

of these three methods, since all of them are needed for the investigation of his problems. No less must we demand that he has a firm grasp of the general results of the anthropological method as applied by various sciences. It alone will give his work that historic perspective which constitutes its higher scientific value.

A last word as to the value that the anthropological method is assuming in the general system of our culture and education. I do not wish to refer to its practical value to those who have to deal with foreign races or with national questions. Of greater educational importance is its power to make us understand the roots from which our civilization has sprung, that it impresses us with the relative value of all forms of culture, and thus serves as a check to an exaggerated valuation of the standpoint of our own period, which we are only too liable to consider the ultimate goal of human evolution, thus depriving ourselves of the benefits to be gained from the teachings of other cultures and hindering an objective criticism of our own work.

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PLANT MORPHOLOGY.*

THOSE who organized these congresses left to the guests whom they honored with their invitation a high degree of freedom in the handling of their subject. In the exercise of that freedom, which I gratefully acknowledge, I have decided not to attempt any general dissertation on the present position of plant morphology as a whole, but to discuss certain topics only in the morphology of plants, which at present take a prominent place in that branch of the science of botany. These center round the question of the relation of the axis to the leaf in vascular plants.

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We may, I think, date the foundation of a scientific comparative morphology of plants from the publication of the 'Vergleichende Untersuchungen' of Hofmeister, and his recognition of the fundamental homologies between mosses, ferns and other plants. But notwithstanding the soundness of Hofmeister's comparisons for the alternating generations as a whole, the homologies of the parts remained unsatisfactory; the chief reason for this was that their grouping was not derived from the comparison of nearly allied species; nor does it seem to have been held as important to consider critically whether such parts as were grouped together were or were not comparable as regards their descent. For long years after the publication of the 'Origin of Species' homology had no evolutionary significance in the practise of plant morphology. But in the sister science of zoology this matter was taken up by Ray Lankester, in 1870, in his paper 'On the Use of the Term Homology in Modern Zoology, and the Distinction Between Homogenetic and Homoplastic Agreements.' (Many botanists of the present day would be the better for a careful study of that essay.) He pointed out that the term homology, as then used by zoologists, belonged to the Platonic school, and involved reference to an ideal type. This meaning lay at the back of Goethe's theory of metamorphosis in plants, and it seems to have been somewhat in the same sense that homologies were traced by Hofmeister. Lankester showed that the zoologist's use of the term 'homologous' included various things; he suggested the introduction of a new word to define strict homology by descent; structures which are genetically related in so far as they have a single representative in a common ancestor, he styled 'homogeneous'; those which correspond in form, but are not genetically related, he termed 'homoplastic.'

It is important at once to recognize that the strict 'homogeny' defined by Lankester as that of 'structures which are genetically related in so far as they have a single representative in a common ancestor' can only be traced in the simpler cases of plant form: it implies the repetition of individual parts, so strictly comparable in number and position as to stamp the *individual identity* of those parts in the successive generations. The right hand of a child repeats in position and qualities the right hand of the mother and of the race at large; here is a strict homogeny. In the plant body such individual identity of parts of successive generations is not common. It may be traced, for instance, in the cotyledons, and the first plumular leaves of seedlings of nearly related species, or in their first roots. But as a consequence of that continued embryology, which is so constant a feature in the plant body, the number of the appendages of any individual is liable to be indefinitely increased, while often the absence of strict rule in their relative positions makes their identical comparison in different individuals impossible. This is especially clear in the case of roots of the second, and higher orders; for they do not correspond in exact number or position in seedlings. What we recognize in such cases is then, not the individual identity, but their similarity in other respects; and when we group them under the same head we recognize, not their strict homogeny according to the definition of Lankester, but their essential correspondence, as based upon the similarity of their structure, and of their mode of origin upon, and attachment to, the part which bears them. This is also the case with the antheridia and archegonia of the pteridophytes, which are as a rule definite neither in number nor in arrangement, and are subject to variation in both respects, according to the conditions which

may be imposed upon them by experiment; nevertheless they accurately maintain their structural characters, and their essential correspondence is thus established, but not their individual identity. It is clear that this is a comparison of a more lax order than the recognition of their individual homogeny would be.

