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THE FUNDAMENTAL PROBLEMS OF PRESENT DAY PLANT MORPHOLOGY.[1]

A FEW months ago I was in Jena in order to attend the unveiling of the statue there erected to M. Schleiden. Now there is hardly any other place which has been of so much significance in the development of plant morphology as this small university town. It was there that Goethe, the originator of the term 'morphology,' busied himself with morphological studies, and founded the idealistic system which has influenced our thought—often unsuspectedly—till the present day. There Schleiden, in outspoken opposition to the conceptions of the idealistic morphology, gave new life to the theory of development founded by Caspar Frederick Wolff in a neighboring hall in the middle of the eighteenth century, and so paved the way for the brilliant discoveries of William Hofmeister. And who does not know what meaning Jena has won as the citadel of phylogenetic morphology, first through the work of Haeckel in zoology and later through that of Strasburger in botany? In such a morphological atmosphere the question forces itself upon us, in what relation do the morphological questions of the present stand to those of the past? Are they still unchanged in spite of the immense increase of empirical ma-

[1] Lecture delivered at the Congress of Arts and Science in St. Louis, September 21, 1904, by Professor K. Goebel, University of Munich; translated by Professor F. E. Lloyd. The theme was proposed by the Direction of the Congress. Since the time allowed for the lecture was but forty-five minutes, the various questions could be indicated merely.

terial, and have the methods of their solution only changed? Or have the problems themselves become different?

To reply to this question is not easy, and the answer must vary with the point of view of the one who makes it. For morphology is yet far from being an exact science, the results of which force themselves upon us with the compulsion of necessity. This is due to the difficulty of the materials, a difficulty which compels us to seek for hypotheses and other subjective means of explanation. It thus comes about that views not only concerning the goal of morphology, but also as to the way in which this goal is to be reached, are widely diverse, and my own views concerning the fundamental problems of morphology are certainly far from being approved by all morphologists.

We may, indeed, say that, apart from minor differences, there are in morphology two main trends of thought which, apparently at least, are opposed to each other, one of which we may denominate formal, and the other causal. Causal morphology is that the aim of which is to determine the causes, in the widest sense, of form relations; this kind of morphology is the youngest, and is far less widely diffused than the formal. To us of a later period it may seem like a remarkable pleonasm, to speak of a 'formal morphology.' Morphology is, of course, the doctrine of form, and therefore any morphology appears to be, in the nature of the case, a formal one, and as a matter of fact has been in its historical development. But in spite of this fact this definition is historically justified, for it designates the tendency of morphology which regards form as something which stands alone for itself, and takes cognizance neither of the functions of organs nor of how they have arisen. This formal morphology arose at first out of the necessities of taxonomy. There had first to be contrived a terminology for the distinction and description of single plant forms. From this function morphology soon, however, became distinct, thus constituting an independent discipline which on its part had served taxonomy a more important service than one might have at first expected. For while taxonomy, in order to find its way amid the maze of plant forms, had to keep in view the differential characters and the separation of single forms from each other, morphology found itself under the necessity of determining what was common to the most various forms and was accordingly directed toward more general questions; morphology taught, as Goethe expressed it, 'Die Glieder der Pflanzen im Zusammenhänge zu betrachten, und so das Ganze in der Anschauung gewissermassen zu beherrschen.' It resulted in the knowledge that, when we regard plants singly, manifold as their parts appear, they may yet be referred to a few elementary forms, and further, morphological research showed that the parallelism between different plant forms could be understood most easily under the assumption which we designate the theory of descent. The establishment of the theory of descent was the result of the morphological research. This we must here especially emphasize, for it shows what significance morphology has gained in respect to our general conception of organisms. But the theory of descent has also reacted upon morphological research, to such an extent, indeed, that it has been held that phylogenetic research is to be regarded as the sole business of morphology. Thus, for example, Scott has said:

> The object of modern morphological botany is the accurate comparison of plants, both living and extinct, with the object of tracing their real relationships with one another, and thus of ultimately constructing a genealogical tree of the vegetable kingdom. The problem is thus a purely historical

one, and is perfectly distinct from any of the questions with which physiology has to do.[2]

This position is certainly justified from the standpoint of the paleontologist. For him, for whom nothing but dead material is at hand, there remains nothing else to do than to make known, through careful comparative study, the structure and relationships of those organisms whose remains are available. This is a very important business. The beautiful results of phytopaleontological research, such as have been attained during the last decade in England and France, have very materially furthered our knowledge of plant forms, and have made to live again before our eyes in a most surprising manner and in the finest details of their structure, types long since vanished from the surface of the earth.

