl. XLVIII, Fig. 3.

M. amoenus, Hoffm. Figure in Zuccarini.

M. rubens, Pfeiff. Figure in Pfeiffer, Pl. XVI, Fig. 9.

M. Lehmanni, Miq. Figure in Miquel, *Monographia*, Pl. II.

This genus includes nearly globular strongly-ribbed forms especially characterized by a strong cephalium. I have had no seeds, and the figures above cited are hardly detailed enough to allow conclusions to be drawn from them. All show a globular, or nearly globular, hypocotyl. *M. amoenus* in Zuccarini's figure shows large thick pointed cotyledons, recalling the *Ancistrocactus* division; while *M. rubens*, as given by Pfeiffer, suggests rather *Cephalocactus*, an altogether unlikely difference between these two; while *M. Lehmanni*, in Miquel's picture, is different from the other two. De Candolle's figure of *M. communis* is of interest in showing below the huge swollen stem, two projections which he mistook for cotyledons, but which, as Miquel¹ pointed out, are not so, but were probably two rootlets in that position. The nearly globular structure which he mistook for plumule is combined hypocotyl and epicotyl, with the cotyledons invisible. The presence of a lateral root in that position in Miquel's figure of *M. Lehmanni* confirms this. The beginning of growth of the epicotyl shown by Miquel is insufficient to give a clear idea of it.

15. Genus **Leuchtenbergia**.

L. principis, Fisch. Figure 44.

In this genus is but a single species, a rare and remarkable plant with very long, almost leaf-like, tubercles bearing papery

¹ Ann. Sci. Nat., Bot., 2nd Ser., XIV, 62, 63.

spines and flowers at their summits. The germination and early stages have not been described. I have obtained seeds from Mr. William Tell, of Austin, Texas, who obtained them from a correspondent in Mexico; and as living plants of this species have come from the same source, the identification is to be trusted. The embryo (Fig. 44) is altogether *Echinocactus*-like, with the pointed cotyledons so characteristic of that genus. The hypocotyl is deep red in colour though the first leaves of the epicotyl are white, an unusual feature. The epicotyl develops first two leaves at right angles to the cotyledons, which bear spine-clusters in their axils, and both leaves and clusters are soon carried up on the tops of strongly developed cylindrical tubercles, which, except for those of *Anhalonium*, are larger than those of any Cactaceae I have seen, and this fact is in itself confirmation of the identity of my seeds as of this species. A third tubercle then develops at right angles to the first pair, and later a fourth. The spines are also *Echinocactus*-like, much feathered with hairs, and very different from those of the adult plants, and this feature persists into seedlings of considerable size, as I have seen in a specimen formerly described by me¹. At this writing my specimens have not advanced beyond the stage shown in the figure 44 c, but I hope to obtain from this material the full life-history of this most remarkable of the Cactaceae. But all features show its close connexion with *Echinocactus*, though I cannot say with which division. The nearest approach to the remarkable tubercles of the epicotyl that I have seen is in *E. bicolor*, which has large spirally-arranged tubercles, though they are not so large as in *Leuchtenbergia*.

16. Genus **Mamillaria**.

M. elephantidens, Lem. Figure 45.

M. latimamma, DC. Figure in Goebel, p. 86.

M. radiosa neo-mexicana, Engelm. Figure 46.

M. centricirrha, Lem. Figure in Schumann, in Engler and Prantl, p. 170.

¹ Flora, op. cit., p. 74.

M. Sempervivi, DC. Figure 47.

M. Goodridgii, Scheer. Figure 48.

M. glochidiata, Mart. Figure in Zuccarini, Pl. I, Fig. I, 4.

M. tentaculata, Link and Otto. Figure in Pfeiffer, Pl. XVI, Fig. 8.

This very large genus contains the smallest species of the family, and consists of globular to short cylindrical forms with spirally-arranged tubercles (and never ribs), with spine-clusters at the ends of the tubercles and flowers in their axils. In one division the tubercles have a longitudinal furrow along the upper face, and these connect with the furrowed *Echinocacti* of the division *Thelocactus*. In the other division the furrow is wanting. The explanation of its presence in the one group and its absence in the other I have elsewhere given¹.