But if room for doubt of the strictest homogeny be found in simple cases such as these, what are we to expect from the comparisons of less strictly similar parts of the plant, such as cotyledons, scale leaves, foliage leaves, bracts, sepals, petals, stamens, carpels? How far are these to be held to be homogeneous, or in some less strict sense homologous? Or, going still further, how are we to regard those comparisons which deal with parts of different individuals, species, genera, orders or classes? What degree of homology is to be accorded to them? In proportion as the systematic remoteness of the plants compared increases, and the continuity of the connecting forms is less complete, so the comparisons become more and more doubtful, and the use of the term 'homology' as applied to them more and more lax, until we are finally landed in the region where comparison is little better than surmise. It becomes ultimately a question how far the term 'homology' is to be held as covering these more lax comparisons, which are certainly not examples of 'homogeny' in Lankester's sense, and are only doubtfully correlated together on a basis of comparison of more or less allied forms.

The progress of our science should be leading towards a refinement of the use of the term 'homology'; an approach must be made, however distant it may yet be, to a classification of parts on a basis of descent. But though that may be readily accepted in theory, it is still far from being adopted in the general practise of

plant morphology. None the less, comparison is inevitably leading to the disintegration, on a basis of descent, of the old-accepted categories of parts; of these the most prominent, and at the same time the most debatable, is the category of leaves, and they will lend themselves best to the illustration of the matter in hand.

To those who, like myself, hold the view that the two alternating generations of the Archegoniatae have had a distinct phylogenetic history, it will be clear that their parts can not be truly comparable by descent. The leaf of the vascular plant, accordingly, will not be the correlative of the leaf of a moss. Even those who regard the sporophyte as an unsexed gametophyte will still have to show, on a basis of comparison and development, that the leaves of the two generations are of common descent. I am not aware that this has yet been done by them.

But the phylogenetic distinctness of the leaves in the sporophyte and gametophyte is not the only example of parallel foliar development. Goebel has shown with much cogency that the foliar appendages of the bryophytes are not all comparable as regards their origin; he remarks, 'It is characteristic that the leaf formation in the liverworts has arisen independently in quite a number of series' ('*Organographie*,' p. 261), and has shown that they must have been produced in different ways. Here then is polyphyleticism in high degree, seen in the origin of those parts of the gametophyte which on grounds of descent we have already separated from the foliar appendages of the sporophyte.

Such results as these for the gametophyte lead us to enquire into the views current as to the origin of foliar differentiation in vascular plants. In discussing such questions, it is to be remembered that in different stocks the foliar condition of the sporophyte as we see it may have been

achieved in different ways, just as investigators have found reason to believe that it was in the gametophyte. We have no right to assume that the leaf was formed once for all in the descent of the sporophyte. But at the moment we are unprovided with any definite proof how it occurred. All the evidence on the point is necessarily indirect, since no intermediate types are known between foliar and non-foliar sporophytes. Physiological experiment has as yet nothing to say on the subject. The fossil history of the origin of the foliar state in the neutral generation is lost, for the foliar character antedated the earliest known fossil-sporophytes. There remain the facts of development of the individual, and comparison, while anatomical detail may have some bearing also on the question; but all of these, as indirect lines of evidence, fall short of demonstration, and accordingly it is impossible to come at present to any decision on the point. For the purposes of this discussion, however, we shall proceed on the supposition that all leaves of the sporophyte generation originated in essentially the same way, though not necessarily along the same phyletic line.

There are at least three alternatives possible for the origin of the foliar differentiation of the shoot, in any progressive line of evolution of vascular sporophytes: (1) That the prototype of the leaf was of prior existence, the axis being a part which gradually asserted itself as a basis for the insertion of those appendages; the leaf in such a case would be from the first the predominant part in the construction of the shoot. (2) That the axis and leaf are the result of differentiation of an indifferent branch-system, of which the limbs were originally all alike; in this case neither leaf nor axis would predominate from the first. (3) That the axis preexisted, and the foliar appendages arose as outgrowths upon it; in

this case the axis would be from the first the predominant part.

