

The Origin of Plant-Structures by Self-Adaptation to the Environment, exemplified by Desert or Xerophilous Plants. By the Rev. GEORGE HENSLOW, M.A., F.L.S., &c.

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(PLATE XII.)

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I. *Introductory Observations on the Characteristic Features of Plants of Deserts and Arid Countries.*

THE general *facies* of the flora of a country with a relatively dry soil and atmosphere is very observable; and when it is found to be the same in widely separated countries—as in the desert regions of North Africa, in the arid districts of India and Thibet, of Afghanistan, in parts of Australia, in S. Africa, in Brazil*, &c.,—

* For an interesting description of the plants growing in a very dry region of Brazil, but probably of less intensity than that of the African deserts, the reader is referred to a paper by M. Ed. Warming entitled, “Lagoa Santa (Brésil), Étude de Géographie Botanique,” *Rev. gén. de Bot.* 1893, p. 145. Many peculiarities mentioned by that author correspond more or less exactly with those I have described in this paper.

Grisebach also compares the S. African region (Kalahari) with the Soudan:—“Les autres formes végétales sont les mêmes qu’on retrouve dans d’autres steppes et déserts, ou bien elles signalent l’intime affinité du Kalahari et du Soudan. À la première catégorie appartiennent les plantes grasses (*Euphorbia*, *Mesembryanthemum*), les végétaux bulbeux qui ouvrent rapidement leurs fleurs après les orages d’été (ex. *Amaryllis*); parmi les arbustes, les formes de *Spartium* (ex. *Lebeckia*), de l’Oléandre (par l’entremise d’une Rubiacée, le *Vangueria*), et du Myrte (par une Ébénacée, l’*Euclea*); enfin, les arbustes à feuilles velues, particulièrement fréquents dans la savane” (*Tarchonanthus*).” (*Vég. du Globe*, vol. ii. pp. 255, 256.)

so that these several countries afford either the same or "representative plants," one infers (but of course at first merely on *à priori* grounds) that most probably similar causes have produced these similar results. A closer inspection shows that the similarities in the vegetative system of such plants, which often have no affinity between them whatever, can be carried down into the minutest details of histological structure; and that a large proportion of such structures at least are always serviceable to the plants in resisting the deteriorating effects of an insufficient supply of water, as well as of an excess of radiation and other hindrances to such vigorous growth as is maintained in moister climes.

We thus begin to suspect, indeed very strongly, that the various peculiarities (such, *e. g.*, as the densely hirsute clothing and the consolidation of the mechanical tissues) are the direct results of the dry climatal conditions surrounding the plants; and that the unfavourable environment actually brings about the production of just those kinds of structure which are best able to resist the injurious effects of the climate, and so enables the plant to survive under them. Such, at least, is the result of my own observations on the plants of the Egyptian deserts.

The distribution of similar forms of plants under similar conditions illustrates another fact. We speak of "chalk-loving," "sand-loving," and other kinds of plants frequenting special environments; but these phrases seem to be, to a great extent, misnomers. Plants by no means all or always "love" the soils alluded to, in which they are often found. Many flourish quite as well, if not better, in a totally different soil. Having, however, been located in them for many generations, they have become so adapted to the peculiar conditions of the soil and climate, *by assuming such structures as are the best under the circumstances*, that they now succeed in them; but at the same time many are always tacitly protesting, so to say, against their environment; for they at once show how much more vigorous they can become when they are grown in a different and more congenial soil*.

Similarly we might just as well speak of desert-loving plants, corresponding to the term "xerophile;" but we know what an intense struggle for existence they have to maintain. Nevertheless they have become so inured to their difficulties, that

* See Battandier's observations, Bull. Soc. Bot. de Fr. 1887, p. 189

when seeds of desert plants are sown in ordinary garden-soil many fail to grow at all*; just as, while some water-plants grow more vigorously on land, others cannot live if exposed to the air. Or, again, with regard to many maritime plants, they will grow quite as well, if not better, away from the sea, either by altering their structure as Samphire does, by developing flat and thin leaves, or else they may retain their usual features, this being due to heredity. Thus *Salsola Kali*, the Prickly Glasswort of our sandy sea-shores, has become one of the worst weeds ever introduced into American wheat-fields. One year's damage in Dakota alone is estimated at 2,000,000 dollars. It is described as taking complete possession of the soil, while its spiny nature makes it objectionable to horses and other animals (Farmer's Bulletin, No. 10, 1893). In this case the plant has not lost its spines by growing in a richer soil, and illustrates the fact that hereditary influences often, if not always, *tend*, more or less, to resist the effects of a changed environment. And just as new adaptations can easily become fixed in some cases, but with great difficulty in others, as in cultivating wild plants; so, conversely, while some features are instantly lost, others are as rigidly retained, though it may be in a modified form. What, however, may be called the general "plasticity" of plants is now so well recognized, that it affords us a perfectly adequate means in accounting for the self-adaptation of plants, although it is far from being necessarily applicable in every feature.

I will now give some special characteristic features of desert plants, and then compare them with others growing in arid districts to show the more or less great similarity which prevails.

II. *General Morphological Characters*†.

On first entering the desert near Cairo, where plants are to be found,—namely, along the lines of watercourses, which are

* According to Dr. E. Sickenberger in Cairo and to my own experiments at home.

† The best work I am acquainted with on the structure of desert plants is one by Dr. G. Volkens, entitled "Die Flora der aegyptisch-arabischen Wüste auf Grundlage anatomisch-physiologischer Forschungen dargestellt," and the epitome "Zur Flora der aegyptisch-arabischen Wüste, eine vorläufige Skizze." He gives eighteen plates (4to) illustrative of the anatomy of a well-selected series of types. I have fortunately been able to collect a large number of the same plants myself in the deserts around Cairo; and for nearly all the

dry all the year round excepting in February and March, while no plants occur on the higher ground at all,—the general appearance is of low bushes or isolated tufts of a nearly uniform grey colour. The plants are never crowded or cover the ground like an English roadside. In other words, they do not struggle for an existence with one another, but only with their inhospitable inorganic environment*. The grey colour is mainly due to intense hairiness, which subdues the green hue of chlorophyll. A few plants only, comparatively speaking, have no hair, and are consequently greener, as the species of *Zygophyllum*, which are fleshy-leaved plants; but a coating of wax is of frequent occurrence, and this aids in giving a glaucous hue.

The hair and the wax, as well as the fleshy character of the leaves, are adaptations to arrest the loss of water by transpiration during the summer.

III. *Spinescent Characters.*

The next obvious feature is the stunted character of the bushes, three feet being about the maximum height (*Zilla myagroides*), with gnarled stems at the base. This is often coupled with a spinescent character, either in the branches (as *Zilla*), foliage (as *Echinops*), or stipules (*Egonia*) and bracts (*Centaurea*). These features are, we may say undoubtedly, in the

rest I am greatly indebted to the kindness of Prof. E. Sickenberger, of the School of Medicine, Cairo; so that I have been able to examine anatomically nearly the whole series described by Dr. Volkens, and have thus been able to supplement his observations in some degree in points he has not recorded. I would also refer the reader to the writings of M. P. Maury, Assoc. Franç. pour l'Avancement des Sci., Congrès de Toulouse, 1887; also Morot's Journ. de Bot. ii. 1888, Rev. Bibl. p. 101.

* Similarly of the desert regions of Beluchistan, Dr. Aitchison says:—"The barren character of the country and the want of indigenous trees is due to the extreme dryness of the soil and aridity of the atmosphere.... The struggle of plant-life for existence is great. The plants which are seen to exist through it all are either annuals or those possessing great root-stocks, tubers, tuberous roots, rhizomes, bulbs, or other such structural developments as assist them to baffle and survive through the extremes of temperatures."—"A Summary of the Botanical Features of the Country traversed by the Afghan Delimitation Commission during 1884-5," Trans. and Proc. Bot. Soc. Edinb. 1889 (read April 11th, 1889), p. 42.

main due to a want of water *, which always prevents the formation of cellular tissue ; while this deficiency of parenchyma is associated with a hardening of the fibro-vascular mechanical elements. The converse conditions are sometimes witnessed, *e. g.* in a plant of *Zilla myagroides*, which was the only species raised from seed out of many sown in the Botanic Garden of Cairo by Dr. E. Sickenberger. It not only bore well-developed leaves, but the spines, though formed through the forces of heredity, were very slender and subflaccid instead of being intensely rigid.

As an interesting illustration of a highly spinescent plant belonging to the Cucurbitaceæ, an order in which it would be least expected, is the Narras plant of Caffraria (*Acanthosicyos horrida*). It grows on the sandy downs on the sea-coast. It has no leaves, but double spines studded all over the branches, forming impenetrable bushes which spread widely and attain the height of a man. It is curious that although the seeds germinate readily, all attempts to cultivate it in Europe have failed ; just as Dr. Sickenberger and I failed with the numerous desert plants of Egypt, for, as stated, he was only successful with *Zilla myagroides*. Another remarkably spinescent plant is *Aciphylla squarrosa* of the order Umbelliferae, described by Sir J. D. Hooker in his 'New Zealand Flora,' vol. i. p. 87.

The hardening of the mechanical tissues generally, which so often results in special spiny processes, is brought about by drought and other conditions of the environment, and is one of the best means for resisting the intense heat of the desert.

M. de Candolle † called attention to this fact. He says :—"Very hard wood resists heat because it encloses but little aqueous juices, so there is but little to evaporate." Similarly he remarks upon the great value of cork for resisting both extreme

* So Mr. Belt, in 'The Naturalist in Nicaragua,' says (p. 46) :—"This spiny character of vegetation seems to be characteristic of dry rocky places and tracts of country liable to great drought."

Similarly Grisebach, describing the flora of Kalahari, South Africa, and alluding to spinescent species of *Acacia*, says :—"Tous ils portent des épines qui, chez *A. horrida*, ont 5 à 8 centimètres de longueur. La division limitée du feuillage et l'exiguïté des surfaces sont autant de traits en rapport avec le développement des organes piquants et de la sécheresse du sol" (*La Végét. du Globe*, ii. p. 252). He also alludes to similar features of the Tibetan flora (i. p. 614).

† "Essai élémentaire de Géographie Botanique," Dict. des Sci. Nat. vol. xviii.

cold as well as extreme dry heat; as there will be a greater number of cells in the layers of cork filled with air, thus making bad conductors between the external air and the cambium layer and alburnum. Thus old trees resist cold better than young ones. On the other hand, endogenous trees having no bark only grow in warm climates. In some, as the Date, the bases of the leaves, especially if they decompose into a hairy covering, may supply the place of it.

The evidence in support of the assertion that spines are the direct outcome of the environment also rests upon the well-known fact that there are many instances of plants losing their spines altogether when grown under other circumstances. This variableness in the spinescent character of plants is no new observation. Thus, G. G. Küchelbecker, in a 'Dissertatio botanico-physica de spinis plantarum' (A.D. 1756), wrote as follows:—"Sunt autem quaedam plantae quae eundem semper et vbique seruant in extensione superficiei habitum, cum contra ea aliae, pro varia soli et culturae indole, formam hanc alias sibi propriam deponant, vel tamen maximam sui partem mutant, ita vt, quae glabrae antea erant, nunc inaequalitatem magis minusue eminentem induant, atque suum plane deposuisse videantur habitum superficiei pristinum" (pp. 9, 10). He then refers to Linnæus's *Philos. Bot.* p. 215, § 272:—"Spinosae arbores cultura saepius deponunt spinas in hortis Hirsuties loco et aetate facillime deponitur." Again, *l. c.* p. 247, § 316:—"Solum mutat plantas, vnde varietates enascuntur, et, mutato eodem, redeunt. Hinc *Acanthi* molles et aculeati; *Cinarae* aculeatae et non aculeatae."

Similarly, at the present day Pears, species of Rose and of *Prunus*, &c., are well known to lose their spines under cultivation. *Ononis spinosa*, L., has an excessively spiny variety, *horrida*, growing in maritime sands. It is much less spiny in waste places by roadsides, &c., and becomes the variety *inermis* elsewhere. This latter form of the "subspecies" *repens* can be produced, temporarily at least, at will; for when the ordinary spiny form *O. spinosa* is grown either in a very rich soil or with an abundance of water and a moist atmosphere, whether the plants be raised from cuttings or seeds, they gradually lose their spines; those first formed under these conditions are much reduced in size and in rigidity. Hereditary influence is too strong to arrest them at first altogether; although none are produced later on vigorous

shoots growing in a saturated atmosphere. They reappear as soon as the same plants are allowed to grow in the ordinary way. It may be added that when the spines are arrested, the peculiar odour of *O. repens* is present, and the flowers also are larger and are like those characteristic of that subspecies *.