Throughout this genus the embryos show a very succulent and usually nearly globular hypocotyl, with cotyledons always small, sometimes indeed so small as to have been considered wanting. They are usually rounded, but sometimes more or less pointed.

In the division with the furrow I have had seeds only of *M. elephantidens*, which have produced an embryo of remarkably large size (Fig. 45), with an elongated hypocotyl and rather broad rounded cotyledons, suggesting the *Cephalocactus* division of *Echinocactus*, with which however it is scarcely at all possible that *Mamillaria* has directly any affinities. Since Goebel's figure of *M. latimamma* shows the same elongated hypocotyl, it is possible this is a common characteristic of this division. In this connexion the embryos and seeds of *M. macromeris* would be of especial interest. If this furrowed division of *Mamillaria* is derived, as other considerations seem to show that it is, from the *Thelocactus* division of *Echinocactus*, then the large size and elongated hypocotyl must be re-acquired and not primitive, for neither character appears in *E. Scheerii* (Fig. 43), a good representative of *Thelocactus*. The epicotyl in *M. elephantidens* develops the clusters spirally on short tubercles, with no

¹ In *Flora*, op. cit., p. 75.

trace of rib-formation. I have not observed the beginning of the splitting of the vegetative points on the tubercles, but no doubt it comes about there precisely as in *E. Scheerii*.

M. radiosa neo-mexicana belongs also with the grooved forms; its cotyledons (Fig. 46) are pointed, a feature very rare in this genus, but their small size would prevent any confusion of this with a small *Echinocactus*.

In the furrowless division occur the smallest embryos, and of the several species I have studied all are much alike. As shown by *M. Goodridgii* and *Sempervivi* the hypocotyl is very swollen, larger above the middle and with small rounded cotyledons. In the development of the epicotyl in this division I have not yet determined the very important point of the exact mode of appearance of the vegetative point which in the adults stands in the axils of the tubercles and produces the flowers. Theoretically this ought to appear as it does in the furrowed *Echinocacti* and furrowed *Mamillariae*, i.e. the point which on the first formed tubercles is single should on some of the later become stretched out, and in still later ones the stretching should go yet farther so as to separate it into two parts, and so on, the stretching taking place at earlier and earlier stages in the growth of the mamilla until finally it occurs before this has become raised from the main stem.

17. Genus *Anhalonium*.

A. fissuratum, Engelm. Figure 49; also in Goebel, Pl. II, Fig. 7.

A. prismaticum, Lem. Figure 50.

This small, but morphologically very important, genus contains only small somewhat *Mamillaria*-like forms with angular tubercles and no visible spines. They are flattened above and in shape like a top with the greater part buried in the earth. The tubercles show two types, one with a furrow and one without, in this showing parallelism with *Mamillaria*.

Important though this genus is, but a single good figure

of its embryos or seedlings has been published, that given by Goebel, cited above. In the embryos of both *A. fissuratum* and *A. prismaticum* which I have studied, the hypocotyls are very succulent and somewhat elongated. The cotyledons are hemispherical, merging without visible boundary into the hypocotyl, rather broad, so that the groove between them is much longer than in any of the *Mamillariae* I have studied (compare Fig. 49 *c* and 50 *b* with 47 *c* and 48 *c*), and in this respect, as well as in the way in which they merge without break into the hypocotyl, they are much more like *E. horizontalonius* (Fig. 38) than like any *Mamillaria*. The rather abrupt ending of the groove and its slight broadening there is also characteristic of both *Anhalonium* and *E. horizontalonius*, and it is not marked in any *Mamillaria* I have seen. This fact however can hardly mean relationship, but merely coincidence, for the two vegetative points to the tubercle show a close relationship with *Mamillaria* and an origin from *Thelocactus*. I think it most likely that *Anhalonium* has come off from *Thelocactus* independently of, but near to, *Mamillaria*.