The first of the above alternatives, viz., that the prototype of the leaf existed from the first, and was indeed the predominant part in the initial composition of the shoot, has been held by certain writers as the basis of origin of the leafy shoot in vascular plants.* On this view not only is the whole shoot regarded as being mainly composed of leaves, but some even contend that the axis has no real existence as a part distinct from the leaf bases.†

This view in its general form represented the plant as constructed on a plan somewhat similar to that of a complex zoophyte. It has more recently culminated in the writings of Celakovsky and Delpino. The former in his theory of shoot-segments ('Sprossgliedlehre') starts from the position that the plant is composed of morphological individuals; the cell, the shoot and the plant stock are recognized as such. The stock is composed of shoots, and the shoot of cells. Braun recognized the shoot as the individual *par excellence*; between the cell and the shoot is a great gulf, which has not yet been filled; 'between the cell and the bud (shoot) there must be intermediate steps, the limitation of which no one has succeeded in defining'; the long sought for individual middle step is the shoot segment (Spross-glied), which is neither leaf only, nor stem segment only, but the leaf together with its stem segment. Now this appears to me to be purely Platonic morphology; the intermediate step *must* occur; we will, therefore, discover and define it. The definition of it consists

* Goethe, 'Die Metamorphose der Pflanzen.' Gaudichaud, *Mem. de l'Acad. d. Sci.*, 1841. Kienitz Gerloff, *Bot. Zeit.*, 1875, p. 55. Celakovsky, 'Unters. ueber die Homologien,' *Pringsh. Jahrb.*, XIV., p. 321, 1884; *Bot. Zeit.*, 1901, Heft. v., VI.

† Delpino, 'Teoria generale della Filotassi.' For ref. see *Bot. Jahresbr.*, VIII., 1880, p. 118, also Vol. XI., 1883, p. 550.

in the drawing of certain transverse and longitudinal lines partitioning the shoot, lines which in the sporophyte have no existence in nature; the assumed necessity of partitioning the shoot into parts of an intermediate category between the whole shoot and the cell brings these assumed limits into existence.

Notwithstanding the ingenuity of the theory as put forward by Celakovsky, in the absence of any structural indication of the limits of the shoot segments in the vast majority of cases the theory does not appear to me to be sufficiently upheld by the facts.

An extreme, and indeed a paradoxical position has been taken on this phytotic question by Delpino. As a consequence of his studies on phyllotaxis he concluded that the axis is simply composed of the fusion of the leaf bases; that the leaves are not appendicular organs, but central organs; that an axis or stem system does not exist, and accordingly that the higher plants are not cormophytes at all, but phyllophytes. There will, I think, be few who will adopt this fantastic view of the shoot.

The second view, that the axis and leaf are the result of differentiation of an indifferent branch system, of which the limbs were originally all alike, has lately been brought into prominence by Potonié.* Taking his initiative from the branching of the leaves in early fossil ferns, he recognizes the frequent occurrence of overtopping ('Uebergipfelung'), that is, the gradual process of assertion of certain limbs of a branch system over others; in the branching of fucoids he finds an analogy for his observations on fern leaves, and draws the following conclusion, that 'the leaves of the higher plants have been derived in the

* 'Lehrbuch d. Pflanzenpalaeontologie,' pp. 156-159. Also 'Ein Blick in die Geschichte d. Bot. Morph. und d. Pericaulomtheorie,' 1903, p. 33, etc.

course of generations from parts of an algal thallus like that of *Fucus*, or at least from alga-like plants, by means of the overtopping of dichotomous branches, 'and the development as leaves of the branches, which thus become lateral.' Dr. Hallier, who adopts Potonié's position, prefers to draw the comparison with liverworts, which show a similar sympodial development of a dichotomous branch system.*

It seems not improbable that the condition of many branched fern leaves may have been derived through a process of 'overtopping' in an indifferent branch system of the leaf itself. But it lies with Potonié to show, on a basis of comparison of forms more nearly related to them than the fucoids, that the relation of axis to leaf in the ferns was so derived; and, further, that such an origin is in any way applicable to other foliar developments in vascular plants, especially pteridophytes such as the lycopods, equisetia and sphenophylls. I am not aware that this has yet been done. But granting that this can be done, the question still remains whether similarity of method of branching is any criterion of comparison as to descent. And especially whether such comparison is valid between widely distant groups, or between the different generations of an antithetic alternation. It is true that Potonié prefers to regard such generations as homologues, as is indeed essential for his view; but that does not prevent others from differing from him, or even considering the fact that the parts compared belong to different generations as fatal to his theory. For my own part, I am not prepared to give up the broad conclusions as to antithetic alternation on so slender a ground as similarity of method of branching represented in them both. For sympodial development of a dichotomous sys-