M. Lothelier † carried out very similar experiments with other spinescent plants. He thus found that by growing *Berberis vulgaris* in a moist atmosphere it bore no spinescent leaves, as the parenchyma was well-formed between the ribs and veins; but in a perfectly arid atmosphere it bore spines only. Intensity of light also favoured their production. He found from a microscopical examination that in a section of a spine exposed to moist air the vessels of the xylem are few in number and the pericycle is not lignified. In a dry air the xylem forms a continuous ligneous circle and the pericycle is also lignified. I have myself repeatedly corroborated this observation of the special consolidation of fibrous tissues in several instances in different species of desert plants. This consolidation of the mechanical elements may be perhaps explained as a secondary result of the relative abundance of the assimilative tissues; the palisade-layers being often two, three, or even four in number, and equally on both sides of a leaf of a desert plant. While there is a great arrest in area of the parenchymatous tissue—due to the feeble water-supply—the organized products are mainly utilized in the lignification of the supportive tissues.

Conversely, if plants be etiolated by being grown in the dark, while the parenchymatous tissues are relatively in excess, such as the pith and cortex, M. Rauwenhoff has shown that the mechanical tissues are greatly reduced, the assimilative tissues being quite incapable of any activity ‡.

Another instance is supplied by our common Water-reed,

* Such were the results of my own experiments in 1891-92. I raised plants from the seeds obtained from these plants in 1893, to see if the hereditary trait of producing spines becomes less pronounced in successive generations. In August the plants had only grown to about five inches in height in consequence of the drought; but up to the date of writing this (Aug. 15th) they had developed no spines.

† *Revue gén. de Bot.* 1890, p. 276; *Bull. Soc. Bot. de Fr.* 1890, p. 176; *Comptes Rendus*, 1891, cxii. p. 110.

‡ "Sur les causes des Formes anormales des Plantes qui croissent dans l'obscurité," *Archives Néerlandaises des Sci. exac. et nat.* t. xii. p. 297.

Phragmites communis. This grass is very abundant in the Nile Valley, growing in places which are not artificially irrigated. It covers large areas of waste ground outside Cairo, forming a stunted growth, the leaves being very short and sharp-pointed. It has been named var. *isarica*. Close to the Nile, however, in Rhoda Island, it grows ten or more feet high, with long leaves almost exactly like the plants in English rivers. In many places the two forms of leaf are on the same stem, sometimes even alternating with each other, suggesting the idea that the leaves were elongated or abbreviated and spinescent, according as the plant happened to have sufficient water at its disposal or not.

In this plant we have, therefore, a varietal character which is quite inconstant, as it varies repeatedly even on the same stem, and which has not become relatively fixed, though deemed worthy of a name.

Such and other facts show how completely relative many varietal and even specific characters may be. They may have every degree of constancy, but they can often and easily change if the environment be altered, till other characters take their place, which may then become relatively fixed in their turn.

I have said that all observations tend to prove that the great reduction of the parenchymatous tissues, with a correlated hardening of the mechanical tissues—so that a spinescent character becomes very characteristic of desert plants—are simply the inevitable results of the action of the environment. That this is so, is corroborated by an experiment of M. Duchartre on the effect of drought upon *Dioscorea Batatas* *.

Some tubers of this plant produced long shoots, but without being allowed to have any water at all. The effect upon the stem was that it acquired excessive rigidity with no heliotropism nor power of climbing. Although the stem was much more slender than normally, there was a marked predominance of the elements of consolidation. The fibres had very thick walls and a minute lumen. The periphery of the central cylinder showed a zone of perceptibly greater thickness than usual, consisting of fibres of small diameter, but with walls of greater thickness than usual. This appears to have been the usual pericyclic zone so common in herbaceous endogenous stems. Similarly, the collen-

* Bull. Soc. Bot. de Fr. 1885, p. 156.

chymatous cords at the angles were quite as much developed as in normally grown stems.

Moreover, all these well-developed mechanical elements of consolidation in the *Dioscorea* were in a greater relative proportion, in consequence of the considerable reduction which the parenchymatous tissues had undergone.

The leaves were small and undifferentiated, the parenchyma between the veins being much arrested; the stomata were undeveloped and the palisade and lax central parenchyma all alike and unformed in character, except that the two of four larger layers in the centre had no chlorophyll.

From the above brief epitome of M. Duchartre's experiment it will be seen that, so far as the small amount of parenchyma and the great density of the mechanical elements of the fibro-vascular tissues are concerned, we have an exact parallel between desert plants and this *Dioscorea* grown without water in the dark. Hence this experiment, together with those referred to above, will suffice to completely justify the conclusion that the indurated character of the mechanical system and also the spinescent features of so many desert plants are simply the immediate results of the effects of the comparatively waterless character of the environment. Lastly, it must be borne in mind that the spinescent character is hereditary, and although the rigidity begins to break down under cultivation in a moist climate and a good soil, the spines may still be formed but become gradually modified and finally disappear, reverting to leafy branches, as has occurred with cultivated pears, plums, and *Ononis*; or back into leaves, as in *Berberis*.

That "xerophilous" peculiarities of plants are not only correlated with but are actually *caused* by the arid conditions of their environment is the conclusion of A. F. W. Schimper*, who has lately studied the flora of Java. He finds that the plants of the shores, alpine plants, those of the solfataras, and epiphytes, although very different from each other in a classificatory sense, all present common characters in being strictly "xerophilous." In all, the leaves are small and thick, there is a strong cuticle,

* "Ueber Schutzmittel des Laubes gegen Transpiration, besonders in der Flora Java's" (Mittheilungen aus den Sitzungsberichten der königl. preuss. Akademie der Wissenschaften zu Berlin, 1890, Heft vii. p. 1045). See also Rev. gén. de Bot. 1892, p. 364.

the stomata being at the bottom of "crypts," the intercellular spaces reduced, hairs more abundant, the water-storage tissues present, &c. The author concludes from his observations that among the causes capable of determining the development of these various adaptations of defence against a temporary or permanent insufficiency of water are the dryness of the atmosphere and soil, a strong insolation and rarefaction of the air, the richness of salts, or a too low temperature of the substratum. The stunted condition of the plants of the solfataras and of the shores would be due to the too great abundance of salts in the substratum, which has the result of reducing the assimilation of carbon.

As a corroboration of the preceding, it may be added that MM. J. Vesque et Ch. Viet* came to the same conclusion, namely, that the fibrovascular structures were much more developed in a dry than in a moist atmosphere.

I will conclude this section by quoting the following corroborative remarks of Grisebach†:—"Au nombre de phénomènes généralement répandus figure le développement des épines, phénomène qui va en croissant avec la sécheresse du climat. Les arbustes épineux plus petits qui habitent les steppes asiatiques et les solitudes du Sahara pénètrent dans les savanes de la contrée basse du Soudan (*Tragacantha, Alhagi*). L'exemple le plus remarquable de ce fait est fourni par le Sider (*Zizyphus Spina-Christi*), qui, sous la forme d'un arbuste ou arbre nain, s'étend depuis la Palestine jusqu'au Sennaar et au Bornou. Mais dans le Soudan le développement des épines n'est point limité aux arbustes asiatiques de petite taille, ou à la forme de Sodada, puisque même les arbres, notamment les Acacias, aussi bien que les plantes grasses, sont également armés d'organes piquants. Dans la Nubie, la majorité des arbres sont épineux, et il paraît que dans certaines parties de l'Abyssinie et dans le Bornou il n'est presque point de végétal ligneux sans épines. Une chose semblable est rapportée par M. Livingstone relativement aux contrées confinant avec le Kalahari, tandis qu'au contraire cette organisation s'évanouit sur le partage des eaux dans la direction du Congo."

* "De l'influence du Milieu sur la Structure anatomique des Végétaux," Ann. Sci. Nat., Bot. sér. 6, tom. xii. 1881, p. 167.

† La Végétation du Globe, ii, p. 197.

IV. *Foliage of Desert Plants.*

Another result of the deficiency of water is the small size of the leaves of desert plants, thereby lessening the surface of the transpiring organs; or else they are suppressed almost, if not quite, altogether, as in *Retama*, *Anabasis*, *Ephedra*, and *Tamarix*. Many plants produce moderate-sized leaves in the early spring as soon as the rainy season commences, but none or very small ones later on, as *Zilla*, *Alhagi*, *Statice*, &c. The inrolled margins of the leaves, which make them assume the form of a more or less closed cylinder, is another common contrivance.

Now while this reduction of surface is beneficial by lessening transpiration, we must remember that it is simply the result of drought. This is proved in several ways: first, one and the same plant will produce much larger leaves in March or April, when a good supply of water is at hand, but minute leaves in June, when the supply is deficient; secondly, if the same plant be grown in the Nile Valley it ceases to produce the smaller summer foliage and resembles the ordinary herbaceous leaves of temperate climates. Thus *Salvia lanigera* growing in the Delta has flat leaves, eight inches in length; but when in the Desert they are only about two and a half inches long, with the margins inrolled. A similar variability is a common phenomenon and is well known; for numerous instances might be given of leaves varying in form and structure on the same plant or on different individuals, according as they develop at different times or under different circumstances—or, again, if the plant have been transplanted, say, from a hot to a cold, or from a dry to a wet locality; or, again, from a low to a high altitude or *vice versâ*. Mr. Groom records a case of an orchid, *Renanthera albescens*, which naturally scrambles over plants growing on hot open sandy heaths. The specimen had been transferred to the botanic garden, Singapore, where it was growing under the shade of a well-foliaged tree. As might be expected, the form and anatomical details of the new leaves became much altered. Mr. Groom gives a series of comparisons showing how the cuticle decreased in thickness, while the dimension of the leaf increased in length but was diminished in thickness, &c.*

Mr. Scott Elliot† has independently arrived at a very similar

* 'Annals of Botany,' vii. p. 152.

† "Notes on the Regional Distribution of the Cape Flora," Trans. Bot. Soc. Edinb. 1891, p. 241.

result as to the cause of the small size of the leaves of the "ericaceous" type which prevails in parts of the Cape and of Australia. He observes :—"The climate [of the Karoo] is characterized by a long and dry summer and by plenty of wind. Such conditions obviously favour transpiration . . . Hence the small and excessively coriaceous leaves of these plants without much spongy parenchyma are thoroughly suited to the climate. We may even, I think, go a step further and say that the physical conditions have produced this form . . . With regard to leaves certain observations, which are not yet extensive enough for publication, as to the variation in size and texture of the leaf in the same species in different habitats, strongly incline me to believe that the smallness, cuticularization, and want of spongy parenchyma in the leaf all follow directly from such conditions." Similarly M. E. Warming attributes a similar result to climate, especially the dryness of the atmosphere on the Campos of Lagoa Santa in Brazil. He writes :—"Lorsque les feuilles ne sont pas tomenteuses sur les deux faces, elles sont ordinairement raides et coriaces ; les feuilles de plusieurs espèces, agitées par le vent, font entendre un bruit de cliquetis ou de crécelle très extraordinaire ; tels sont certains *Salvertia*, *Vochysia*, le *Palicourea rigida* ou *streptitans* et certains *Bombax*. La majorité des espèces arborescentes ont les feuilles dures et coriaces, à quelque famille qu'elles appartiennent" *.

Besides the general reduction in size of the leaves, plants in the desert reach the *subaphyllous* and *aphyllous* conditions. The degradation in the size and form of the leaf passes through many degrees till the leafless stage is reached, as in *Ephedra* and *Retama*. Just short of that, the leaves are minute, scale-like, closely adpressed against the stem, and assume the appearance of the foliage of *Thuja*, *Cupressus*, &c. In the desert this form is well seen in *Anabasis reticulata* and *Salsola Pachoi*. Such leaves may terminate in sharp points, as in *Cornulaca macrantha*, and as seen in our English *Salsola Kali*. This last-named genus, as also *Tamarix*, adopts both forms, just as *Retinospora* may have them, even on the same plant.

That drought is the main cause is inferred from the fact that similar forms occur in plants in rocky and arid mountain regions at high elevations. Thus while the New Zealand nearly

* *Op. cit.* p. 155 [*supra*, p. 218].

aphyllous species of *Veronica* live at an elevation of 7000 feet, *V. thujoides* is found at a lower but still high elevation. Similarly *Thujas* (*Biotas*) are trees and shrubs of considerable elevation. So many coincidences here offer the same grounds in support of the contention that similar causes have brought about similar results and produced these mimetic forms in genera of widely different orders. Thus *Tamarix* in Africa may be said to represent *Haloxylon Ammodendron* of Beluchistan and the Oriental steppes (Aitchison and Grisebach), *Casuarina* of Australia, the *Thujas* of Japan and California, *Veronica thujoides* of New Zealand, &c.