But does this limitation of morphology to the comparative phylogenetic method which is imposed upon the paleontologist exist also for the morphological study of living plants?

There are many of the opinion of Scott; and, indeed, a special 'phylogenetic method,' which is said to be a characteristic of modern morphology, has even been talked of.

Were this the case, then the only difference between the morphology of the present and the earlier, idealistic morphology would consist in this, that in the place of the general ideas with which this operates, as, e. g., 'type,' 'plan of organization,' etc., there would be found phylogenetic conceptions. Such general abstractions are, however, even now difficult to escape, since we can set forth real descent-series only in the fewest instances, and, accordingly, we can not actually point out the stem forms. Yet Darwin himself said:

> We have seen that the members of the same class, independently of their habits of life, resemble each other in the general plan of their organization. This resemblance is often expressed by the term 'unity of type'; or by saying that the several parts and organs in the different species of the class are homologous. The whole subject is included under the general term of Morphology. This is one of the most interesting departments of natural history, and may almost be said to be its very soul.[3]

The significance of formal morphology can not be more forcibly expressed than it was by Darwin. And yet we see that, in Germany at least, interest in morphological problems has greatly decreased. Morphological treatises have become relatively less numerous; morphological books, even such excellent ones as, *e. g.*, Eichler's 'Blüthendiagramme,' do not pass through a second edition, while anatomical and physiological works appear repeatedly in new editions; evidently meeting the demands of the botanical public more fully than morphological works. This may be referred to reasons which lie partly without and partly within morphology itself; both turn out to be true. Histology, cytology and experimental physiology have developed remarkably; new methods in this field promise new results; particular lines of work, however, such as descriptive anatomy, are especially favored because the perfection of the methods of research have quite materially lightened the task of working through a vast array of materials, especially for those to whom the other fields of botanical study are more or less unfamiliar.

But the reasons for the phenomenon which lie within the field of morphology are also clear. Some parts of morphology are well worked out, as, *e. g.*, the doctrine of the more obvious form relations of plants, and the homologies, at least in the large, are determined, although in the matter of detail much remains vague and offers a wide field for exhaustive studies in development. More and more, however, these

[2] Address to the botanical section, British Association for the Advancement of Science, Liverpool, 1896.

[3] 'Origin of Species,' 2: 142.

studies bear the stamp of repetition and complement, from which the stimulus of newness is wanting, or they are carried on upon materials which are very difficult to obtain. The constructions of the idealistic morphology, however, often proved to be untenable.

But the first experiments towards a causal morphology, brought disillusion. For only a short time lived the hope of being able to answer, *e. g.*, the question as to the arrangement of leaves through the effect of mechanical factors, or to refer the form-relations of a plant to the direct influences of gravity and light on the plant. It soon became evident, however, that such involved problems are not to be unraveled by such simple means, and this may well have resulted in the suppression of interest in morphology.

At this point phylogenetic morphology appeared to take on a new lease of life. This, however, in natural science is connected, on the one hand, with the appearance of a new, creative (?) idea, and, on the other hand, with the discovery of new methods. Now the theory of descent has powerfully stimulated morphological research. But has it brought to it, as, *e. g.*, Strasburger has held, a new method, the phylogenetic? Alexander Braun has already properly answered this question in the negative.

Scott, also, has maintained that historical morphology (as regards both living and fossil plants) is dependent upon comparative study, that is, makes use of the same method as was in evidence before the appearance of the theory of descent; indeed, the most important homologies in the plant kingdom became known through Hofmeister at a time when the idea of descent was far from that general acceptation which it at first gained through the life work of Darwin.