tem (and this is all that such 'overtopping' actually is) has occurred in cases where it can not be held to have resulted in a branching which is foliar; and of this instances can be found without going so far afield as the Fucaceæ. If this be so, then little value need be attached to the comparison of such branchings in plants not nearly allied to one another; these may be held to be quite distinct examples of a general phenomenon, without the one being in any sense the prototype of the other. Such reflections as these indicate that the comparison in mode of branching between the leaves of ferns and the thallus of fucoids, which forms the groundwork of the view of Potonié (or between the ferns and the thalloid liverworts, as may be preferred by others), are not to be held as more than distant analogies; consequently they are no demonstration of the origin of the leaf by a process of 'overtopping.'

There remains the third view, which, however, is no new one; for there have not been wanting those who have assigned a more prominent place to the axis in the initial differentiation of the shoot. Perhaps the most explicit statement on this point is that by Alexander Braun, who remarks in his 'Rejuvenescence in Nature' (English edition, p. 107), referring to phytonic theories, that 'all these attempts to compose the plant of leaves are wrecked upon the fact of the existence of the stem as an original, independent and connected structure, the more or less distinct articulation of which certainly depends upon the leaf formation, but the first formation of which precedes that of the leaves.' Unger also in his botanical letters to a friend (No. VIII.), described how 'The first endeavor is directed towards the building up with cell-elements of an axis'—'those variously formed supplementary organs which are termed leaves originate laterally upon it'

* 'Beitrage z. Morph. d. Sporophylle u. d. Trophophylls,' Hamburg, 1902.

and he concludes that 'we may [therefore] say with perfect justice that the plant * * * is, as regards form, essentially a system of axes.' Naegeli contemplated a somewhat similar origin of the leafy shoot, as an alternative possibility; in fact, that the apex of a sporogonium-like body elongated directly into that of the leafy stem, in which case the axis would be the persistent and prominent part, and the leaves be from the first subsidiary, and lateral appendages. In my theory of the strobilus in archegoniate plants the central idea was somewhat similar to this. It may be briefly stated thus: There seems good reason to hold that a body of radial construction, having distinction of apex and base, and localized apical growth as its leading characters, existed prior to the development of lateral appendages in the sporophyte; for such a body is seen in certain bryophyte sporogonia, while the prior existence of the axis and lateral origin of the appendages upon it are general for normal leafy shoots. The view thus put forward is, indeed, the mere reading of the story of the evolution of leaves in terms of their normal individual development. I have recently shown that all pteridophyte shoots may be regarded as derivatives from the radial strobiloid type, with relatively small leaves, which would thus have come into existence.

It is natural to look to the pteridophytes for guidance as to the origin of foliar development in the sporophyte, for they are the most primitive plants with leafy sporophytes. They may be disposed according to the prevalent size of their leaves in a series, leading from microphyllous to megaphyllous types. I have lately shown that such a seriation is not according to one feature only, but that certain other characters which have been summarized as 'filicineous' tend to follow with the increasing prominence of the leaf. This

indicates that such seriation is a natural arrangement. Now it is possible to hold either that the large-leaved fern-like plants were the more primitive, and the smaller-leaved, derivatives from them by reduction; or, conversely, that the smaller-leaved were the more primitive, and the larger-leaved derivatives from them by leaf-enlargement; other alternative opinions are also possible, such as that the leaf origin has been divergent from some middle type, or that the leaves of vascular plants may have been of polyphyletic origin.* For the moment we shall leave these latter alternatives aside.

Much of the difference of view as to foliar origin centers round the question whether originally the leaf was relatively large or small. Those who hold that the large-leaved forms were the more primitive will be naturally disposed towards the view of the original preponderance of the leaf