V. Succulent Plants.

Although spinescence and hairiness are the prevailing features in the desert plants near Cairo, some few are decidedly succulent, as the species of *Zygophyllum*. That this feature is one of the direct results of the intense heat (probably influenced by the presence of salts in the soil), inducing the formation of a thick cuticle, which, in turn, involves the retention of water and the development of succulent aquiferous tissues, I think cannot be doubted. The presence of salts has been proved by M. Lesage to be the immediate cause of succulency in maritime plants of temperate climates*; and he succeeded in making plants succulent which are not so ordinarily. On the other hand, the structure of "rock plants," such as *Sedums*, *Haworthias*, &c., is correlated with their arid and stony surroundings (probably without the aid of salts), and is obviously one of the many adaptations for the storage of water.

That the succulency is due to the direct action of the environment, is shown by the results of experiments in which the normal succulency is made to disappear when a new combination of surrounding conditions is supplied to the plant. Thus M. Battandier† cultivated *Sedum Olusianum*, and the leaves at once began to assume a flatter character, and he remarks as a coincidence that the two species *S. stellatum* and *S. tuberosum*, which are not rupicolous in France, but inhabit wet places, have flat leaves. On the other hand, I have found the leaves of *S. stellatum* growing in cracks between flat slabs of rock in Malta,

* The succulency of several members of the *Chenopodiaceæ* which frequent saline marshes and deserts may be now attributed to the same cause.

† Bull. Soc. Bot. de Fr. 1887, p. 191.

in an exposed heated spot, to be more or less cylindrical. M. Battandier also says that two other species which are not rupicolous but grow in dry earth, viz. *Sedum rubens* and *S. Magnoli*, have flat leaves in a wet season but cylindrical leaves in a dry one.

Similarly the common maritime fleshy Samphire of temperate climates, *Crithmum maritimum*, when cultivated in a garden became luxuriant and bore flat and smooth leaves.

Centaurea crassifolia, a plant peculiar to the Maltese islands, growing in hot rocky valleys, has thick succulent leaves which survive during the hot season; but in March, when it begins to produce its new foliage, before the hot summer has approached, I found that the leaves were nearly as thin as in ordinary plants.

As another example, M. Costantin observed* that *Salsola Kali*, a common inhabitant of maritime salt marshes, grows up sandy rivers, when it passes into *S. Tragus* by losing its fleshy leaves.

The most elaborate series of experiments to test the source of the succulency of the maritime plants has been carried out by M. Lesage†, who shows conclusively that the presence of salt is at least a potent cause in its production. He succeeded in *making* plants, such as garden cress, succulent by watering with salt water. He also testifies to the hereditary effect, in that seed obtained from plants of cress which were somewhat succulent in the first year's experiment became still more so in the following.

The increased substance of the leaf is accompanied by a greater development of palisade-tissue with diminished intercellular passages and a less proportion of chlorophyll. This latter result is correlated with a relative decrease in the amount of starch produced.

From all the above facts, natural and experimental, the conclusion is inevitable that while succulency is of benefit to the plants under the conditions in which they grow, especially by enabling them to store water during the hot and dry season, it is in all cases actually brought about by the direct action of the environment itself, coupled with the responsiveness of the protoplasm of the plant.

* Journ. de Bot., 15 mars 1887.

† Rev. gén. de Bot. vol. ii, pp. 55, 106, 163; see also Comptes Rendus, cxii. 1891, p. 672.

VI. *Protection of Buds.*

A feature very characteristic of the African desert grasses may be here mentioned—namely, the retention of the leaf-sheaths, so that the annual buds are carefully protected against drought when they appear in the spring. Similarly the *Paronychiaceæ* are provided with scarious stipules completely concealing the buds within them. Similarly *Lavandula atriplicifolia* has a spike of densely overlapping bracts (resembling the “wheat-eared” monstrous form of *Dianthus*) protecting the flower-buds. M. Warming noticed the same thing in Brazil. He thus writes :—“ Dans le groupe des Glumiflores (Cypéracées et Graminées) les feuilles sont étroites et raides ; presque toutes les espèces de ce groupe sont tuniquées au sens où M. Hackel a employé ce mot pour la première fois en 1889, c’est-à-dire que les bourgeons demeurent enveloppés et protégés par la base des feuilles qui persistent pendant longtemps, comme cela a lieu aussi dans le *Posidonia oceanica* (*Andropogon*, *Rhynchospora*, *Scirpus* sp., etc.).” In the African deserts numerous species of *Aristida* illustrate this fact. Lastly, it may be added that bulb-scales may become almost “woody” (*Allium Crameri*, &c.).

VII. *Roots.*

The organs hitherto considered are mostly above ground, but roots also exhibit features of self-adaptation to desert life in the enormous *length* they sometimes attain. Dr. G. Volkens describes * how a young plant of *Monsonia nivea* of one year’s growth may be seen between July and January to have a small rosette of three or four leaves, while the roots may be twenty inches in length. Other plants may have roots two or more metres long. The *Colocynth*, he observes, has an enormous length of root in order to maintain its existence. It stands singly, has large herbaceous leaves without any means of preventing an excess of transpiration, as a cut shoot fades within five minutes ; and yet it flourishes unshadowed through the whole summer.

The great length of root in certain desert plants has been also noticed elsewhere. Thus Dr. Aitchison observed in Beluchistan that “several of the *Astragali* (*A. kahircus*, *auganus*, *buchtormensis*) have long whip-like roots, the bark of which is employed as twine by the people. These roots are extracted in a very neat way, by attaching a loop of twine to the crown, passing a stick through the other end and making it act as a lever” †.

* *Op. cit.* p. 7 [*supra*, p. 220].† *Op. cit.* p. 431 [*supra*, p. 221].

M. de Candolle has also called attention to the advantages of long roots in enabling the plants to resist extremes of temperature. He says:—"L'action de la température est très-sensible à la surface des sols, et l'est moins à une certaine profondeur; d'où il résulte, 1^o, que, dans un terrain donné, les plantes à racines profondes résistent mieux aux extrêmes de la température que celles à racines superficielles; 2^o, qu'une plante donnée résiste mieux aux extrêmes de la température dans un terrain plus compacte, ou moins bon conducteur du calorique, ou moins doué de la faculté rayonnante, que dans un sol ou trop léger ou bon conducteur, ou rayonnant fortement le calorique; 3^o, la nature des plantes et celle du sol étant données, les plantes résistent mieux au froid dans une atmosphère sèche, et à la chaleur dans une atmosphère humide" *.

The cause of the long tap-roots of so many desert plants is the well-known responsive power of the apices to moisture, or hydrotropism. Similar phenomena may not infrequently be seen in England. Thus if, for example, the tip of the root of a seedling turnip gets into a field drain-pipe, it may grow to a length of some yards, of course never producing the turnip †. As water is often to be found at various depths below the surface of the desert, the roots stimulated by ascending moisture continue to grow downwards till they attain very great lengths.

DURATION.—Some desert plants are usually annuals, the majority being perennials. A feature, however, which Dr. Volkens notices is that these characters are particularly liable to change in desert plants according to circumstances. Plants which normally live but one year, as species of *Savignya*, *Poly-carpon*, *Malva*, *Trigonella*, *Ifloga*, &c., may survive two or more years; while perennials, like *Capparis*, *Tamarix*, *Nitraria*, *Retama*, *Acacia*, &c., may become annuals. The fact is that it simply depends upon the depth to which the primary tap-root descends so as to secure a more continuous supply of water below the surface, which enables the plant to survive the hot season.

Mr. Scott Elliot has observed the same fact in South Africa ‡. In speaking of the prevalence of the "ericaceous" type, including 350 species of *Erica* itself, he remarks:—"It is not, I think,

* 'Essai élémentaire de Géographie Botanique,' Dict. Sci. Nat. tom. xviii.

† I have such a specimen, which was brought to the late Prof. J. S. Henslow by a villager in Suffolk about the year 1850.

‡ *Op. cit.*, Trans. Bot. Soc. Ed. 1891, p. 244 [*supra*, p. 228].

hard to see why this type should obtain so largely in the S.W. district. There is, to begin with, no winter worthy of the name; and therefore annuals would, when becoming acclimatised, probably cease dying at the end of the year, because there is no reason why they should. Certain European annuals of cultivation have, in fact, become perennials."

Now the annual, biennial, or perennial character of plants is often regarded as specific; but it is one which can be easily changed, and may then become hereditary: thus the garden form of the carrot is *now* biennial, but normally, as a wild plant, *Daucus Carota*, it is an annual. This is simply the result of sowing the seed of the original wild form *late in the season*. The consequence was that the plants did not blossom till the following year. Then, by selection, this biennial feature has been fixed, and is now hereditary.

Poa annua, if grown in plenty of moisture, at once becomes a perennial; as it does also on the Alps, just as several other annuals at lower altitudes, as well as latitudes, become perennial when growing at higher altitudes and latitudes.

Mr. Th. Holm* has recorded a number of examples of American plants which are ordinarily annuals, but become perennial under exceptional conditions. They include *Hypericum nudicaule*, *Delphinium Consolida*, *Cyperus flavescens*, *Carex cyperoides*, and species of grasses and Crucifers which are annuals in Europe, but perennials in the United States, and particularly so near Washington. For example, *Arabis dentata*, which is typically biennial, and *A. lyrata*, which is normally annual or biennial, have formed perennial specimens. On the contrary, *A. lævigata*, said to be perennial by Hildebrandt, is not at all rare as a biennial near Washington.

This change in duration may be accompanied by a change in the period of flowering; or the period of flowering may change without a plant altering its duration of life. These alterations may become permanent. Thus, Sir J. D. Hooker† noticed how the stock and mignonette become perennials in Tasmania; on the other hand, the castor-oil becomes an annual in England.

As a remarkable instance of a plant having undergone a complete change of season in flowering, *Oxalis cernua* may be

* "On the Vitality of some Annual Plants," Amer. Journ. Sci. xlii. 1891, p. 304; also Rev. gén. de Bot. 1892, p. 364.

† Animals and Plants under Domest. ii. p. 305.

mentioned. This is a native of the Cape of Good Hope, and flowers in the winter, *i. e.* July; but throughout the whole of the Mediterranean border, where it has become dispersed since 1806, it blossoms from November to April*.

Mr. Darwin has so fully discussed, under the head "Acclimatization"†, the variability of plants in adapting themselves to climate, and so becoming "precocious" or "late" in flowering, that I need not enter upon this subject. All I would contend for is that such variations of habit are simply due to the responsiveness of protoplasm to the environmental conditions, and that, when once acquired, they all tend to and may become hereditary traits.

In corroboration of this I will conclude with the following observations by the late Dr. Lindley‡:—"It often happens that, as in peas, the tendency in such plants to advance or retard their season of ripening *was originally connected with the soil or climate* in which they grew. A plant which for years is cultivated in a warm dry soil, where it ripens in forty days, *will acquire habits of great excitability*: and when sown in another soil will, for a season or so, retain its habit of rapid maturity; and the reverse will happen to an annual from a cold and wet soil. But as the latter will gradually become excitable and precocious if sown for a succession of seasons in a dry warm soil, so will the former lose those habits, and become late and less excitable."

VIII. *Histological Peculiarities of Desert Plants.*

Although the morphological features of desert plants are obviously adaptive, the histological elements illustrate the same fact even in the most minute details§.

EPIDERMIS AND CUTICLE.—Commencing with the epidermis, a thickened cuticle in various degrees is of well nigh universal occurrence. There is also very frequently a superficial layer of wax. The cuticle is often covered with waved lines or ridges, especially on elevated cells, and the hairs with tubercles.

* See my paper on "The Northern Distribution of *Oxalis cernua*, Thunb." Proc. Linn. Soc. 1890-92, p. 31.

† Animals and Plants under Domestic, ii. p. 305.

‡ 'Theory of Horticulture,' p. 465. (The italics are mine.)

§ The reader might consult M. Vesque's descriptions and figures of species of *Capparis*, showing how their anatomical structure conformed to their habits. "L'Espèce végétale considérée au point de vue de l'anatomie comparée," Ann. Sci. Nat. sér. 6, t. xiii. 1882, p. 5.

M. Dufour* found experimentally that the thickness of the external and lateral walls of epidermal cells is greater under sunlight than is that of the same species when grown in the shade; and the cuticle is also much more developed under sunlight.

It need hardly be pointed out that in the desert the sunlight and glare reflected from the sand are very powerful, and therefore, *cæteris paribus*, the intensification of those elements mentioned is just what would be, on *à priori* grounds, expected from M. Dufour's experiments. But the thickness of the cuticle tends powerfully to prevent the loss of water, which is the end and aim of all desert plants in their adaptations to the climate.