The method has then from first to last remained the same: the most comprehensive comparison not only of mature forms, but also their development. A special 'phylogenetic method' there is not, but only a phylogenetic conception of morphological problems. These are, however, just as at first was the case with idealistic morphology, purely formal. Modern morphology, in my sense, however, differs from the older in this, that it goes beyond the method of mere comparison. It allows the setting up of genetic trees to rest for the while, since, with our present knowledge, this meets with insuperable difficulties and has brought almost as much disappointment as the idealistic morphology. For just this reason, namely, because we are persuaded that no other forces have been at work during the phylogenetic history than those which now control the development of each particular organism, do we wish, first of all, more exactly to learn what these are. We are concerned not alone with the determination of the single successive stages of development. These must, of course, be followed, but in addition we should follow all phenomena which may be got at by our means of observation, whether directly, by the microscope, or by chemical analysis. We may, therefore, say: The basal problem of the present day morphology is not phylogenetic development, but development in general. We must, therefore, take our departure from the investigation of individual development (of ontogeny), for only this lies before us complete and without any break, and further, because the study of ontogeny only may proceed from the experimental point of view. An understanding of development is possible only when the conclusions, to which the observation of the phenomena of development has led us, rest upon experimental proof; in other words, when we ask questions of Nature, and obtain our answers to them.

Every little step—and with such only

are we now concerned—beyond the mere descriptive consideration of development is here of significance, and brings the possibility of further progress. And small indeed, I may add, appears to be such advance to those who, from the beginnings of phylogenetic morphology have, like Sisyphus, sustained their courage to roll again and again up the mountain the rock of phylogeny as often as it has rolled down.

It may now be attempted to examine somewhat more closely in certain particular examples the relation between phylogenetic and causal morphology. One of the changes which phylogenetic morphology has brought with it is that it seeks to ascertain which form is 'primitive' and which derived. Idealistic morphology has borne in upon us no conviction on this question, since it derives all forms from a type which is present only as a conception. But phylogenetic morphology must, on the one hand, always reckon with the possibility of polyphyletic development, and, on the other hand, it can operate not only with reversionary structures, as did the idealistic morphology, but must be far more concerned in determining which forms within the series which it proposes stand nearest the common point of derivation. It seeks then with diligence after 'primitive' forms. But in this search we meet with great difficulties. In the first place, we are inclined to regard those forms as primitive which have simple form-relations, and unmarked division of labor. But such forms may also have arisen by reversion, and if one looks over botanical literature, he sees, at least so far as the relationships between the larger groups are concerned, there exists no agreement as to which forms are to be regarded as primitive and which derived; often opinion on this point changes with the fashion. Thus the thallose liverworts have up till now been regarded as more primitive than the foliose, because the vegetative body of the former is much more simple in construction than that of the latter, and between them there are found gentle gradations. Recently, however, the attempt has been made to derive the thallose from the foliose forms. This is not the place to examine the evidence for or against such derivation. How vacillating is the point of view from which it is judged what form is primitive is shown by the various positions which have from time to time been given to the apetalous dicotyledons.

The old morphology regarded these as reduced forms because their flowers are less fully differentiated than those of most of the other dicotyledons. Eichler has, however, already shown that there is no ground for maintaining that the corolla in the 'Iuliflorae' and 'Centrospermae' has suffered reduction; and on this point we can only agree with him. But must they, because the perianth shows simpler form relations and also because the number relations within the flower are not always constant, be therefore primitive? Even if we admit that these groups have a great geological age, it is not proved that they stand as regards their total organization on a lower plane of development; old and primitive forms are the same only when it can be shown that the former stand nearer to the stem forms of the angiosperms than other forms. If this is not capable of proof, then the old forms may just as well be the end terms of long developmental series as others, only that the differentiation of organs has not taken place to the same degree as in the others. Now, we do not know the stem forms if the angiosperms, and they may never, perhaps, be known. But even if we content ourselves by reconstructing them on the basis of comparative study, I can find no reason, *e. g.*, to regard the Cupuliferae as primitive forms, while I can find many reasons for not doing so.