* The view recently advanced by Professor Lignier ('Equisetales, et Sphenophyllales. Leur origine filicinienne commune,' *Bull. Soc. Linn. de Normandie*, Serie 5, Vol. 7, Caen, 1903) is analogous to that of Potonié, though differing from it in detail. It involves the ranking of the lycopod leaf as a 'phylloid,' the leaf of the fern as a true leaf, or 'phyllome,' differentiated from an indifferent system of 'cauloids,' on which the 'phylloid' appendages had become abortive. It regards the leaves of equiseta and sphenophylls as phyllomes, reduced from the larger-leaved fern-type. The argument is chiefly based on comparisons as to branching and anatomical structure. I do not think that these grounds suffice to override the probability that the leaves of lycopods are essentially of the same nature as those of the sphenophylls or equiseta (compare my 'Studies,' No. V.). Professor Lignier's view further involves the acceptance of homologous alternation, while he makes no mention of the chromosome-differences of the two generations. Such difficulties do not arise if the leaves of the sphenophylls and equiseta are regarded as being in the upward rather than the downward scale of development, a view of them which would equally harmonize with the anatomical comparisons of Professor Lignier.

over the axis, and will favor some phytonic theory; those who hold the smaller-leaved forms to be the more primitive will probably adopt a strobiloid theory of origin of the leafy sporophyte. I propose to offer some remarks on the relative probability of these alternative views.

If large-leaved prototypes be assumed generally for vascular plants, this naturally involves a widespread reduction, since small-leaved forms are numerous now, and have been from the earliest times of which we have any record. Reduction is a ready weapon in the hands of the speculative morphologist, and it has often been used with more freedom than discretion. But reduction should never be assumed in order to meet the demands of convenience of comparison, nor as a cover for doubt. The justification of a view involving reduction must be found in its physiological probability in the case in question, and this should be backed by comparisons of form and of anatomical structure; the conclusion should also be in accordance with the paleontological record. All suggested cases of reduction where such justification is absent should be looked upon as doubtful.

Convincing evidence of reduction of leaf complexity in an evolutionary sequence, supported on all these grounds, has been adduced in the progression from ferns, through cycado-filicinean forms, to the cycads; and it applies with special force in the case of their sporophylls. Ferns, which are essentially shade-loving and typically zoidiogamic, or amphibious, may be understood to have given rise to the cycado-filices, and cycads, which are more xerophytic, and show that essential character of land plants—the seed habit. Not only is such a progression physiologically probable, but it is supported by paleontological evidence, as well as by detailed facts of anatomy, and of reproductive morphology. The case for reduction of leaf complexity seems to

be here fully made out, and somewhat similar arguments will also apply for other types of gymnosperms.

The facts relating to the vascular system of the shoot have also their bearing on the question of the relative size of primitive leaves. The origin of the leaf trace from the axial stele in conifers, and also in angiosperms, has been shown by Dr. Jeffrey to be of the type styled by him phyllosiphonic. This is specially characteristic of those plants where the leaf is essentially the dominating influence in the shoot. In this I see a probability, which their physiological position as land-growing plants would justify, that the seed-bearing plants at large were descended from a large-leaved ancestry, and had undergone reduction of leaf complexity in their descent. But while we thus recognize a probability of widespread reduction producing relatively smaller-leaved forms, it does not follow that *all* small-leaved vascular plants originated thus. On this point the anatomical evidence is of importance, as bearing on the origin of the small-leaved strobiloid pteridophytes. Of these (putting aside the hydropterids as being a special reduction problem in themselves), there remain the Lycopodiales, the Equisetales and the Sphenophyllales, which are all cladosisiphonic in the terminology of Dr. Jeffrey. The question will largely turn upon the meaning of this anatomical feature. I take it to be as follows: The cladosisiphonic character is the anatomical expression of the dominance of the axis in the shoot. Here the leaf trace is merely an external appendage on the stele, which is hardly disturbed by its insertion. This type is seen in certain small-leaved pteridophytes. The phyllosiphonic character, on the other hand, is the anatomical expression of the dominance of the leaf over the axis in the shoot. Here the insertion of the vascular supply of the leaf profoundly disturbs the

vascular arrangement in the axis. It is characteristic of certain large-leaved pteridophytes, and is seen also generally in seed plants.

It is a fact of importance that, in the individual life, the one or the other type is usually constant; but in certain ferns the progression may be traced from the cladophonic in the young plant to the phyllosiphonic in the mature, thus suggesting a similar progression in descent, viz., that the large-leaved phyllosiphonic ferns were derived from a smaller-leaved cladophonic stock. Of the converse, viz., the progression from the phyllosiphonic to the cladophonic state in the individual life, I know of no example among the pteridophytes, though it is true that there is some approach to it in the Marsileaceæ. Thus the anatomical evidence indicates a probability that, even in large-leaved ferns, the cladophonic was the primitive type; but that the phyllosiphonic, once initiated, is as a rule maintained; this is shown by its persistence in the seed plants, even where the leaf has been reduced in size.