Dr. Volken† observed that a considerable number of xerophile plants are protected against a too energetic transpiration by the existence on the surface, outside the cuticle, of a thick layer of a sort of varnish, very brilliant in appearance. It is in great part soluble in alcohol, and without doubt of a resinous nature. An interesting fact, from the point of view of geographical botany, is that such plants are peculiar to the southern hemisphere.

The presence of wax on the surface of leaves was long ago observed by Mulder to be closely correlated with chlorophyll; so that when we find the palisadic layers much increased, as they are in desert plants, we should, *à priori*, expect a specially increased layer of wax. The production of this substance is dependent ultimately upon the increased amount of light [and heat?], which appears to deoxidize chlorophyll, and to leave wax as one of the products; hence the epidermis becomes colourless and the cuticle coated with wax, as the wax increases with the loss of water. Upon this Mr. Herbert Spencer observes:—"The deposit of waxy substances next to the outer surface of the cuticular layer in leaves is probably initiated by the evaporation [transpiration?] which it eventually checks" ‡.

When the external walls of epidermal cells are flat, the cuticle is generally smooth; when, on the contrary, each cell forms a convexity towards the exterior, it is nearly always ornamented, either with parallel and straight or undulating striæ, or they may be more or less reticulated, &c. The above features

* Ann. des Sci. Nat., Bot. sér. 7, tom. v. p. 311, t. viii.

† "Ueber Pflanzen mit lackirten Blättern," Berichte der deutschen botan. Gesellschaft, Bd. viii. Heft 4, p. 120 (1890).

‡ 'Principles of Biology,' ii. p. 245.

are common in desert plants. M. Vesque offers the following interpretation *:—"Il serait bien difficile de déterminer le rôle de ces dessins cuticulaires par l'expérience; mais étant donnée cette circonstance singulière que les épidermes plans en sont ordinairement dépourvus, tandis que les parties convexes en présentent presque toujours, il est permis d'émettre une hypothèse à mes yeux fort plausible. Chaque cellule convexe représente en effet une lentille convergente qui, malgré ses faibles dimensions peut, surtout dans les pays chauds, notablement surélever la température en un point déterminé de la cellule épidermique; il est donc important, dans ce cas, de remplacer la vitre lisse par une vitre cannelée qui a pour effet de disperser, d'égaleriser la lumière incidente; de cette manière on comprend pourquoi, dans un grand nombre de cas, les cellules convexes qui avoisinent les stomates ou les poils enfoncés au-dessous du niveau de l'épiderme et celles qui se relèvent en petites saillies autour de la base des poils sont striées tandis que les autres ne le sont pas."

As far as sheets of glass with striated and reticulated surfaces can imitate a cuticle, I find that a sheet of sensitive paper is not darkened to the same extent under them as under a clear sheet of glass of the same thickness when fully exposed, and for the same time, to sunlight; though nothing could be deduced from any differences of temperature under the same circumstances.

PILOSISM.—Since a more or less excessive hairiness is a characteristic feature of the great majority of plants growing in hot and barren deserts, the question arises as to what is the cause. Now any extra outgrowth, even if it be but epidermal trichomes, implies the presence of more nutritive materials at the disposal of the plant at the spot than when they are not formed at all. M. Mer, who studied the question, came to the conclusion that, *ceteris paribus*, hairs are due to a localized extra nourishment, and therefore frequently occur upon the ribs and veins, *i. e.* immediately over the channels of sap. He thinks this view is supported by such a case, *e. g.*, as *Rhus Cotinus*, in which the abortive pedicels, which bear no fruit, develop a large amount of hairs, while the pedicels which bear fruit have few or none. The excess of hair is therefore presumably due to a compensatory distribution of sap.

* *Op. cit.* p. 34 [*supra*, p. 235, note].

M. Aug. Pyr. de Candolle came to the same conclusion in 1827 ; for he thus wrote about *Rhus Cotinus* :—"Peut-être la sève destinée à nourrir les fruits ne trouvant plus d'emploi, lorsque ceux-ci ont avorté, produit-elle ce développement extraordinaire de poils. Quelques filets d'étamines (*Verbascum*, *Tradescantia*) deviennent aussi poilus quand les anthères avortent, et probablement par la même cause"*.

Dr. M. T. Masters observes, when speaking of the hair on the barren pedicels of *Rhus Cotinus*, or the "Wig-plant," as it is called :—"A similar production of hair may be noticed in many cases where the development of a branch or of a flower is arrested ; and this occurs with especial frequency where the arrest in growth is due to the puncture of an insect, or to the formation of a gall"†.

As an illustration of this last-mentioned fact, it may be often noticed how *Veronica Chamædrys* terminates its shoots with an excessively woolly globular bud. A similar thing happens to a heath, *Erica scoparia*, common on the hills around Cannes. In the latter plant the abnormal leaves are broad, ovate, and densely hairy ; while the ordinary leaves are linear and glabrous. These globular structures in both plants are due to the irritation set up by the presence of grubs. The axis and the innermost leaves are arrested at the apex, while in compensation the lower leaves of the bud alter their character, enlarge and become densely clothed with hair ‡.

The fact of hairs being developed over and about the fibro-vascular cords is of common occurrence, and, under the above aspect, becomes very significant in such cases as in desert-grasses, lavender, &c. Pfitzer observes, "Almost all grasses inhabiting very dry localities have leaves with well-marked longitudinal folds"§, the stomata being situated within the grooves, while the ridges correspond to the vascular and fibrous cords. The tooth-like (or branched, as *e. g.* on the calyx of Lavender) hairs of the grasses project like *chevaux-de-frise* over the grooves. They have swollen bases capable of imbibing moisture ; and so in all

* 'Organographie Végétale,' tom. i. pp. 111, 112.

† 'Teratology,' p. 472.

‡ I have elsewhere called attention to this fact in its analogy with the results of the irritating action of the pollen-tube. See 'Origin of Floral Structures,' p. 164 *seqq.*

§ Quoted by De Bary, *Comp. Anat. &c.* p. 50.

probability absorb dew, as well as protect the surfaces against a loss of water. The marginal inrolling of the blade is, of course, an additional protection. To such an extent does this occur, that many blades of desert-grasses are perfectly cylindrical; the upper surface, which is the especially grooved one, being entirely concealed from view, as may be well seen in Volken's figure of *Aristida ciliata* *.[•] In some cases, as in this grass, certain hairs assume a papillate form immediately over the stomata.

As another illustration which seems to support M. Mer's contention that hairs are, *cæteris paribus*, a result of compensation, M. Lesage † found in a root of the second order of *Phaseolus*, which was much longer than the primary root, that the portion *outside* the water was covered with numerous root-hairs; *near* the water these hairs were elongated, while *in* the water they were much shorter, and finally disappeared altogether. In a transverse section it was seen that the cortical layers in the air contained smaller elements than those in the water; and in the central cylinder the xylem was proportionally more lignified in the aerial portion.

The root of the bean was made the subject of similar observations. It was found that when numerous secondary roots were suppressed, the primary root was covered with numerous absorbing hairs.

The above interpretation will, therefore, satisfactorily explain the existence of the hairiness of plants in the deserts; for drought, aided by the barrenness of the soil, tends to arrest the development of parenchymatous tissues; and in proportion as this arrest is excessive, so is the compensating process of the production of hairs. Hence, just as with plenty of water or a good soil, as obtains under cultivation, plants tend to become less hairy than in the wild state, as *e.g.* the parsnip, so, conversely, under aridity and a poor soil, hairiness becomes a characteristic and hereditary feature.

Here again, therefore, if the above explanation of M. Mer's be true, the very conditions which bring about the production of an excessive clothing of hair are precisely those against the severity of which this dense clothing is one of the very best of protections.

The above interpretation receives indirectly an additional

* *Op. cit.* pl. xvii. fig. 4 [*supra*, p. 220].

† *Comptes Rendus*, cxiii. 1891, p. 109.

countenance from the fact that just those desert plants which *do* develop much parenchyma and become exceedingly fleshy, as the *Aloinæ*, *Euphorbiæ*, *Cactaceæ*, *Zygophyllum*, &c., are generally entirely hairless.

Intense hairiness is certainly one of the most conspicuous features of desert plants, and is an invaluable means of lessening the heat by forming a non-conducting surface; and, on the other hand, is a means of absorbing dew during the summer when no rain falls.

Dr. G. Volkens remarks that a multitude of cases establish the empirical deduction that drought is correlated with the presence of much hair, though what the real causal connection may be is not so clear to him*. He observed that as transpiration tends to increase, so does the relative quantity of hair, till (it may be added) the quantity becomes so great as to check the very process which may have had something to do with bringing it about.

In desert plants the hairs are of different forms. They may be stiff, straight, and adpressed to the surface, all lying in one direction; or the "needles" are interlacing; or the hairs may be of a twisted cottony character and cover the surface with a layer of wool; or, again, they may be stellate and flat, the branches interlacing so as to produce a dense coating of felt; or they may be bladdery and filled with water. These latter may finally collapse, dry up, and form a glassy sheet.

There are also peculiarities in the structure of the hairs themselves which are remarkable. In many cases the cavity is quite filled up with the exception of the broad basal part of the cell, while the outer surface may be densely coated with wax, either entirely or with "gashes" and "pores" (*Diploaxis Harra*), or else the basal portion is quite devoid of it (*Heliotropium luteum*), so that water can readily pass from without into the interior. Dr. Volkens observes, with regard to the filling up of the lumen with cellulose matter, that this is connected with the swelling up of the inner membrane, and shows (by treatment with suitable reagents) that it is a substance which, when water is absorbed, can hold it fast with great strength. This, of course, greatly retards transpiration.

I have found in some cases, besides the closely applied felt, that there are taller branching hairs standing much above the

* He makes no allusion to M. Mer's observations, which were probably therefore unknown to him.

level (*Erucaria aleppica*). These I take to be specially absorbing hairs, as well as all which have no wax, or at least places where it is wanting.

As a special peculiarity, I have found in *Cocculus Leaba* a basket-like arrangement of hairs round the axillary buds. This would presumably retain a large drop of dew, by means of which the bud would be benefited.

Besides being actual absorbents of dew*, it may be borne in mind that not only does the felt collect the dew-drops, which get entangled in it and so get absorbed, but it parts with them by evaporation much more slowly than does a smooth leaf, as I have tested by experiment with many kinds of leaves.

Now, as Dr. Volkens observes, though *suspected*, he cannot say for certain how or why the hairiness is produced. But, besides, the reasonable interpretation of M. Mer which I have given above, that hairiness is a direct result of the environment upon the plant, is established by numerous cases. In the first place we have "the argument of coincidences," as I would call it; but when we find that a change of habitat brings about a greater or less degree of hairiness, the *probabilities* accumulate till they amount to a moral conviction, which is further established by experimental verification. Thus, for example, the hairiness of wild plants tends to decrease under cultivation, as in the wild parsnip. Linnæus observed this fact nearly two hundred years ago for he says†:—"Spinas et hirsutiem . . . plantæ sæpius exuunt a loco vel cultura." *Ranunculus repens* growing in a dry barren gravelly soil is very hairy, but another plant growing in water ten feet from the former, which I have preserved, is scarcely hairy at all.

M. Battandier observes‡ that *Bellis atlantica*, with leaves covered with a true velvet having a long pile, at the summit of the mountain Blida, when cultivated in Algeria, bore leaves less and less velvety till they finally became as glabrous as the *Bellis* of Algeria.

Similarly *Allium Chamæmoly*, when cultivated for eight years, lost its villosity which it had on the summit of Zaccar. So also

* For proof that plants *can* absorb rain and dew by their green parts, I would refer the reader to my paper "On the Absorption of Rain and Dew by the Green Parts of Plants," Journ. Linn. Soc., Bot. xvii. p. 313.

† Philos. Bot. § 272.

‡ Bull. Soc. Bot. de Fr. 1887, p. 193.

Cerastium Boissieri, which is white and tomentose at the summit of Aït-Ouabau, became glabrous and of a beautiful green at Algiers.

Hairiness is well known to be a most variable character, and although it is recognized as specific when constant and abundant, as in *Verbascum*, and therefore less variable, it obviously becomes much less important when it fluctuates.

It may be observed here that the hairiness as an hereditary character varies greatly. Thus, M. Battandier found that *Bellis atlantica* varied *when transplanted*, yet when raised by seed in Algeria did not show similar modifications; similarly *Allium Chamæmoly*, though it was less villous, remained more hairy than its congener after cultivation as well as by sowing. On the other hand, seedlings of *Pastinaca sativa* raised in a prepared border in the botanic gardens of the Cirencester Agricultural College became less and less hairy, and finally quite glabrous*.