The development of the epicotyl in both species is remarkable. The first tubercles are long and slender (Fig. 49 *d* and 50 *c*; also Goebel, Plate II, Fig. 7), and bear several feathered spines at their tips. The whole appearance of these tubercles strongly recalls that of the adult tubercles of *Leuchtenbergia*, and it is very difficult indeed to resist the belief that they are in some way connected. But the markedly pointed cotyledons of *Leuchtenbergia* in contrast with the very low rounded ones in *Anhalonium* makes any direct relationship well-nigh impossible, and we must attribute the resemblance of the tubercles to parallelism and not to any direct connexion. On the other hand, following the hint given by the cotyledons, it is not at all difficult to imagine the pronounced tubercles of a form like *E. horizontalonius* (Fig. 38 *d*) growing out into the tubercles of *Anhalonium*. As the epicotyl becomes older the new tubercles become broader and flatter, and pass gradually over into the well-known angular tubercles of the adults.

I have not yet been able to determine the important point of the mode of formation of the inner vegetative point, but have no doubt it comes about as in *Thelocacti* and *Mamillaria*. It should be particularly plain in *A. fissuratum*.

A feature which is prominent in this genus and not found in any other Cactaceae, so far as I know, is the early growth in succulence of the root along with the hypocotyl. The root, shortly after the embryo is out of the seed, instead of remaining small, begins to swell not only as fast as, but often faster than, the hypocotyl. For a time a constriction marks the boundary between the two (shown in Fig. 50c), but later this disappears, and in the adult plant the true epicotyledonary stem is extremely short, while the great visible part below the tubercles is really root, as Goebel has already surmised. This unusual succulence of the root is no doubt correlated with the half-buried habit of the plant. Succulent roots of another kind occur also in *Cereus tuberosus*, *Echinocactus nupinus*, and perhaps other species.

18. Genus *Pelecyphora*.

This genus, with its single odd species, is but slightly removed from *Mamillaria*, with which it is no doubt connected through a form like *M. micromeris*, which somewhat closely approaches it in many characters. From my seeds several embryos were produced which, however, did not differ from those of the smaller kinds of *Mamillaria*. The cotyledons were very minute on a nearly globular hypocotyl.

SUMMARY OF THE FORM-FACTORS OF EMBRYOS AND SEEDLINGS.

We may now group together the facts just described and note to what conclusions they point. Taking first the germinated embryos, it is plain that as a whole there is, from *Pereskia* through *Cereus* and *Echinocactus* to *Mamillaria*, a progressive condensation in bulk, and diminution of surface

brought about by the increasing approach to a spherical form of the hypocotyl, and diminution of the cotyledons. The only marked exception to this is found in the Platopuntiae, climbing Cerei, Phyllocacti, and *Rhipsalis*; but in these cases, as I have already pointed out, there is in common a return to a more mesophytic habit, which amply explains the larger spread of surface and consequent relative increase of cotyledon and diminution of hypocotyl. This progressive condensation of the embryos, however, runs strictly parallel to the condensation in the adults, and in both cases is least in *Pereskia*, more in *Opuntia*, yet more in *Cereus*, still more in *Echinocactus*, and most of all—indeed reaching near to its utmost possible theoretical limit—in the nearly globular forms in *Mamillaria*. In the adults this condensation is due to adaptation to a more and more desert habitat. There is however this important difference to be noted between the two series, that in the progressive condensation the embryos lag behind the adults, and this is plainest in the diminution of the cotyledons. Thus in *Opuntia* the leaves are very evident in both adults and embryos, but even here the cotyledons have diminished from those of *Pereskia* less than have the leaves of *Opuntia* diminished from those of *Pereskia*; in *Cereus* this is yet more evident, for here the cotyledons are still large and broad, while the leaves of the adults are reduced to small scales and often are but tiny rudiments. In *Echinocactus* the cotyledons are still somewhat prominent, but the leaves of the adults are represented only as microscopic rudiments soon merging into the stem in later growth, while in *Mamillaria* the leaves are as in *Echinocactus*, and the cotyledons themselves are nearing the vanishing-point. It is true there are some seeming exceptions to this rule, as in the *Cephalocactus* division of *Echinocactus*, but in reality, as this is one of the most condensed of the divisions of the genus, it illustrates and does not contradict the rule. Indeed, as far as my material allows of a judgment, it seems plain that the same principle applies within the limits of each genus, i. e. the more condensed the adults, the more succulent the hypocotyl

and the less developed the cotyledons, and the lagging of the embryos behind the adults is probably true here also. The latter principle may be found true where a single species of a given genus suddenly deviates from the normal for that genus. This lagging behind amply explains why adult and embryo do not always correspond. But however it may be in details, I think there is no doubt that the ground-form of the embryos is imposed by the ground-form of the adults, though not so much by the immediately preceding as by the more remotely preceding ancestors.