Here may be cited chalazogamy, which elsewhere occurs in forms which may be regarded as degenerate; the facts that only a few of the ovules develop further; that at the time of anthesis they are in many forms not yet present, and finally the dicliny of the flowers. There has been much contention over the question whether the androgynous flowers of these forms are to be admitted to be the original form or not. Let us look at, *e. g.*, the Cupuliferæ. Most of the forms have diclinous flowers. In *Castanea vesca,* however, androgynous flowers occur regularly, and in the male flowers rudiments of the ovary, in the female flowers staminodia are often evident. But we know that for reduced organs all gradations occur from nearly complete development to almost entire disappearance. From the formal standpoint, then, the androgynous flowers may, with at least as much justice, be regarded as primitive as the diclinous ones, which, more recently, have been thus branded. Just this question is, however, fitted to clear up the difference between pure phylogenetic and causal morphology. The latter says: By the mere comparison of forms morphological questions may not at all be decided. We must first of all become more closely acquainted with the forms to be compared, by seeking to determine the conditions under which, in living plants, the configuration of parts is produced. Concerning the flowers of the Cupuliferæ the question then arises: is the occurrence of male and female flowers dependent upon different conditions and are these other than those under which androgynous flowers arise? As a matter of fact, it may be determined that, *e. g.*, in the oak the female flowers always occur in those parts of the twig which are stronger, that is, better nourished than those in which the male flowers occur. This offers us, however, only a point of departure for a more exhaustive research. When we know better the relation between the formation of flowers and the total activity of the plant, when we have the ability at will to cause it to produce male, female or androgynous flowers, when we further know how it is determined that the oak usually brings to development only one out of six ovules, and why the pollen tube follows a different path than the usual, then may we further discuss the question whether the Cupuliferæ are primitive or not—for then shall we have better grounds for phylogenetic conclusions than we have at present, and we shall then recognize with great probability the changes which have taken place in these organs as phenomena resulting from changes in the total organization of these plants.

So, as the matter now stands, we can not deceive ourselves on this point, that the constructions of the old morphology, although confined almost entirely to *vestigial* series, nevertheless stood on firmer ground than the modern speculations on the question of primitive forms. Starting with a completely endowed form, we can follow the reduction of form through intergradations and, by reference to vestigial organs, often with convincing certainty. But by what means shall we judge a rudimentary organ? Is it more than a gratuitous assumption, when, as recently was the case, a certain botanist declares the lodicules of grasses to be not a perigone, but a rudiment (*Ansatz*) of a perigone? Whereby may one recognize a rudiment, *i. e.*, the attempt to form something new, an attempt which, however, has remained nothing more? In what way may we distinguish such a rudiment from a vestigial organ? And, finally, after one has broken faith with the old vestigial series, is it not still more of the stamp of formal morphology if he contents himself in arranging forms in series and then comes to a standstill when he tries to decide at which end

stand the primitive and at which end the derived forms? At any rate, such a limitation brings out the better the true condition of our knowledge, for such an arrangement of forms in a series is about the best service that formal morphology can do. This service is, to be sure, no small one, for it enhances broad critical comparison and is, therefore, the result of hard work. But the desire to give this arrangement in series a genetic bearing has oftentimes led us to untenable propositions and explanations. Just as we have little ground for assigning the Cupuliferæ to a primitive position, so have we as little evidence for regarding the Casuarinæ also in the same light. The latter have been placed by a recent systematist at the apex of his system because there has been an inclination to find in them a sort of 'missing link' between angiosperms and gymnosperms. I may, perhaps, mention that I had regarded such a view as incorrect, even before the evidence was adduced by an American botanist (Frye) that *Casuarina* has evidently nothing which marks it off from other angiosperms. Many of my fellow botanists have been inclined to point out as a further example of the fruitlessness of the search for primitive forms those Bryophytes which have been regarded by me as primitive; and I readily admit that here also we can not point out any conclusive evidence for their primitive position, but only for a greater or less subjective probability. Numerous other examples (as, *e. g.,* the supposed primitive monocotyledons) may be pointed out, which show that the phylogenetic morphology has overrated the prospects of results in search for primitive forms, stimulating as this has been.

This may be seen also if we notice the attitude of phylogenetic morphology to the problem, which the old morphology dubbed with the not very fortunately chosen name of metamorphosis, and which historically is that of homologies. Here, also, it may be shown that the problems have remained the same while only the attempts to reach a solution have changed.

The idealistic morphology believes that all organs of the higher plants may be traced back to caulome, phyllome and trichome; it conceived this process not as a real one, but was content with a conceptual arrangement of different plant organs in these categories, which were really nothing but abstractions.