Having thus gained a valuable sidelight from anatomy, we may now return to our central question, of the initial relation of leaf to axis. Of the three theories already noted, the theory of overtopping as applied to the origin of the leaf, may in my opinion be dismissed, as it is not based upon comparison of nearly related forms, while the sympodial development of a dichotomous system, on which it is founded, is a general phenomenon of branching, restricted neither to leaves nor to the sporophyte generation. As to the other two, the facts whether of external form or of internal structure seem to me to indicate this conclusion: that the strobiloid condition was primitive for certain types, such as the Equisetales, Lycopodiales and Sphenophyllales; that in them the leaf was from the first a minor appendage upon

the dominating axis; and anatomically they have never broken away from the cladophonic structure, which is the internal expression of their microphyllous, strobiloid state. That the Filicales and also the Ophioglossales were probably derived from a microphyllous strobiloid ancestry, and achieved the phyllosiphonic structure as a consequence of leaf enlargement, this being the derivative rather than the primitive condition; its derivation is even illustrated in the individual life of some ferns. From the Filicales the phyllosiphonic structure was probably handed on to the seed plants, and by them retained, notwithstanding the subsequent leaf reduction which followed on their adaptation to an exposed land habitat. Thus a strobiloid origin may be attributed to all the main types of vascular plants. It seems to me to harmonize more readily with the facts than any phytonic theory does.

A prototype, which was probably a prevalent, though perhaps not a general, one for the pteridophytes, may then be sketched as an upright, radial, strobiloid structure, consisting of a predominant axis, bearing relatively small and simple appendages. On our theory the origin of those appendages in descent would be the same as it is to-day in the individual development, viz., by the outgrowth of regions of the superficial tissue of the axis to form them. The axis would preexist in descent, as it actually does in the normal developing shoot. The origin of these appendages may have occurred independently along divers lines of descent, and the appendages would in that case be not homogeneous in the strict sense. Thus there would be no common prototype of the leaf, no morphological abstraction, or archetypic form of that part. More than one category of appendages might even be produced on the same individual shoot, differing in their function on their first appearance. Such has perhaps been

the case in the calamarian strobilus, where the leaf tooth can not be readily homologized with the sporangiophore. These suggestions will suffice to indicate how elastic a strobiloid theory is, and how its application will cover various types of construction, even such as are shown by the most complex cones of pteridophytes.

From the comparison of living species there is good reason for thinking that all the primitive leaves in certain types, such as the lycopods, were sporophylls, and that a subsequent differentiation took place, by abortion of the sporangia; thus a sterile vegetative region became defined from a fertile upper region. It may be a question whether this origin by sterilization of sporophylls is applicable to foliage leaves at large. Nevertheless, analogy, not only with other vascular plants but also with the bryophytes, suggests that a similar differentiation of a sterile from a fertile region has been a general phenomenon in the neutral generation. At first in the simpler pteridophytes these regions were essentially similar to one another in form, as is still seen to be the case in some lycopods. Later, however, the sterile and fertile regions took divergent lines of development in accordance with their difference of function. The differentiation reaches its climax in the higher flowering plants. The inflorescence, or flower, on this view, though produced later than the vegetative region in the individual life, embodies the more primitive parts, viz., those which bear the sporangia and spores. The vegetative region is in its origin mostly, if not wholly, secondary. The physiological reasonableness of this view is too obvious to need insistence. As the self-nutritive powers of the gametophyte fell off in the adaptation to the land habit, the nutritive function was taken up by the new vegetative system thus intercalated between sexual fusion and spore production.