When we turn to consider the dynamics of the connexion between adults and embryos, exactly how it is that the former can influence the latter, we face a difficult question. At a first glance one might explain it as due to the fact that as embryos and adults live in the same places, and hence under much the same conditions of dryness; and since condensation or spread of surface is chiefly determined by dryness of the habitat, therefore the spread of surface must correspond in adults and embryos, i. e. through independent adaptation of each to the same external conditions. But only a little observation is needed to disprove this: for on the one hand the germinated embryos live under very different external conditions from the adults, in that they are growing only at the time of the yearly rains; and on the other, *Cereus*, *Echinocactus*, *Opuntia*, and *Mamillaria* embryos grow side by side on the same desert and thrive equally well, though of such extremely different forms. Direct adaptation therefore to the surroundings, except in the case of those with a re-acquired mesophytic habit as *Phyllocactus*, can have but little to do with the form of the embryos. Again, one may suppose that the shape of the seed determines that of the embryo; but this simply replaces the difficult question at issue by the very much more difficult one of how the adult plant is able to influence the form of its seeds so that these will mould an embryo answering in form to itself. Moreover the relative size of cotyledons and hypocotyl is not in the least degree affected by the shape of the seed. In some minor particulars however,

I think the seed does influence the form of the embryo, as for example in the difference of size between the two cotyledons in many species, particularly *Platopuntiae*. Observation shows that the smaller is on the concave side, covered by the convex larger one. Again, possibly the forking of the tip of one cotyledon in *Cereus Bonplandi* may be due to this, and certainly the one-sidedness of the root in *E. myriostigma* and *E. capricornis*, and the slight asymmetry in both planes noticed in nearly all cotyledons and hypocotyls, including the slight pointing to one side of the pointed cotyledons in *Cereus* and *Echinocactus*. But such are very minor effects.

Of course in any given generation the form of the embryo, aside from slight irritable responses to light, &c., is determined by heredity. But heredity is but the sum and resultant of past experiences, and hence in the present case is largely a study of the facts of past environments. This suggests an explanation which I believe to be the true one, i.e. that the form of the adults, like any other character, once acquired—it matters not for our present purpose how—as it becomes more and more fixed and intensified, tends to work back into earlier and earlier stages in the ontogeny of the successive individuals; until finally, a character adaptively acquired by the adults works back into the epicotyl, of which I have shown many cases in this paper, and finally into the embryo itself. But while the working back into the epicotyl may be comparatively rapid, the passage into the embryo seems to be very slow, as is explained by the considerable lagging of those behind the adults, due no doubt to the fact that the embryos have a set of activities of their own in their early life which keeps them from being too plastic to other influences working upon them.

In summary then the shapes of the embryos in Cactaceae seem to be determined by three leading factors. First, the ground-form of the embryos answers in general to the ground-form of the adults, and alters with the latter by the working back of newly acquired characters. Second, there is an occasional expansion of surface, with increased cotyledons

and relatively diminished hypocotyl, allowed by exposure to more mesophytic habitat. Third, some minor details of outline are due to the position of the embryos in the seed.