As a spontaneous variety, *Malva parviflora* may be mentioned; as grown in the Nile Valley as a culinary vegetable it is not very hairy, the hairs being stellate, having only a few rays, sometimes two only. As a desert plant, where it appears as a small annual for a few weeks only, the stellate hairs increase their number of rays. Similarly *Erodium laciniatum* is much less hairy when growing in waste ground on Rhoda Island in the Nile by Cairo than when in the desert. I find that the main differences between the two forms may be summed up as follows:—Hypodermic collenchyma is much thicker in the petiole of the desert form. The upper epidermis has its cells similar in size but with more hairs. The lower epidermis has cells which are much smaller than those of the Nile Valley form. The palisade, consisting of two rows of cells, is identical in both cases below the upper epidermis; but while there is a lax mesophyll of rounded cells on the lower side in the Nile Valley form, the corresponding cells are somewhat elongated in shape, thus tending to assume the palisadic type characteristic of the lower side as well as of the upper in the desert form. Hairs of the latter are more numerous in the proportion of 24 to 10 for the same area.

STOMATA.—These structures are frequently sunk below the

* Prof. Buckman raised the "domesticated" variety alluded to in 1847, which he called the "Student." It is still regarded as the "best variety" in cultivation, according to Messrs. Sutton & Sons of Reading (1894).

level of the outer surface of the leaf and may occur on both sides. The depression in which they lie is either in consequence of the great thickness of the outer wall of the epidermis (*Allium Cræmeri*, *Pityranthus tortuosus*, &c.), or because the epidermis itself lines cavities in the parenchyma which are either naked or clothed with hairs covering over the stomata, as in the grass *Danthonia Forskåli*, very like the well-known case of *Nerium Oleander*, to which M. Vesque adds *Capparis Breynia*. The *Oleander* has narrow, rigid, more or less erect leaves which are well suited to live in a dry atmosphere. In a specimen growing at Cannes there was a thick cuticle and two layers of thick-walled hypodermic cells, a palisade-tissue of two layers on the upper side and of one layer on the lower. A lax mesophyll of green cells fills up the central space. The stomata are on the bottom of the epidermal cavities.

In a leaf gathered from a tree in Cairo, there were slight differences, in that there happened to be no palisade-cells on the lower side at all, the lax mesophyll reaching to the hypodermic layer. Such differences are probably accidental; but they show clearly how easily the anatomy of a leaf conforms to slight differences of illumination, &c.

In desert plants the guard-cells are often so thick-walled that the lumen is nearly obliterated; and, contrary to what is generally supposed to be the case in temperate regions, Dr. Volkenš shows that they often close during the day and are open at night*. Perhaps the arrested moisture due to the check to transpiration may cause turgescence by day, which closes the slit, while the cessation at night brings about a relaxation; or it may be the result of a more complicated action between the guard-cells and the adjacent epidermal cells. It is, however, difficult to say without a very close investigation into the phenomena on the living plants in their natural conditions.

IX. *Assimilative Tissues.*

The chlorophyll-tissue of an ordinary dorsi-ventral leaf is typically differentiated into a palisadic layer below the upper epidermis and a spongy layer above the lower epidermis. It is well known that in those plants in which the leaf is normally reversed in position, as *Alstræmeria*, the relative positions of

* Die Flora der ægypt.-arab. Wüste, p. 47.

these two layers are also reversed. This inversion can be more or less decidedly brought about by compelling certain leaves to develop their surfaces reversed. Moreover, when leaves assume a vertical position, so as to be equally illuminated on both sides, then the epidermis and subjacent palisadic tissue are also more or less alike, as in some grasses, the phyllodes of Australian Acacias, the pendulous falcate leaves of gum-trees, though the first-formed horizontal leaves on the same gum-trees are dorsiventral in structure like ordinary horizontal leaves*.

The preceding facts all conspire to prove that the differentiation of the mesophyll into palisadic tissue is the direct result of illumination; and that, as the upper surface of normally horizontal leaves receives more light than the lower, the differentiation of the chlorophyll-cells into an elongated form parallel to the incident light is the direct outcome, *cæteris paribus*, of that external agent.

A significant fact with regard to these alterations is that the change evinces itself by degrees. Thus in young leaves of *Alstroemeria psittacina*, M. Dufour † shows that it is only partially effected. Thus the first leaf stands vertically. It possesses few stomata, and is nearly alike on both sides. The second leaf is still nearly vertical, being only twisted towards the apex. It has stomata on both faces at the base, but at the point shows many upon the upper, but none on the lower side. The subsequent leaves have the petiole twisted and are completely reversed in position; their petioles have a small number of stomata on the two faces in the limb, exclusively upon the

* The chief differences between the two forms of leaves in *Eucalyptus* I find to be as follow:—In the horizontal leaf the upper epidermis is composed of small cells and there are no stomata. There is a palisade-tissue of one layer of cells, with lax mesophyll below the lower epidermis. This latter has larger cells than the upper and is provided with stomata. The pendulous leaf is a good deal thicker than the horizontal. Both epidermides are provided with a very dense cuticle in which the stomata are deep-seated. There are four rows of palisade-cells on both sides with a chlorophyllous mesophyll between them. The petiole is flattened so that the leaf can swing much in the same way as that of the Poplar. The horizontal leaves in *E. Globulus* are sessile.

M. G. Briosi has written a voluminous work with many plates upon the leaves of *Eucalyptus Globulus*, Labill., to which the reader is referred for numerous details ('Intorno alla Anatomia delle foglie dell' *Eucalyptus Globulus*, Labill.,' 95 p. et 23 pl., Milano, 1891).

† Bull. Soc. Bot. de Fr., 28 mai, 1886, p. 269. The author here gives several references to the literature of the subject.

superior face, now become the lower in position. Another interesting point is that in young leaves the mesophyll is homogeneous; but the cells under the upper epidermis are rather larger at first in the older leaves, showing an hereditary tendency to develop palisade-tissue; but later on the influence of the light soon renders the cells below the—now reversed—inferior side much longer than the others.

The needle-like leaves of the Norway Spruce prove, according to the careful investigations of M. Mer *, to be most remarkably sensitive to light—becoming more quadrilateral with a uniform palisade-tissue as the leaf grows exposed, but flatter and more dorsi-ventral when it is more shaded on the same tree.

He also observes the remarkable result of frost setting up a “habit” in the tree, as follows :—“Trees planted isolated have some modifications. They become more bushy, from the development of lateral buds, which are arrested in forests. When the young shoots are struck by frosts in the spring it happens at times that, without reaching the point of death, they lose their turgescence. They become soft, and their extremity turns towards the ground. Lignification supervenes before they have recovered their turgescence, and they remain thus definitely curved. When the terminal bud is not destroyed it develops its succeeding shoot the following year in this position. If one places it vertically, the terminal bud turns downwards, and the branch in course of development preserves this situation; or rather its extremity tends to elevate itself by a slight curvature. This depends upon its degree of vigour and the time during growth when the experiment is made.”

This passage is very suggestive as a cause of “weeping” varieties of trees, by a *temporary* injury producing a *permanent* effect in the growth, though not to the extent of being hereditary.

Again, Dr. F. Noll † has shown that external influences determine not only the *direction* of some organs, but also the *position* in which they are formed; as, *e. g.*, the development of the gemmæ of *Marchantia*, of aerial roots on climbing plants, &c. In other and more numerous cases the formation of fresh organs appears to be independent of external forces, and to be determined only by the internal, *i. e.* hereditary, forces in the

* Bull. Soc. Bot. de Fr. 1883, p. 40.

† See Journ. Roy. Micr. Soc. 1891, p. 490.

plants; as, for instance, in the dorsi-ventral structure of many parts of plants. In *Bryopsis* the reversal of the plant brings about a corresponding internal organic transformation.

M. Warming notes the same feature in the leaves of plants growing in the arid campos of Lagoa Santa. He says *:—"La direction des feuilles accuse également la sécheresse du climat; beaucoup d'entre elles ont habituellement une direction verticale ou sont au moins très relevées, de manière à n'être frappées par les rayons solaires que sous un angle aigu. Certaines espèces ont des feuilles très réduites et quelques-unes sont aphyllées; elles appartiennent à des familles très différentes." The reader will perceive that this description would apply equally well to many desert plants of the northern hemisphere.

Applying the preceding observations to desert plants:—If a leaf be small, narrow, and moreover assume a more or less vertical position, as is so generally the case, so that it is illuminated nearly equally on both sides, we should expect to find on *à priori* grounds that it would have palisade-tissue on both sides. Such is precisely the case with innumerable desert plants. The only and indeed relatively rare exceptions are in the leaves of such plants as develop their foliage during the rainy season, as annuals, or in "Nile Valley" plants which happen to secure a place in the borders of the desert. Such have a more or less characteristic spongy parenchyma on the underside; while transitions from this to true palisadic tissue are easy to be found. The typical chlorophyll-tissue in leaves of true desert plants is therefore palisadic on both sides, the cells being arranged in from one to four or even five superposed rows. These sometimes meet in the middle (*Zizyphus Spina-Christi*), in others there is a central layer of short rounded cells (*Cassia obovata*), the usual lax merenchyma being entirely wanting.

In addition to the typical palisadic cells at right angles to the surface, large cells palisadic in shape may be arranged in cylinders around the fibro-vascular bundles. This is particularly well seen in grasses; but within this cylinder is a second, of chlorophyllous cells, which are quadrate and short in form. This peculiar arrangement of a double cylinder of green cells is not confined to grasses, but occurs in exogens, as *Tribulus alatus*, *Atriplex Halimus*, &c.; so that in all cases the fibro-vascular cords are densely imbedded in chlorophyllous tissue.

* *Op. cit.* p. 155 [*supra*, p. 218].

In some cases the inner sheath is colourless and acts as a water-storage tissue (*Oligomeris subulata*). It is, I think, really homologous with the endoderm.

M. Dufour* found that chlorophyllous tissue is much more developed in sunlight than in shade; and it may be added that a similar phenomenon occurs in Alpine plants and plants of high latitudes as compared with the same species growing at low altitudes and latitudes. In these cases the deeper green tint is also due to the uninterrupted sunlight. Hence it is not surprising to find the chlorophyll-tissues reach a high development under the intense light in the desert, whether from the sun direct, or reflected upwards from the sand.

X. Ligneous Tissues.

Messrs. Dr. D. H. Scott and G. Brebner have described† the histology of *Acantholimon glumaceum* (Plumbagineæ), and Prof. D. Oliver had previously examined‡ that of *Acanthophyllum* as well (Caryophyllæ). These are both desert plants; and I might now add a great many more anomalous and subanomalous stems of plants growing in the North-African deserts, some of which Dr. G. Volkens has described and figured§. The general conclusion deducible from a study of their peculiarities is that these are due to the climatal conditions under which they grow. Summing them up, they may be enumerated as follows:—There is a general tendency to lignification; with an absence of medullary rays (*Zilla myagroides*, *Bassia muricata*); if they be present, they are comparatively few and have thick walls (*Farsetia africana*, *Helianthemum kahiricum*, *Ochradenus baccata*); the fibro-vascular cords may form “islands,” as seen in a transverse section, imbedded in dense tissue (*Statice pruinosa*, *Atriplex leucoclada*, *Pityranthus tortuosus*); the “wedges” of wood may fail to form a regular zone, but be more or less isolated and imbedded in water-storage tissue (*Tamarix mannifera*, *Anabasis articulata*). The wood may be deeply indented with cortical invasions, as Prof. Oliver has shown to be the case in *Acanthophyllum*. Dr. Scott observes that this is due to the fact

* Ann. des Sci. Nat., Bot. sér. 7, tom. v. p. 311.

† Ann. of Bot. vol. v. p. 259.

‡ Trans. Linn. Soc. vol. xxii. p. 289.

§ Die Flora der ägyptisch-arabischen Wüste, &c.

that the zone does not close up after having early parted with a cord for an appendicular organ. I think we may attribute this failure to a want of activity in the formation of wood, which may be correlated to the insufficiency of foliage during the hot months*. Perhaps the curious cavities described† by Prof. D. Oliver in a species of *Acantholimon* as occurring in the wood may be attributed to the same cause.

As other examples of anomalous stems, Dr. Volkens describes and figures that of *Gypsophila Rokejeka*: the pericycle (which is often very active in the Caryophyllæ) puts on a very dense zone of thick-walled sclerenchyma, in lieu of xylem, which in this plant is comparatively feeble. A similar result occurs in *Telephium sphærospermum*, of the allied order Paronychiaceæ. I have found an analogous result of pericyclic activity in *Iphiona mucronata*. Inside a cortex there are zones of square, oblong, or irregular shaped patches of sclerogen imbedded in a parenchymatous tissue‡, and only isolated patches of xylem around the medulla, all being imbedded in a "stereome-zone." *Astragalus Forskålîi* has a very anomalous stem. It has large cords of liber outside a zone of cork, then another series outside the phloem, a third, *complete* zone in the middle of that tissue. An anomalous xylem follows surrounding a medulla in the centre of which is a column of collenchyma! To this I would add the stem of *Anabasis articulata*, which has only rudiments of leaves, opposite and distichous. All the elements, as seen in a transverse section, make up four series of crescent-shaped structures around an hourglass-shaped pith. Taking a "wedge," there is sclerenchyma forming the angle, then a zone of large vessels and wood-fibres, then cortical parenchyma, and sclerenchyma outside.