This is in brief outline the strobiloid theory of the shoot in vascular plants, as arising out of the facts of antithetic alternation. It will be seen that it is essentially in harmony with the view of Braun, upheld also by Sachs, that the shoot is the real morphological unit, of which leaf and axis are correlative parts. Those who adopt it will find their position simplified in regard to another question which has recently taken afresh a prominent place in morphological discussions, viz., the theory of cortication (*Berindungstheorie*). It is held by Potonié, and a similar view was also maintained by Celakovsky, that the stem has centrally an axial nature, peripherally a leaf nature. The primitive axis (*Urcaulom*) acquires in the course of generations, by coalescence with the basal parts of its primitive leafy appendages (*Urblätter*), a mantle,—a ‘*Pericaulom*.’ This is what we commonly designate the cortex, which is thus regarded as not being axile in origin, but foliar. In accordance, however, with our strobiloid theory we may presume that, as is seen in some of the bryophytes, the simple sporophyte consisted originally of a central region—a primitive stele—and a peripheral region, a primitive cortex. From the latter sprang the appendages, as superficial outgrowths, just as at the present day the leaves originate upon the cortex of the axis. The cortex in such cases would be, from the first, part of the primitive axis, and the outgrowths processes from it. The primitive cortex from which the appendages sprang may remain a continuous, undifferentiated band, as it actually does appear in the vast majority of leafy sporophytes; or it may be in certain cases more or less clearly marked off into regions surrounding the insertion of the individual leaves. But in the fact that these special cases exist I see no sufficient foundation for the view that each leaf is, in shoots at

large, connected with a definite area of extended leaf-base; and still less for the theory that in vascular plants the cortex originated from such coalescent leaf bases. Our theory of the strobilus would, indeed, presuppose that close relation of cortex and appendage, and absence of limit between them, which is so common a feature in vascular plants; and furthermore, it will readily cover the facts where the cortex is delimited into definite areas round the leaf bases; but it does not recognize any necessity for generalizing from such cases of special delimitation that the cortex is foliar in its origin, in shoots of vascular plants at large. It would be more ready to suggest the converse, viz., that the leaves were cortical in their origin, as, indeed, they are in the ontogeny.

Discussions such as these on phytonic theory, or theory of cortication, are liable to develop into mere scholastic contests. They originated in the present case in the use of terms in an unprecise sense, and the subsequent attempt to attain precision. Both these theories have proceeded from the assumption that the 'leaf' is an abstract entity, distinct from the stem. Difficulties arise when the attempt is made to carry out that distinction sharply in practice, for this is nothing less than the attempt to define precisely things which in point of fact appear neither uniform nor precise in nature. The strict definition of terms used in morphological science is doubtless in itself a desirable thing; but it must be so conducted as to harmonize with the facts of individual development, while at the same time it must not violate evolutionary probability. As a matter of fact, neither in the mature state nor in the ontogenetic or phylogenetic development of the leaf does the structure suggest its sharp delimitation from the axis as a general feature in the shoots of ordinary vascular plants.

My present position with regard to the phytonic theories and the theory of cortication is frankly destructive; for in the first place, if the evidence from the gametophyte generation be discounted, the facts of segmentation in the sporophyte are of the slenderest; further, I do not think that morphological insight will be advanced by attempts to define precisely the limits of the parts of the vascular shoot; it seems more in accordance with nature to accept for vascular plants the view of Braun and of Sachs, that the shoot is the original unit. What is first urgently required, in order to decide such questions, is the correct recognition of the phyletic lines which eventuated in the various appendages as we see them. Then may follow definitions of the parts, which may or may not succeed in assigning their strict limits. When this is accomplished a terminology may follow which shall segregate parts which have had a separate phyletic origin. Thus an evolutionary morphology of the shoot would be built up. But it is useless to accept the thesis merely in the abstract that the basis of morphology must be in phylogeny; the principle must also be put in practice, and be ultimately reflected in our methods, and in the definition of our terms.

A step in this direction will be the recognition that at present the word 'leaf' is loosely applied; it is, indeed, a temporary makeshift borrowed from colloquial language, and used in a descriptive rather than in a strictly scientific sense. It designates collectively objects which have, it is true, formal and functional, and even topographical, features in common, but have not had the same phyletic history. There is every probability that the word 'leaf' will continue to be used in this merely popular sense.