The form-factors of the epicotyl are simpler than those of the embryos, and from what has been said in the preceding pages it will appear that we have in the epicotyls remarkably clear examples of the working back of the characters of the adults. The first leaves of the epicotyl (very small except in *Pereskia* and *Opuntia*), and indeed often the cotyledons themselves, produce axillary buds which at once develop the characteristic spine-clusters. This is true in all of the species that I have examined throughout this family; the very first formed axillary structures are true spines. There seems to be abundant evidence that the spines in this family really are metamorphosed leaves and not emergences or other dermal or epidermal structures; and recalling the principle of repetition of phylogeny in ontogeny, one would expect to find in these first formed axillary clusters some trace of a leaf-nature showing in the spines, which is never the case. This fact, however, is not necessarily evidence for a non-phyllome origin of the spines, since it may, and probably does, mean simply that the production of leaf-spines from axillary buds is very old, preceding the differentiation into genera, which indeed *Pereskia* proves to us is the case. It may be that this ancient habit of producing axillary spine-clusters is the oldest existent characteristic of the family, and may yet give the key to its still unknown phylogeny. The epicotyl of course tends to repeat its hereditary characters, and does so until these are obliterated by the working back of new ones, and it is the different stages of the working back of these which give us the very fine examples of repetition of phylogeny in ontogeny which appear in the climbing Cerei, Phyllocacti, *Rhipsalis*, &c. Taking the family as a whole we may picture successive waves, as it were, of characters acquired by adaptation in the adults sweeping back into the later seedlings, and wiping out earlier characters. The more superficial features of these waves do not however affect the

embryo, for the transition from epicotyl to embryo forms a barrier against which the crests of the waves are broken, and behind which only the influence of the ground-swell, as it were, is felt. It is the condition of these waves at this moment which gives us the present embryology of the family.

PHYLOGENY OF THE GENERA.

We may now summarize what the preceding facts indicate as to the phylogeny of the genera. Taking them all into account, together with others drawn from the comparative anatomy of the adults, and to some extent others from the floral and fruit anatomy, the relationships appear to be as expressed in the following diagram. The outline of the main trunks and branches is intended to express the appearance of the whole group as it appears to us at the present day, while the axial lines are intended to represent the probable historical relations of the different genera, their place and relative time of origin from one another.

All considerations show that *Pereskia* is nearest to the original stem-form of the family, and that *Opuntia* is derived from it, though the connecting forms still existing make of them a single trunk. From *Opuntia* came off *Cereus*, and our columnar Cerei are nearest to the primitive form as their cotyledons show, though the original Cerei must have been somewhat tubercled after the manner of *Opuntia* rather than strongly ribbed. From columnar Cerei came off in succession *Echinopsis*, *Echinocereus*, and *Pilocereus*, and from the last *Cephalocereus*. Well down in the stem of the columnar Cerei came off the climbing forms, giving another incipient genus, and from these came first of all *Pfeiffera*, with its early branch *Rhipsalis*, and later *Hariota*, and *Phyllocactus* with its branch *Epiphyllum*. From the columnar Cerei again, but low down and near *Echinopsis*, came off *Echinocactus*, which soon gave off as a branch the furrowed forms which gradually changed from the ribbed to the tubercled forms. These tubercled Echinocacti, with their furrow, gave rise to the

Mamillariae with a furrow, and these in turn by its disappearance to the smooth tubercled forms, and from these came finally the most specialized of all of the genera, *Pelecypora*. Returning to the Echinocacti, we find *Melocactus* as a later branch, and as earlier ones *Leuchtenbergia* and *Anhalonium*. The relations of the two latter are somewhat

puzzling. Though the embryos of *Anhalonium* in some ways recall the *Cephalocactus* division of *Echinocactus*, yet the presence of two growing-points in each tubercle places it near *Mamillaria* and relates it to *Thelocactus*, and it has probably come off from the latter near to but independently of *Mamillaria*. As to *Leuchtenbergia*, the pointed cotyledons

and single growing-points to the tubercles suggest an origin from *Echinocactus* in some division other than *Thelocactus*, but at present I have no further data. It must come from near a form with the ribs replaced by tubercles.

Since my materials were chosen especially to represent the embryology of the genera and leading groups, and hence only rarely include closely related species, it does not give a fair idea of the extent to which embryology can be used in this family as a clue to the relationships of closely related or doubtful species. Obviously a large amount of accurate data and a thorough knowledge of the principles controlling form-changes must be accumulated, and the present study needs to be supplemented by a minute study of the embryology of groups of related species, and this I hope to make in the form of morphological life-histories of certain species. I have no doubt that the very stable characters of the embryos, and the remarkable way in which the epicotyls so often show the characters of the immediate ancestry, will make them of great systematic importance. And when to this we add the fact that most of the genera and many of the species in this new family are still in the nascent state, and that most of the connecting links are still in existence, I think it will be possible to recover the phylogeny of genera and species in this family to an altogether rare degree of completeness.