That thereby the reproductive organs were left entirely out of consideration—these were referred to modifications of vegetative organs—is explained in part by the fact that they occur in the higher plants less frequently as peculiar parts, and often completely disappear in teratological growths, which are with predilection turned to account in theoretical considerations; and in part because of the view that for morphology the function of an organ is a matter of indifference, and that accordingly in morphological considerations it can have no significance whether an organ has developed as a glandular hair, chaffy scale or as an archegonium, so long as it has developed out of the outer cell-layer of the plant body! This standpoint, a complex one, indeed, needs no especial discussion more. Let us, on the other hand, see how phylogenetic morphology has come to terms with the problem of metamorphosis. As an example I select a passage from a prominent American work, in which Coulter and Chamberlain express themselves concerning the leaf structures of flowers as follows:

> While sepals and petals may be regarded as often leaves more or less modified to serve as floral envelopes, and are not so different from leaves in structure and function as to deserve a separate morphological category, the same claim can not be made for stamens and carpels. They are very ancient structures of uncertain origin, for it is quite as likely that leaves are transformed

sporophylls as that sporophylls are transformed leaves. * * * To call a stamen a modified leaf is no more sound morphology than to call a sporangium derived from a single superficial cell a modified trichome. The cases of 'reversion' cited are easily regarded as cases of replacement. Lateral members frequently replace one another, but this does not mean that one is a transformation of the other.[4]

We see that in this verdict the emphasis is laid on the historical development, but at the same time this is pointed out to be unknown to us. With this latter conclusion I am in complete harmony, but the accentuation of the historical-phylogenetic factor has, on the other hand, led to a conception of the ontogenetic problem, in which I can perceive no advance upon the old morphology; there is rather avoidance of the problem than an attempt to solve it. This, however, is connected with the purely formal conception, as the phylogenetic morphology employs it. Let us examine the matter in question. For a long time we have known that often in the room of the stamens—to confine ourselves to these—flower leaves or foliage leaves or occasionally even carpels arise. The idealistic morphology says that this proves that the stamens are 'leaves,' for these can be modified the one into the other. Coulter and Chamberlain, however, deny that a stamen fundament may be transformed into a flower leaf; they find only a 'replacement' of one 'lateral member' by another. It should be remarked that 'leaves' exist in nature as little as 'lateral members.' Both notions are mere mental abstractions, not the expression of the facts of observation. We speak of the replacement of one organ by another if these have nothing more in common than the place of origin. Thus we see that in the foliose liverworts a branch often arises in the position of a leaf-lobe. No one has observed any intermediate form between these; the lateral shoot in reality takes only the position of a leaf-lobe. The relation between the stamens and the organs which 'replace' them is, however, quite different. We speak of a transformation of an organ A into an organ B when B not only stands in the position of A, but also corresponds with A in the earlier stages of its development, and later strikes out on its own line of development. If this is the case, we should expect to find between A and B intermediate forms which are different according to the developmental stage at which A is caused to develop further as B. To use an analogy: Replacement and transformation behave as two fluids which are, and two fluids which are not miscible; in the first case the inner structure is different, and in the second there is a correspondence. The comparison is a limping one, but still gives us a fair illustration.

As a matter of fact, we do find every intermediate step between stamens and flower leaves, and we can not doubt that these have come into existence because a stamen, or, in other words, a stamen fundament, has at different stages of its development received a stimulus which has caused it to develop into a flower leaf. We find correspondingly, that the earlier developmental stages of a stamen and a flower leaf are parallel throughout, while in the above cited example of the branch and a leaf-lobe of a Jungermanniaceous liverwort the developmental history are throughout different, as is shown by the arrangement of cells. In the case of stamens, therefore, there occurs not a replacement, but a transformation. And, indeed, a limited one. Not any 'lateral members' you please may arise instead of stamens, but only and always those which we subsume under the concept leaf, because they evidently have peculiarities in common. Besides, there are also normal flowers which exhibit all intergradations between flower

[4] Coulter and Chamberlain, 'Morphology of the Angiosperms,' p. 22.

leaves and stamens. The former Coulter and Chamberlain would regard as leaves, the latter not; where, however, is the line of separation between them?

From the limited power of transformation possessed by organs it results that in causal morphology the problem is then not a phylogenetic, but an ontogenetic one. Whether sporophylls or foliage leaves are the older phylogenetically may be disregarded. For it appears more important first to determine why the power of transformation is limited, why a shoot-thorn or a shoot-tendril may be transformed only into a shoot, a stamen or a carpel only into a 'leaf'; and second, what conditions are determinative thereto.

The first step toward the solution of the problem is that we learn to call out experimentally and at will such transformations as we have heretofore occasionally observed as 'abnormalities.'