It may be observed that the four wedges, roughly resembling a Maltese cross, here appear to be correlated to the positions of the rudimentary leaves; the xylem tissues failing just where no leaves occur.

As long as the shoots are young and green, one may add to

* I find that Grisebach confirms this idea, for in speaking of the partially developed wood in *Haloxylon Ammodendron* he says:—"La suppression du feuillage détermine la croissance incomplète du corps ligneux" (*La Vég. du Globe*, i. p. 630).

† *L. c.* tab. 51. fig. 24.

‡ Dr. Volkens figures a section of a *young* stem; but does not appear to have noticed the development of pericycle.

the above peculiarities of stems the great thickness of the cuticular surface of the epidermis, which is not infrequently clothed with hair like that of the foliage; the great depth of the palisadic layer, which often consists of three, four, or more zones of elongated cells (e. g. *Zilla*), the cortex acting as a storage-tissue for water, subsequently passing over into cork.

Now, when we observe how often the different members of the tissue of stems of woody desert plants are thus variously disposed and constructed, while at the same time there are certain general features very commonly to be seen throughout, I think we cannot fail to arrive at the conclusion that these structures are simply the outcome of the environment in which such plants live. This view is corroborated by experiments, for they prove that the great tendency to lignification of the tissues, as already shown for the spinescent features, is a result of a deficiency of water, and they at once tend to disappear when desert plants grow in an ordinary prepared soil of cultivation.

This, for example, is well seen in several species which frequent both the Desert and the Nile Valley, and in the plant of *Zilla myagroides* already alluded to, which was raised from seed in Cairo. The spines were quite flexible, the pericyclic sclerenchyma, which is very dense and thick-walled in the desert plants, being very greatly reduced under cultivation.

We have also seen, from Duchartre's experiment with *Batatas*, that the absence of sufficient water is a direct cause—in conjunction with the responsiveness of protoplasm—of a comparative increase of lignification. To this we may add the great defection of foliage in the hot summer months, when the formation of tissues is proportionally arrested. We can thus realize how anomalies in the structure of the stems may well be expected, though we may not be able to explain in the case of every individual stem the direct connection between cause and effect.

XI. *Water-storage Tissues.*

One of the most characteristic features of desert plants is their system of storing water. Commencing with the epidermis, certain of the cells form rounded or oval elongated bladders bulging on both sides; or they may elongate into hairs, the lower part acting as a storehouse of water, or they may assume the form of bladders supported on short pedicels. As an example is the familiar ice-plant which occurs about Alexandria, being so

called because the water-cells are so conspicuous over the surface of the leaf. Many other plants are provided with them, but they are not so conspicuous to the naked eye; thus species of *Reseda* (as *R. arabica*), *Gypsophila Rokejeka*, *Malcolmia ægyptiaca*, *Heliotropium arboreum*, *Hyoscyamus muticus**, &c. *Atriplex leuoclada* has globular water-cells on slender supports; in this, as in *Atriplex Halimus*, the hairs finally collapse, and by sticking together form a sort of protecting sheath all over the surface of the leaf.

In the interior of the leaf the chlorophyll-tissue is sometimes so abundant that the leaf is perfectly green throughout; in other cases the central tissue is nearly or quite devoid of chlorophyll-grains and acts as a storage-tissue. In *Atriplex Halimus* the outer layer of palisade-cells is clear and utilized as storage; while in some, as *Nitraria retusa*, large isolated storage-cells lie imbedded within the palisadic tissue, some others of the elongated cells being reservoirs of tannin.

Of the above varieties the central storage-tissue is the most important and is well seen, as it occupies by far the greater space, in such succulent leaves as those of *Mesembryanthemum* and *Aloë*.

Sign. Arcangeli has lately observed that *Atriplex nummularia* possesses below the epidermis of the leaves an uncoloured parenchyma which covers the assimilative layer and represents a tissue of water-storage†.

In stems the cortex and medulla act as storage-tissues, the former gradually passing into cork, which of course is a great protective tissue in many desert plants.

Of subterranean structures the bulb-scales of species of *Allium*, *Pancratium*, &c., and the cortical region of roots of grasses, may act as storage-organs.

In some exogens the roots and subterranean stems assume special forms which act as reservoirs. Thus, in the genus *Erodium* there are three desert species which develop tuberous structures on the roots, which Dr. Volkens proved to be water- and not starch-storing tissues. This observation has been

* The epidermal water-cells give a pale green colour to the leaf, and render it difficult to dry completely, except after many days in the press; perhaps because the water in all the plants is more or less thickened by gummy or other matter.

† "Sulla struttura delle foglie dell' *A. nummularia*, Lindl., in relazione alla assimilazione" (Nuovo Giorn. Bot. Ital. vol. xxii. p. 426).

corroborated on quite independent grounds by M. Hackel*, who has called attention to similar structures and their usage in certain grasses of dry climates; these being singular developments of the lowest internodes of the culms, shoots, and basal leaves.

He distinguishes them as tuberous or bulbous grasses and tunicated grasses. Tuberous grasses are such as *Phleum pratense*, var. *nodosum*, Gaud., and *Arrhenatherum avenaceum*, var. *nodosum* (*Avena nodosa*, L.), of which one or more of the basal internodes of the culm and shoots attain a tuberous development; while *Poa bulbosa*, L., represents a bulbous grass, since the bases of some of the sheaths of the leaves have increased in thickness and form a bulb very much like that of *Allium*†. He observes that these tuberous and bulbous forms only occur in countries with periods of dry seasons, and none have been observed in the moist parts of tropical regions.

It is very interesting to learn that the author does not consider these tubers and bulbs to be reservoirs of starch or sugar, as are the similar organs of Liliaceæ, Iridaceæ, &c., though being structurally homologous with these; but physiologically they are water-reservoirs, just as Dr. Volken's maintains with regard to the tuberous roots of species of *Erodium* in the deserts of Africa.

What is particularly to be noticed is that Hackel has shown that *Poa bulbosa*, on being cultivated in moist soil, almost lost the bulbous character, clearly proving therefore that these productions are the direct result of a dry environment.

These tuberous swellings on grasses are therefore clearly analogous with those on the roots of *Erodium*. Thus *E. hirtum* has globular, potato-like tubercles; *E. Hussoni*, finger-shaped; and long spindle-like roots occur in *E. glaucophyllum*.

They all contain a storage-tissue protected externally by a strong, many-layered cortical coating. Their position being between the absorbing root-apices and the foliar transpiring surfaces, they act as reservoirs and regulate the supply of water.

Bulbs of species of *Allium*, as *A. Crameri*, &c., are similarly adapted to the desert, storing water within the inner scales,

* "Ueber einige Eigenthuemlichkeiten der Graeser troekener Klimate," Verhandlungen der k. k. zool.-botan. Gesellsch. Wien, Jahrgang 1890, p. 125.

† Dr. Aitchison observed *Poa bulbosa* to be "the most common grass covering the great plains in Beluchistan" (*l. c.* p. 432) [*supra*, p. 221].

whilst the outermost series become almost woody in texture, as a protection against the hot sand in which they lie.

The cortex of roots acts as a storage-tissue in many plants, as in *Gypsophila Rokejeka*, and grasses, such as species of *Danthonia*, while the axis in both is densely woody.

A cause may be suggested for the development of the hypertrophied condition of the cortex and medulla of roots, which act as water-storage tissues, in the excessive heat which the sand surrounding the roots acquires from the sun. In the hottest months and hours of the day, the temperature may rise to about 130° F. (*Volkens*).

Now M. E. Prillieux* has shown experimentally how an abnormal excess of heat in the soil affects the roots of beans, &c., in a precisely analogous manner, by enlarging the cells of the cortex and pith. While, however, in this latter case the distention of the parenchymatous tissue is, of course, abnormal and pathological, in the desert plants it has become a characteristic important and hereditary feature.

M. Battandier also calls attention to the fact that there are plants in which certain buds swell into tubercles capable of enduring the dry season, while the rest of the plant perishes; such are *Saxifraga globulifera* and *Sedum amplexicaule*. In Malta there are several species of *Ranunculus*, such as *R. bullatus*, which produce "root-tubercles," which are thus enabled to survive the parching summer and can live therefore on the most exposed surfaces round the fortifications of Valetta. *Romulea Bulbocodium* and *Iris Sisyrhynchium* are similarly enabled to live and abound in barren rocky grounds of Malta. This island has also fifteen species of *Allium*, nine of *Ophrys*, and eight of *Orchis*, as well as many other bulbous plants, which can thus survive the intense summer heat to which they are subjected; annuals being in a decided minority except as weeds of cultivation.

From M. Hackel's observations on the tuberous processes in grasses which are formed in dry soil and disappear elsewhere, we, at least, have a strong suspicion, if nothing more, that all such structures are the outcome of the environment itself. This is also the conclusion of Mr. Scott Elliot, who notices how numerous are bulbous and tuberous plants in the Karoo of S. Africa. He says:—"Many orders have developed bulbs which

* "Altérations produites dans les plantes par la culture dans un Sol surchauffé," Ann. des Sci. Nat. sér. 6, t. x. 1880, p. 347.

usually show no trace of them ; *e. g.* the whole section *Hoarea* of *Pelargonium* is bulbous." This feature he attributes to the "direct influence of the climate" *.

Finally, with regard to the origin of water-storage tissues generally, I would suggest it to be primarily due to the accumulation of water within the plant in consequence of the arrest of transpiration. This latter function is impeded, in turn, by the formation of a thick and often waxy cuticle and a dense clothing of hair, as well as by the secretion of substances (such as tannin, gum, mucilage, resinous matter, salts, &c.) which thicken the water and so render it less capable of vaporization. But all these features, which thus bring about the very best structures to enable the plants to survive the injurious effects of the climate, are simply the direct outcome of the excessive heat and light coupled with the deficiency of water in the desert.

XII. Secretions.

These are of various kinds and appear to play an important part in arresting a loss of water. Thus, tannin is abundant in some desert plants, betraying itself by a yellowish appearance in the epidermal cells (*Monsonia*, *Erodium*, *Astragalus*, *Tamarix*, *Linaria*, *Centaurea*, &c.), as well as, of course, by the agency of iron salts. Dr. Volken alludes to Warming's suggestion that tannin, in connection with the hygroscopical capacity of acids, would afford a protection against desiccation †. In alluding to this supposed use of tannin, it may be mentioned that Sachs regards it as a waste product in metabolism ‡, though fungi when attacking oak-wood appear to consume it §.

On the other hand, Mr. S. Le M. Moore remarks that "tannic acid may have a more general relation to the turgescence of cells. Moreover, tannin is most likely used up in the lignification of the cell-wall" ||. As lignification is a prominent feature of desert plants, there may be perhaps more than a mere accidental coincidence.

Another kind of secretion is that of strong scented ethereal oils, glandular hairs being a common feature on desert plants. Species of *Artemisia* are characteristic plants of the deserts of

* "Notes on the Regional Distribution of the Cape Flora," Trans. Bot. Soc. Edinb. 1891, p. 241.

† Zur Flora der ägyptisch-arab. Wüste, Skizze, p. 14.

‡ Physiology, &c., p. 328.

§ *Op. cit.* p. 388.

|| Journ. Linn. Soc., Bot. xxvii. p. 538.

Africa and Beluchistan; *Pulicaria arabica* has a particularly powerful odour. Since Dr. Tyndall has shown how minute quantities of such oils diffused through the air are capable of arresting radiant heat, it has been suggested that this is one of the many resources to which desert plants appeal in order to reduce the ill-effects of the heated atmosphere which surrounds them; and just as the presence and quantity of opium, hasheesh, aconitine, &c. secreted by plants varies greatly with the climate, so it is reasonable, in the absence of strict investigations, to assume that these oils are in an excess through the intense heat and other conditions of the climate of deserts.