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EXPLANATION OF FIGURES IN PLATE XXVI.

Illustrating Professor Ganong's paper on the Cactaceae.

All figures drawn from nature with camera lucida. The species of *Pereskia* and *Opuntia* are natural size; all others are two and a half times natural size, unless otherwise explained. Letters *a*, *b*, *c* designate different views of the same specimen. Average specimens were always selected for drawing.

Fig. 1. *Pereskia aculeata*.

Fig. 2. *Opuntia bernardina*: *c*, cross-section of cotyledon $\times 5$; *d*, do. of hypocotyl $\times 5$; *e*, specimen from which buds were removed, and which had grown to double size.

Fig. 3. *O. echinocarpa*: *c*, specimen bearing a bud in the fork near the tip of a cotyledon.

Fig. 4. *O. basilaris ramosa*.

Fig. 5. *O. vulgaris*: *c*, cross-section of cotyledon $\times 5$; *d*, do. of hypocotyl $\times 5$.

Fig. 6. *O. Ficus-indica*.

Fig. 7. *O. Engelmanni occidentalis*.

Fig. 8. *Cereus Thurberi*.

Fig. 9. *Cereus giganteus*.

Fig. 10. *C. peruvianus*.

Fig. 11. *C. Hystrix*.

Fig. 12. *C. Bonplandi*: *c*, older specimen showing removal of axillary buds away from epicotyl.

Fig. 13. *C. Martianus*.

Fig. 14. *C. grandiflorus*.

Fig. 15. *C. nycticaulis*.

Fig. 16. *C. spinulosus*.

Fig. 17. *C. triangularis*: *c*, specimen issuing from seed to show hair-collar and basal swelling $\times 5$; *d*, older specimen to show do. $\times 5$.

Fig. 18. *Phyllocactus Ackermanni*.

Fig. 19. *P. anguliger*.

Fig. 20. *P. phyllanthoides grandiflorus*.

Fig. 21. *P. Phyllanthus*: *a*, *b*, younger specimen; *c*, *d*, older specimen.

Fig. 22. *Pilocereus Houletii*.

Fig. 23. *Cephalocereus senilis*.

Fig. 24. *Echinocereus pectinatus rigidissimus*.

Fig. 25. *E. phoeniceus*.

Fig. 26. *E. Engelmanni*.

Fig. 27. *E. procumbens*.

Fig. 28. *E. tuberosus*.

Fig. 29. *Echinopsis Zuccariniana*.

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- Fig. 30. *E. Eyriesii*.
- Fig. 31. *Rhipsalis Cassytha*.
- Fig. 32. *Echinocactus Wislizeni*: *d*, older specimen.
- Fig. 33. *E. viridescens*.
- Fig. 34. *E. texensis*.
- Fig. 35. *E. longihamatus*.
- Fig. 36. *E. cornigerus*.
- Fig. 37. *E. ingens*.
- Fig. 38. *E. horizontalis*: *d*, older specimen to show epicotyl.
- Fig. 39. *E. Williamsii*.
- Fig. 40. *E. myriostigma*.
- Fig. 41. *E. capricornis*: *c*, older specimen.
- Fig. 42. *E. lophothele*.
- Fig. 43. *E. Scheerii*.
- Fig. 44. *Leuchtenbergia principis*: *c*, older specimen to show tubercles.
- Fig. 45. *Mamillaria elephantidens*.
- Fig. 46. *M. radiosa neo-mexicana*.
- Fig. 47. *M. Sempervivi*.
- Fig. 48. *M. Goodridgii*.
- Fig. 49. *Anhalonium fissuratum*: *d*, older specimen to show tubercles.
- Fig. 50. *A. prismaticum*: *c*, older specimen to show tubercles and smaller root.

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