This has been successful in experimental morphology in a great number of cases, and in the future will be still more so. To be sure, we are still unable to induce the transformation of stamens into flower leaves at will—we only deceive ourselves when we believe that the art of the plant breeder has succeeded in doing this, for in reality all he has done is to isolate such races which have occurred in nature with more or less doubled flowers—and in this regard we stand in contrast to the fungi and insects, the activities of which, as Peyritsch and others have shown, often—unconsciously of course—call forth such transformations. Yet it has been possible to change scale leaves (cataphylls) and sporophylls into foliage leaves, inflorescences into vegetative shoots and, *vice versa*, plagiotropous into orthotropous shoots, hypogæous into epigæous, not to mention the interesting results which have been obtained by Klebs in his studies of the lower plants.

Let us take, for example, the just mentioned transformations of scale leaves into foliage leaves and of sporophylls into sterile leaves. Here developmental study and experiment immediately encroach on each other. Development has shown that, *e. g.*, the bud-scales of many trees which in their definitive condition are very different from the foliage leaves, yet parallel them developmentally in an extraordinary degree; and that many bud scales possess the fundament of a leaf blade which has failed to develop and has thus become vestigial. Similarly, the fundaments of the foliage leaf and the sporophyll in *Onoclea* are the same up to a quite late stage of development, beyond which each follows its own course. These facts gave occasion to the question whether or not it were possible to influence the development at will, and so to cause a scale leaf or a sporophyll to grow from a fundament which otherwise would develop into a foliage leaf. It has been shown that such transformations may be occasioned in a simple way, and the developmental correspondence makes such a limited transformation without further difficulty capable of being understood. And since seedlings produce, apart from the cotyledons and certain adaptations in hypogæous germination, only foliage leaves, which are arranged for the work of photosynthesis; since further it is seen that all foliage leaves of one and the same plant, different as they appear externally, yet in reality follow one and the same course of development, which, as we have seen, is remarked also in scale leaves and sporophylls; I accordingly come to the view that other leaf organs are derived from foliage leaf fundaments through a change in the course of development occurring at an earlier or later period of growth. This conception has found many opponents, some of them for the reason that they have not been able to free themselves from the purely historical conception of the problem.

But the historical question can not help us over the ontogenetic problem any more than the solution of the latter alone can answer the historical question. Even if it were proved in all cases that sporophylls, flower leaves, sepals, etc., are transformed foliage leaves, it would remain undecided that these are phylogenetically older than the former. This phylogenetic problem, however, is with our present means and knowledge not subject to solution with certainty, while the ontogenetic problem, on the contrary, is. Problems, however, which may not be solved appear to me less important than those which may.

To be sure, the solution of the ontogenetic problem is hedged about with great difficulties. For the results which have already accrued, valuable as they may be, take their importance from the fact that they lay the foundation for the future work: what changes take place during transformation, and upon what outer and inner conditions are they dependent? We may comfort ourselves as little as could Goethe at one time with the view that flowers differ from the vegetative shoot in a refinement of the sap; rather would we know what change of the materials, and what other changes, are connected with the order of successive developmental stages of the flower. This, to us as good as unacquired knowledge, should give us a more penetrating glance into the nature of development than we have as yet had. To just this purpose plants are especially well adapted, for experience has shown us that the development of a plant is not produced as is the melody in a music box, in a definite order so long as the outer source of power is present to start it; for the experiments of the last few years indicate rather 'that the form relations of chlorophyll-bearing plants are not predetermined in the germ cell, but in the course of development.'[5] As a result we can not only arrest development at any particular stage, but we can also cause fundaments to unfold which were previously 'latent.' Historical morphology has contented itself as regards the unfolding of latent fundaments also with an historical explanation of the facts. The observation, *e. g.*, that instead of the seed scale of the Abietineae under certain circumstances an axillary shoot appears, has been used by prominent botanists to support the conclusion that the seed scale has arisen phylogenetically from a shoot. Such an hypothesis would get beyond the rank of pure supposition if a living or fossil form certainly related to the Abietineæ could be pointed out, the cones of which bear in the axils of the cover scales shoots possessed of macrosporophylls. As long as such proof is not forthcoming, we stand opposed to a phylogenetic explanation of this observation 'kuehl bis ans Herz hinan.' We seek rather to establish the conditions under which the fundaments, which otherwise become seed scales, develop into shoots, and hold before us therewith the possibility that the forebears of the Abietineæ could have borne their ovules upon axillary outgrowth of the cover scales, which, indeed, possessed the ability under certain circumstances which disturbed the normal development to form shoots, but which phylogenetically does not need to have been at any time an axillary shoot.