Another of the more interesting secretions may be here mentioned, viz., of certain mineral salts, which by their hygrometric properties enable the plants to absorb dew from the air during the hotter months and thus transmit it to the tissues within. *Reaumuria hirtella*, species of *Tamarix*, *Frankenia pulverulenta*, species of *Statice* * and *Cressa* are the more remarkable instances. The first-named plant having developed its new foliage in early spring, when water is comparatively copious, the leaves in the early mornings appear covered with dew-like drops, no doubt due to root-pressure. As the sun mounts the water evaporates, and the plant is now covered with a dust-like secretion of chlorides of sodium, of calcium, and of magnesium; the two latter being of less proportion than the first. There are special, two-celled glands which secrete these salts. Later on, after the rainy period is over, these excessively hygrometric salts absorb dew, which is transmitted to the plant, and thus enable it to retain its bright green character all through the hot season †. In a similar manner a large number of very lofty *Tamarix* trees

* See Mr. J. Wilson's paper on "Mucilage and other Glands of the *Plumbaginæ*," Ann. of Bot. iv. 1890, p. 231.

† I had a curious experience with this plant when drying it in a press for my herbarium. Placing freshly gathered specimens in the usual way between drying-papers, I proceeded to change them after three days. To my surprise I found the sheets perfectly saturated where the specimens were lying. They themselves were covered with dew-like drops, although under strong pressure. The salts had in fact rapidly drawn out the moisture from within the plant. After fresh papers were supplied the plant dried quickly.

There are some peculiarities in the anatomy of the leaf of *Reaumuria* which Dr. Volkens does not allude to, though he has figured the two-celled salt-glands, &c. One is the remarkable forms the "tracheides" of the leaves assume. Instead of being more or less straight tubes, they bulge into bag-like processes of three or four sides, or else assume various irregular shapes. They are thick-

grow outside Cairo, but not quite on the desert. They never receive any water by artificial irrigation whatever, yet are in a very flourishing condition.

Halophytic plants, and others yielding ethereal oils, though not uncommon in the Egyptian deserts, in consequence of the general presence of salts in the sand, are of course especially characteristic of more saline areas, as of the Asiatic steppes. These extensive regions agree with the more Southern deserts in excessive aridity and heat; and consequently we find the same characteristic features in the plants of both alike, such as the production of spines, hairy epidermis, saline sap, and the secretion of ethereal oils. The *Chenopodiaceæ* are especially characteristic of both regions, the salts of soda imbibed by the roots and retained within the plant rendering the water less easy of evaporation.

Similarly there is a great secretion of ethereal oil in consequence of intense heat. Thus Grisebach observes that Arabia is on this account distinguished by its aromatic and resinous plants, of which several are equally indigenous in the steppes of the East*. While, however, these environmental conditions are the direct causes of the secretion of the oils, these latter, in their turn, aid in checking the loss of water. Thus Grisebach observes:—"Les huiles éthérées paraissent également agir d'une manière restrictive à l'égard de la dépense de la vapeur aqueuse, lorsque les organes de végétation sont richement pourvus de ces éléments aromatiques. L'huile s'évapore plus facilement que l'eau, et entoure chaque feuille d'une atmosphère imprégnée de vapeurs odoriférantes. On sait que les vapeurs de substances différentes restent indépendantes les unes des autres dans un espace qui en est saturé, mais il n'en est pas de même lorsqu'elles sont dégagées avec rapidité des liquides, dans des conditions où il ne peut être question de saturation. Sans doute, cette rapidité est retardée en présence d'une autre vapeur susceptible de se produire plus aisément. C'est l'huile éthérée seule que la

walled, but provided with numerous small transverse slits. They suggest the idea that they are means of temporarily storing water until it is required to be transmitted elsewhere; and would seem to support M. Vesque's view of the use of vessels, or rather tracheides, as "réservoirs vasiformes." *Op. cit.* p. 38 [*supra*, p. 227].

* Vég. du Globe, ii. p. 129.

plante rejette comme une substance d'évacuation, tandis qu'elle doit retenir autant que possible l'eau de sa sève, lorsqu'il s'agit de prolonger la durée de ces fonctions vitales. Un rôle de certaine importance pourrait également revenir au phénomène de réfrigération produit par l'évaporation, au moment du passage rapide des huiles éthérées à l'état de vapeur, phénomène qui réagit contre la température communiquée par l'insolation aux feuilles, dont le degré de chaleur détermine aussi la marche de l'évaporation" *.

Mount Sinai appears to show like characteristic features of desert plants to a considerable height, viz. 7035 ft.; for Mr. R. M. Redhead, in some notes upon the flora, remarks †:—"During our ascent of Gebel Mûsa, followed by that of Ras-es-Sâfsafeh, two points especially struck me,—first the great preponderance of scented and especially Labiate plants; and, secondly, the very woolly, tomentose character of those not labiated." He also speaks of "a very fragrant *Tanacetum* or *Artemisia* with pinnated downy leaves *Satureja montana* and *S. Juliana*, I think, have an odour greatly resembling the incense used by the Greek Church, and are gathered by the monks for some ecclesiastical purpose. *Salvia clandestina* has woolly pinnatifid leaves." This last mentioned species of *Salvia* is a most variable one, and has given rise to much discussion and nomenclature. If, however, the effect of the environment be kept in view, which causes the variations, I think the passage from the European *S. Verbenaca* with large flowers and glabrous leaves to the S. European and Desert forms will be probably found to be exemplified by a gradual reduction of the leaf so as to become more deeply indented or of the "coronipifoloid" type, by the glabrous surface passing through a pilose condition till it becomes tomentose as described by Mr. Redhead; while the flower, adapted to insects, runs through the usual degradations till it becomes cleistogamous. Bentham thus speaks of *S. controversa*, which *S. clandestina* connects with *S. Verbenaca* ‡:—"It appears that in the ordinary *clandestine* state of this plant the corolla is abortive, as frequently occurs in *S. Verbenaca* and *S. clandestina*, especially in their more southern stations."

* Vég. du Globe, i. p. 628.

† "Notes on the Flora of the Desert of Sinai," Journ. Linn. Soc., Bot. ix. p. 208.

‡ Labiat. Gen. et Sp. p. 719.

XIII. *General Summary of Observations on Desert Plants.*

Very many additional instances might be given in illustration of the preceding observations, but enough has been stated to bear out the contention, first, that we are justified in concluding, from innumerable coincidences between *structure* and *environment*, that there is some common relation between them of cause and effect; secondly, that all parts of plants are subject to variations, and that while, on the one hand, they may be merely casual, accidental, transient, and of no classificatory value whatever, yet on the other they may become more and more persistent and characteristic, and thence hereditary; affording the systematist features which he may pronounce as varietal or specific, as the case may be. Lastly, seeing how by experimental evidence plants can lose or take on such characters according as they are grown away from or in the normal environment, with which they are associated, the *cumulative evidence* amounts practically to a demonstration that varietal and specific characters are solely acquired through the direct action of the environment.

XIV. *Self-fertilization of the Flowers of Desert Plants.*

In walking along the dry watercourses or "wadys" of the deserts around Cairo, one cannot fail to notice the almost entire absence of conspicuous flowers. This fact is correlated with the paucity of insects. On a closer inspection it is found that a great many, probably the large majority, of flowers are self-fertilizing, the process of pollination being often associated with certain degenerate conditions of the organs of the flowers, as compared with allies of other countries which are adapted to insect visitors.

In my paper on "Self-Fertilization" * I drew up a list of characters some one or more of which are to be found in numerous weeds of cultivation and other plants which are habitually autogamous. Several of these conditions are characteristic of the flowers of Desert plants as well as other special features not therein mentioned.

The general conclusion arrived at by a study of the flowers of the Desert is in complete accordance with those I have elsewhere given †; namely, that flowers which have been adapted to insects,

* Trans. Linn. Soc. ser. II, Bot. i. (1879) p. 317 etc.

† 'Origin of Floral Structures,' Chaps. xxvi. and xxvii.

and therefore endowed with conspicuous and brightly coloured, often irregular corollas, honey, and other details, have to a great degree lost these features by a degenerating process. For if those structures which are correlated with insects were originally brought into existence by these visitors themselves, as I have endeavoured to prove, and if they be not "kept up" by the constantly applied stimulus of their visits, then the protandry, so general in conspicuous flowers, gives way, homogamy follows, and self-fertilization or autogamy is the final result, coupled with numerous degradations in all the floral organs. There are certain orders and genera which are particularly well represented in the Deserts, and I propose selecting a few species as being specially interesting from the peculiarities of their flowers.

The first order to be mentioned is CRUCIFERÆ, represented by over thirty species. A very common plant and one of the largest is the prickly bush *Zilla myagroides*. Another common plant is *Diploaxis Harra*. These two agree closely in the structure of their flowers. The former has small, dull, brownish-pink veined petals; the latter, small pale yellow flowers: in both they are about half an inch in length. The petals of these, as of others of the Cruciferæ and Caryophyllæ, are narrow wedge-shaped or clavate in outline*, never having the broad limb and slender claw of insect-visited cruciferous flowers, such as those of the Wallflower. The two orifices seen from above in the last-named flower are closed up in these Desert plants; while the anthers closely surround the stigma, which in *Diploaxis* is globular, a form which I have shown to be characteristic of British and other self-fertilizing species (*e. g.* Shepherd's Purse and *Pringlea antiscorbutica* of Kerguelen's Island). There are no honey-secreting glands.

Summarizing the peculiarities of several other cruciferous plants, one may note that the flowers are always very small, the petals being narrow, often notched irregularly at the top (*Savignya*, Pl. XII. fig. 3). The colour of the corolla is often brownish pink above, sometimes passing into pale yellow below (*Malcolmia ægyptiaca*, *Zilla myagroides*, *Fursetia ægyptiaca*). The anthers are usually elongated, "linear-sagittate," and always either just above or closely applied to the stigmas (*Malcolmia ægyptiaca*, Pl. XII. fig. 4; *Fursetia ægyptiaca*). The filaments may be curved inwards, bringing the anthers into close contact

* See Pl. XII. figs. 1, 2, 3, and 8.

with the stigmas (*Diplotaxis Harra*). The glands are more or less rudimentary and honeyless or wanting. The pistil may have the two stigmatic lobes adpressed (*Erucaria aleppica*, Pl. XII. fig. 5; *Matthiola livida*, *Malcolmia ægyptiaca*). This would seem to be the preliminary stage, before arriving at the globular condition which occurs in *Diplotaxis Harra*, &c., just as in our common Shepherd's Purse. The pollination takes place in half-opened flowers; and in all the cases which I have personally examined the pollen-tubes were abundantly inserted and undoubtedly issuing from the anthers in contact with the stigmas.

RESEDACEÆ has six species of *Reseda*, *Ochradenus baccatus*, *Oligomeris subulata*, and the very common *Caylusea canescens*. This last has about 5 or 6 distinct carpels, which are in the rudimentary condition of being always open from stigma to base, resembling follicles which have burst completely down the ventral suture. There are numerous ovules grouped together forming a cluster at the base of the carpels (Pl. XII. fig. 7). The minute stigmas are completely surrounded by the numerous anthers and are pollinated by them. The pollen-tubes pass down the inner surface, finally issuing in a great bundle at the base, and then penetrate the inverted ovules. The genus *Reseda* is represented by very small-flowered scentless and self-fertilizing species, the unilateral subcircular disk being much reduced in size.

CARYOPHYLLÆ.—Of this order, *Silene villosa* (Pl. XII. fig. 8) resembles the Crucifæræ in the form of the petals, being irregularly notched at the top and tapering from above downwards. They are also inconspicuously coloured. The anthers are situated just above the stigmas. *Gypsophila Rokejeka* is also a common plant of the northern part of the Eastern Desert. The flowers are only about one sixth of an inch in size.

PARONYCHIACEÆ is represented by twelve species. The flowers are extremely minute and more or less concealed by scarious stipules. They belong to the genera *Robbairaea*, *Polycarpon* (our self-fertilizing *P. tetraphyllum* occurs throughout the cultivated areas), *Polycarpea* (Pl. XII. fig. 9), *Paronychia*, &c.

TAMARICACEÆ has seven species. Their minute flowers have globular stigmas covered with pollen from the anthers surrounding them (*Tamarix mannifera*). In *Reaumuria hirtella* (Pl. XII. fig. 10) the anthers surround the stigmas in the manner common to many self-fertilizing flowers.

GERANIACEÆ has seven species of *Erodium* growing in the Desert; while the British autogamous species *Geranium dissectum*, *G. molle*, *Erodium moschatum* and *E. cicutarium* are common in the cultivated districts; *E. cicutarium* having also established itself in the Desert as well. In the one or two species of *Erodium* which I have had the opportunity of examining, as also of *Monsonia nivea*, the pollen-tubes were visible, the pollen having evidently escaped from the anthers which were crowding round the stigmas.