The question of the significance of metamorphosis leads us into another field of morphology. The above-cited examples show that the transformation of organs always goes on hand in hand with a change of function. This gives us the occasion to take up a further problem of modern morphology: the relation between form and function. The old morphology believed that it should keep away from this question because it held that the function of an organ had nothing to do with its 'morphological meaning.' Just recently we

[5] Goebel, 'Flora,' 1895, p. 115.

have heard that morphology has to do with 'members' and not with the 'organs' of a plant. The fact that 'members' and 'organs' mean one and the same thing, and that for the organism their members are organs, or tools, shows that here again is a purely artificial and therefore untenable abstraction. Morphology stiffens to a dead schematism when it does not take the plant for what it really is—a living body the functions of which are carried on in intimate relation to the outside world. It was the powerful influence of Darwinism that turned more attention again to the function of single plant organs, for, according to one view, which has many adherents, all form relations arise through adaptation. D. H. Scott has given clear expression to this view in the sentence, 'all the characters which the morphologist has to compare are, or have been, adaptive.'

This is a widely disseminated conception, but is by no means as widely accepted. Above all, it must be pointed out that it is not the result of observation, but is a theory, which enjoys by no means general acquiescence. True, the conclusion drawn depends upon the meaning given to the word 'adaptive.' But take it as you will, in the Lamarckian or in the Darwinian sense, in reviewing the phenomena of adaptation we come face to face with the problem: are the form characters fixed adaptational characters solely, or have we to distinguish between organization and adaptational characters? There are several grounds which have led to the belief that organization and adaptational characters coincide. Chiefly the brilliant results which investigation concerning the functional significance of structures as well in the flower as in the vegetation organs has had in the last decade. It was evident that structures to which were earlier ascribed no sort of function yet have such. And if none was found, there yet remained the possibility that the structures concerned had earlier been useful as adaptations. It is, however, clear that we are hereby near to the danger of accepting something as proved which needs rather to be proved. In reality, it seems to me that morphological comparison as well as experiment shows that the distinction between organization and adaptational characters is justified, and that the opinion to which Scott has given expression has arisen from the admission that specific characters have arisen through the accumulation of useful fluctuating variations effected by the survival of the fittest. But we see that in many cases specific characters are not adaptive. If we follow out, *e. g.*, the systematic arrangement of the Liliifloræ, we see that the particular groups differ from each other as to whether the ovary is inferior or superior, and whether it later becomes a capsule or a berry, and, if it is a capsule, whether it is loculicidal or septicidal. Concerning these characters one may well ask whether one can bring the berry or the capsule into relation with the question of adaptation; whether it can be shown that the berry-bearing Liliifloræ occur or have arisen chiefly in those regions where also occur many birds which devour the berries and thus disseminate the seeds. Such a relation can not at present be shown to exist. And who would regard the question whether a capsule opens septicidally, as in the Colchicaceæ, or loculicidally as in the Liliaceæ, as one which stands in relation to adaptation? The method of opening is conditioned by the structure of the fruit in the Colchicaceæ and Liliaceæ, but for the scattering of the seed it is evidently quite a matter of indifference. Shall we conclude that in the past it was otherwise?

Here again we are shown that we get along the best when we start out with the observation of the plants which surround

us, and not with theoretical assumptions and far-reaching phylogenetic hypotheses. The theory of mutations formulated by de Vries with such brilliant results is the result of this kind of patient and step-by-step observation of the now living plant world. The observations of de Vries show us that specific characters arise not through the accumulation of useful variations, but by leaps, and have nothing at all to do with direct adaptation. Such as are disadvantageous in the struggle for existence are weeded out. But selection can not effect the origin of specific or organization characters as such, and this makes it clear to us why—from the human standpoint—one and the same problem may be solved in such different fashions.

The mutation theory of de Vries limits itself to that alone which the observation of the present moment can come at, to the origin of the so-called 'minor species.' But how the division of the plant kingdom into the larger groups has come about, how it has happened that the 'archetypes' have reached such marked development and others have died out or remained in abeyance, are further problems, the solution of which may not so soon be looked for. For this, however, the more intimate knowledge of the factors which regulate the development of the individual from the egg cell to the ripening of the fruit, forms a fundamental starting point. For this purpose plants are especially suitable, since, on the one hand, because of the possession of a *punctum vegetationis,* they are in later life also provided with embryonal tissue, and, on the other hand, because in their form they are more exposed to the influence of the outside world than the majority of animals.