LEGUMINOSÆ.—Of this order the genus *Astragalus* is the most typical, being represented by fourteen species in the Deserts. The flowers of *A. bombycinus* (Pl. XII. figs. 13, 14) are about one inch in length; but in other species they are very minute, the stigmas in all cases being pollinated by the anthers of the same flower and often before the flower expands (e. g. *A. mareoticus*, *A. tribuloides*, and *A. Sieberi*, Pl. XII. fig. 15). In the larger flowers of *A. bombycinus*, in order to place the stigma in the midst of the anthers the long style is bent in the form of the letter N (Pl. XII. fig. 13), a feature which would seem to indicate that ancestrally the style was curved and elevated above the stamens as in the English Broom. A similar adaptation to self-fertilization occurs in *Cassia obovata* (Pl. XII. figs. 11, 12), one of the two species of this genus found in the Deserts. This has small, very conspicuous brownish flowers, half an inch in length. In this flower some of the anthers are very small, twisted, and appear to be abortive, others are elongated on excessively short filaments and stand erect around the ovary. The style is bent abruptly downwards at its base, having the stigmatic end up-turned, so that the pollen can fall directly upon it. There is no true stigma but a “jagged edge” to the styler crifice; a not dissimilar degradation is found in *Linaria Halava* (Pl. XII. fig. 27) and *Pulicaria arabica* (Pl. XII. fig. 16) of the same Desert*.

UMBELLIFERÆ.—This order is only represented in the Deserts by one or two plants, of which *Pityranthus tortuosus* is perhaps the commonest. This plant has extremely minute flowers in small umbels. The anthers shed their pollen while still incurved over the stigmas.

COMPOSITÆ.—Several characteristic plants of this order are

* A somewhat similar structure occurs in the “monstrous” *Myosotis alpestris*, var. “*Victoria*,” in cultivation, as described in the ‘Journal of the Royal Horticultural Society,’ vol. xvi. 1893, pp. xxv, xxvi.

found in the Deserts. Many have very small capitula. Thus the head of *Ifloga spicata* is six tenths of an inch across; that of *Leontodon hispidulum* and of *Brocchia cinerea* being one quarter; while that of *Artemisia monosperma* is only one eighth of an inch. As the flowers of Compositæ are generally more or less fertilized by one another on the same head, a process practically equivalent to self-fertilization—which is also equally common—there is nothing surprising in finding Desert Compositæ setting seed without the aid of insects.

One or two special points of degradation may be mentioned. In *Cotula anthemoides*, *Brocchia cinerea* (Pl. XII. fig. 20), and *Franceœuria crispa* the customary quinary symmetry has become quaternary. In the first-named plant the outer florets have a very rudimentary corolla with a jagged border. In *Senecio ægyptiacus* (Pl. XII. fig. 18), *Franceœuria crispa* (Pl. XII. fig. 19), *Ifloga spicata*, &c. the stigmas remain included within the anther-tube, just as occurs in the Common Groundsel; in *Senecio ægyptiacus* the two stigmas being situated quite at the bottom of the tube. In all the specimens examined the pollen was early shed and the stigmas matured early. *Artemisia monosperma* has almost microscopically minute florets, and, as might be anticipated, it is completely self-fertilizing, the stigmas being tufted (Pl. XII. fig. 17). This is the only genus of Compositæ the pollen of which, according to Mr. C. F. White's researches, is smooth; but I find that it is so also in *Centaurea ægyptiaca* (Pl. XII. fig. 22).

CAMPANULACEÆ.—*Wahlenbergia cervicina* is a small plant of a few inches in height, and cleistogamous (Pl. XII. fig. 23). On cutting the corolla vertically, the curled stigmas are seen to lie in the midst of the anthers, and are of course directly pollinated by them (Pl. XII. fig. 24). A species of *Campanula*, *C. sulphurea*, is found near the great petrified forest a few miles east of Cairo. The corolla is inclined to be funnel-shaped rather than campanulate (Pl. XII. fig. 25). It is of a pale yellow colour, about three quarters of an inch in length. The anthers shed their pollen early and fall down, as is usual in this genus; but the style and stigmas are remarkable in that the former has few collecting hairs (Pl. XII. fig. 26), except just below the stigmas; while these latter are quite mature and pollinated at an early stage.

BORAGINÆÆ.—Of the genus *Heliotropium* four species, and of *Anchusa* three are found in the Deserts. The flowers are very small. Those of *H. luteum* are about one sixth of an inch in

length, those of *Heliotropium Kunzei* and of *H. undulatum* being one eighth. The orifice of the corolla is nearly or quite closed up by the infolding at the throat, and some, if not all, of the anthers curve over the stigmatic ring*. *Lithospermum callosum*, *Arnebia linearis*, and *Anchusa hispida* have the globular stigma situated just below the anthers. In all these species I have seen the pollen-tubes entering the stigmas, the pollen being undoubtedly derived from the anthers surrounding them.

LABIATÆ.—Of this order the Egyptian Deserts contain fifteen species. They are mostly small-flowered; one only, *Salvia palestina*, being large-flowered and evidently adapted to insects in the well-known manner; but this species is confined to the N.E. portion, and, judging by its limited distribution, it is probably a comparatively late arrival. Of genuinely self-fertilized species the following may be mentioned:—

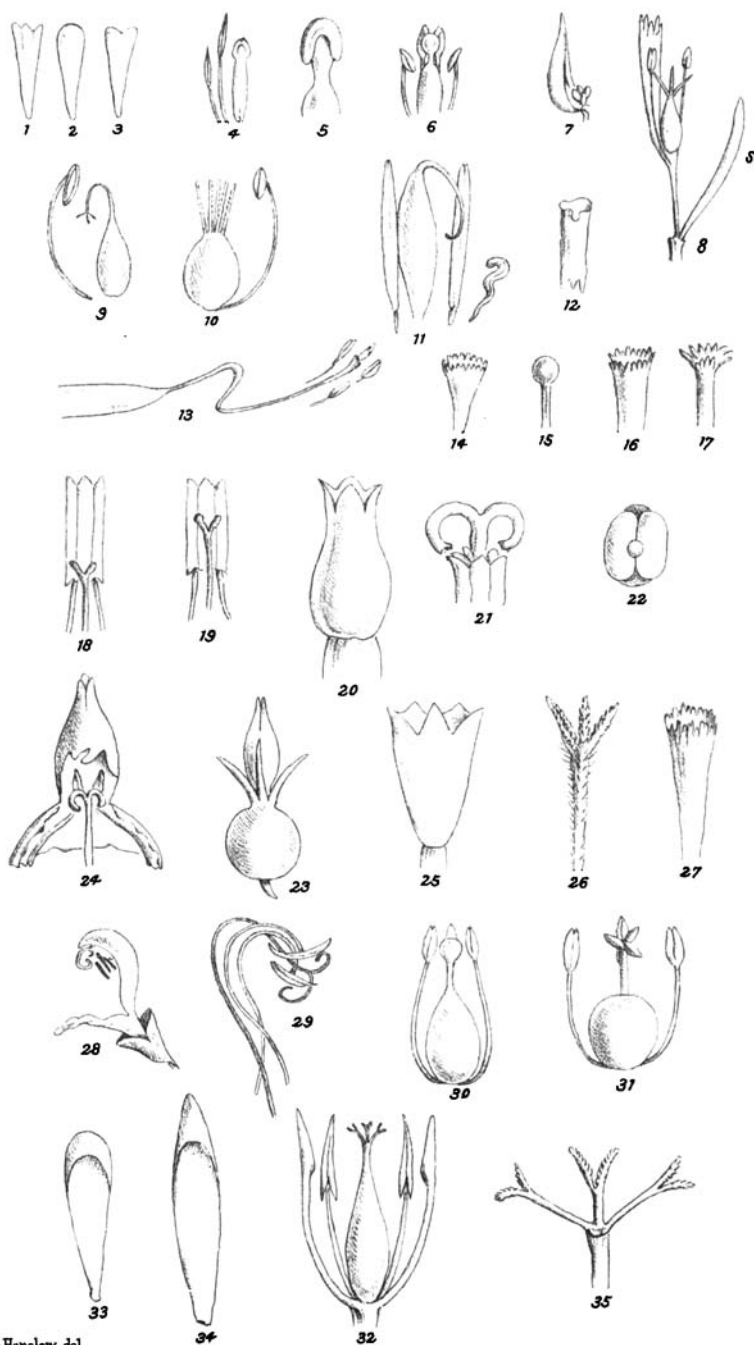
Salvia lanigera (*S. controversa*) (Pl. XII. figs. 28, 29). Though the flowers of this plant are ringent and not at all cleistogamous, the stigmas curl back between the anther-cells, just as in the unopened flowers of *S. clandestina*. *S. ægyptiaca* has minute flowers, about half an inch in length, with the stigmas just below the anther-cell (Pl. XII. fig. 29). *Lavandula atriplicifolia* has a spike consisting of imbricated bracts from which very minute flowers protrude.

SCROPHULARIACÆ.—This order is represented by ten species. *Linaria* has, of course, a flower adapted to insects, but the three species *L. fruticosa*, *L. deserti*, and *L. ægyptiaca* are very small-flowered; they set a profusion of pods, and, judging from dried specimens in the Kew herbarium, they have all the appearance of plants which are independent of insects.

CHENOPODIACÆ.—The members of this order found in the Deserts are all wind- or self-fertilized, as is the case elsewhere. Characteristic Desert species are *Atriplex leucoclada*, *A. Halimus*, *Bassia mucronata*, *Traganum undatum*, *Salsola Pachoi*, *Anabasis articulata*, and *Cornulaca monacantha*. They all have very minute and inconspicuous flowers.

Of **ENDOGENS** the orders best represented in the Deserts are **LILIACÆ** and **GRAMINEÆ**. Of the former *Gagea reticulata*, *Urginea undulata*, *Allium desertorum*, *A. Crameri*, and *Dipcadi erythræum* are found in the north part of the Eastern desert.

* For a suggestion as to the origin of the anomalous position of the stigma in *Heliotropium*, as in *Vinca* &c., see 'Origin of Floral Structures,' p. 135.



G. Henslow del.
A. R. Hammond lith.

Hanbart imp.

ORIGIN OF PLANT STRUCTURES.

The flowers are small and remain only partially open. *Allium Crameri* is one fifth of an inch long, *A. desertorum* one fourth, and *Dipcadi erythræum* one half. In all of these the anthers crowd round the stigmas and pollinate them in the half-opened flowers (Pl. XII. figs. 30, 31). *Dipcadi* is remarkable for having each stigma bifurcated, as in *Euphorbia* (Pl. XII. figs. 32-35); while *Allium desertorum* (Pl. XII. fig. 30) has a globular stigma.

EXPLANATION OF PLATE XII.

- Fig. 1. Petal of *Erucaria aleppica*.
 2. Petal of *Malcolmia ægyptiaca*.
 3. Petal of *Savignya parviflora*.
 4. Stamens and pistil of *Malcolmia ægyptiaca*.
 5. Stigma of *Erucaria aleppica* with closely adpressed stigmatic lobes.
 6. Stamens and pistil of *Savignya parviflora* with globular stigma.
 7. Open carpel and naked ovules of *Caylusea canescens*.
 8. Portion of flower of *Silene villosa* showing position of sepal (s), petal, stamens, and pistil on the gynophore.
 9. Pistil and stamens of *Polycarpæa memphitica*.
 10. Pistil and stamens of *Reaumuria hirtella*.
 11. Pistil and stamens of *Cassia obovata*.
 12. Hollow stigma of *Cassia obovata*.
 13. Style and stigma of *Astragalus bombycinus*.
 14. Stigma of *Astragalus bombycinus*.
 15. Stigma of *Astragalus Sieberi*.
 16. Hollow stigma of *Pulicaria arabica*.
 17. Tufted stigma of *Artemisia monosperma*.
 18. Anthers and stigmas of *Senecio ægyptiacus*.
 19. Anthers and stigmas of *Francaëuria crispa*.
 20. Floret of *Brocchia cinerea*.
 21. Stigmas of *Brocchia cinerea*.
 22. Pollen-grain (smooth) of *Centaurea ægyptiaca*.
 23. Cleistogamous flower of *Wahlenbergia cervicina*.
 24. Corolla of same opened, showing the position of the curved stigmas and anthers.
 25. Corolla of *Campanula sulphurea*.
 26. Stigmas and style of same, nearly devoid of "collecting hairs."
 27. Hollow stigma of *Linaria Helava*.
 28. Flower of *Salvia lanigera*.
 29. Relative positions of anthers and stigmas in the flowers of *Salvia ægyptiaca* and of *S. lanigera*.
 30. Three stamens and pistil of *Allium desertorum*.
 31. Three stamens and pistil of *Allium Crameri*.
 32. Portion of flower of *Dipcadi erythræum*.
 33 & 34. Outer and inner perianth-leaves of same.
 35. Bifurcating stigmas of same.