An especially important means in order to the causal study of development has the research into those phenomena proved itself, which we designate the regeneration of new formations as the result of wounding. The questions: what really takes place when an embryonic cell becomes a permanent cell; the reciprocal influences of separate plant organs, which we call correlation; further the problem of polarity; stand out with great clearness in the phenomena of regeneration. I can, however, at this moment only indicate the problems, and can not point out the steps which have been taken toward their solution. A wide vista spreads out before us. The more must we wonder that of the countless botanical papers which appear each year not more than perhaps a dozen are concerned with the problem of development.

Summing up this brief presentation, it should have been shown that morphology, which originally formed a part of taxonomy, then grew apart from it as an independent discipline. Only when it gives up this separate position will morphology take on new life, for such a position is warranted only historically and not in the facts.

The earlier morphologists would have said that morphology has as little to do with the physiology as with the anatomy of plants, which latter, at the time when systematic botany was in the ascendant, they reckoned also as physiology. For physiology was then everything which was not taxonomy. Nowadays it would be carrying coals to Newcastle to point out the significance of the cell doctrine for morphology. For the understanding of alternation of generations, of inheritance and other phenomena fundamentally important to morphology the doctrine of the cell has become of basic significance. The same is true in a higher degree for the relation between morphology and physiology, for all other tasks of the descriptive natural sciences are, after all, only preliminary attempts at orientation, which at length lead

to experimental questioning, to physiology. Indeed, one may say that morphology is that which is not yet understood physiologically. The separation of the different tasks of botany is not in the nature of things proper, but is only a preliminary means at first to orientate ourselves with reference to the maze of phenomena. The barriers between these tasks must then in the nature of the case fall with further progress. I do not wish to deny the value of phylogenetic investigation, but the results which it has brought forth resemble more the product of creative poetic imagination than that of exact study, *i. e.*, study capable of proof. If the knowledge of the historical development of plant forms hovers before us as an ideal, we shall approach it only when we attack the old problems of morphology, not simply with the old method, that of comparison, but experimentally, and when we regard as the basal problem of morphology not phylogenetic development, but the essence of development in a large sense. Even if we had the story of development spread out clearly before us, we could not content ourselves with the simple determination of the same; for then we should be constrained to ask ourselves, how it has been brought about. But this question brings us straight back to the present, to the problem of individual development. For there is for natural science hardly a more significant word than this of Goethe's: 'was nicht mehr entsteht, können wir uns als entstehend nicht denken. Das Entstandene begreifen wir nicht.' It is then the task of modern morphology to learn more exactly the factors upon which at this time the origin of structures depends. To this task, for which there was at that time but little preparatory work consisting of a few important attempts by the gifted Thomas Knight, Wilhelm Hofmeister, who is known to most of us only as a comparative morphologist, did a too little recognized service. For he pointed out, even before this trend of study became apparent in zoology, that the ill-designated 'Entwickelungsmechanik' pursues essentially the same goal as the causal morphology of botany.

We may regard as a motto this sentence from Hofmeister's 'allgemeiner Morphologie': 'es ist ein Bedürfnis des menschlichen Geistes, eine Vorstellung sich zu bilden über die Bedingungen der Formgestaltung wachsender Organismen im allgemeinen.' This is even now the problem of present day morphology. Comparative consideration, including, of course, the especially important history of development, offers us valuable preparation for the intellectual grasp of the problem, but, above all, for the pursuit of the experimental method.

That the zoologists also have felt this necessity to strike out into new ways besides that of comparative morphological observation shows anew that for all organisms the problems are really the same. Let us then take for our watchword development, not only as a problem, but also for the methods with which we seek to bring ourselves nearer its solution.

SCIENTIFIC BOOKS.

Research Methods in Ecology. By FREDERIC E. CLEMENTS, Ph.D. Lincoln, Nebraska, The University Publishing Company. 1905. Pp. xvii + 334.

This work by Professor Clements is intended by the author as a handbook for investigators and for advanced students of ecology, and not as a text-book of the subject. It, therefore, contains a somewhat elaborate account of methods used by the author in his studies of the last eight years during which a serious attempt has been made by him to discover and to correlate the fundamental points of view in the vast field of vegetation.

The book is presented in four chapters or