This position, with its conservative use of terms fitting awkwardly upon advanc-

ing phyletic ideas, can only be properly understood by glancing back at the history which has produced it. So long as species were regarded as the individual results of creative power, the complexity and variety of their form were relegated to the arcana of the divine mind, and organic nature presented the aspect of a series of isolated pictures; any similarity which these might show was to be regarded as indicative of the underlying divine plan. Now that species have been threaded together by evolutionary theory into developmental sequences, they, like the ribbon of a cinematograph, present phyletic history to the mind with all the vividness of a living drama. While monophyletic views held the field, this seemed comparatively simple; but the conclusions thus arrived at in plant morphology were often palpably improbable. Such difficulties, together with the substantiation of examples of parallel development on a sound comparative basis, led to the modification of monophyletic views, and opened the way for less cramped conceptions. It is now customary to contemplate the plural origin of such leading features as sexual differentiation, foliar development, heterospory, the seed habit, as well as a host of minor characters. On such examples we base a general belief that similar structures may be arrived at by divers evolutionary routes. It is this conception of polyphyleticism that we must make clear in our descriptions, if not even in our terminology.

It will be objected that to carry through a method of designating by the same term only such parts as are shown to be of common descent would produce unwieldy results. Doubtless this is true, but in the terminology of a science it is not so much convenience, as truth and clearness which should be the aim. The choice is open to us either to make the terminology strictly phyletic throughout, which would certainly

be cumbersome, though it would reflect the true position, or, putting phyletic distinctions in the background, to use terms in a more or less comprehensive sense, even grouping together things which we know to have been distinct in phyletic origin. Such a comprehensive sense is conveyed by the expression 'homology of organization,' which, as Goebel points out, 'has only to do with phylogeny in so far as it recognizes a common capacity for development derivable from undifferentiated ancestors.'*

This is, indeed, a collective term for the results of parallel development; it suffers from the danger of suggesting some ideal type, or pattern, towards which evolution has tended.

For my own part, I think it matters little what our terminology be, or what the separation of categories of parts, provided we attach clear meanings to the words we use, and select those words as naturally conveying that meaning. For instance, if we fully realize that the word 'leaf' is used in a sense which is not phylogenetic, but merely descriptive of those lateral appendages on the shoot which are produced exogenously, and in acropetal order, then let it remain, ranking as an expression of 'homology of organization.' But the appendages thus included may for clearness be conveniently divided into 'phyllomes' on the sporophyte and 'phylloids' on the gametophyte, as indeed I suggested some years ago. Nevertheless, these again are not phyletic unities; they include parts with distinct histories which have already been recognized in the gametophyte, while for the sporophyte a more advanced state of the science will probably provide definitions. Meanwhile we consent to a compromise in grouping these together; but the only condition upon which this can be safely done is the clear knowledge that this is a compromise by which we secure a cer-

* 'Organographie,' English edition, p. 19.

tain convenience of description. Moreover, the acceptance of this compromise must not be understood to grant free license to argue from one to another of the forms included, as though they were equivalents; what has resulted in one line of descent can at best only throw a side light on what has happened in another distinct line, and in proportion as the lines involved in a comparison are more remote from one another, their comparison assumes more and more the character of a mere analogy. The danger which our compromise brings with it is that this will not be clearly kept in mind. At all hazards the strict phyletic view should underlie all present morphological discussion, notwithstanding that, for mere convenience, that view may not be clearly reflected in the classification of the parts. This makes me hope that the compromise is only a temporary concession, and that it will give way ultimately to the demands which a more detailed knowledge of descent is sure to bring.

It is well, however, in connection with discussions such as these, to impress upon the lay public that all evolutionary theories are, like other scientific theories, hypotheses incapable of complete proof. No one will appreciate this more fully than biological investigators themselves, for they are in the best position to know how insufficient the evidence actually is, and how liberal a use has to be made of the imagination in bridging over the wide gaps in the series of known forms. The details of a story thus constructed depend so largely on comparative opinion, and in so slight a degree on positive demonstration, that the history as told by competent experts in comparative morphology may vary in material features. A little more weight allowed for certain observed details, or a little less for others, will be sufficient to disturb the balance of the evidence derived from a wide area of fact, and consequently

to distort the historical picture. There is in truth no finality in discussions on the genesis and progress of organic life, or in the kaleidoscopic changes of opinion, since any new fact of importance will in some degree affect the weight accorded to others, and may vary the general result. It will be objected that conclusions which are so plastic are little better than expressions of personal taste; that the study of comparative morphology, is, therefore, calculated to dishearten its votaries, while the non-specialist public, which is compelled to take its information at second hand, will be bewildered, and will conclude that it is useless to pursue a subject which shows so little stability. But, on the other hand, those who follow the progress of morphology with sympathetic care will take heart when they compare its present position with that of a generation ago; it is encouraging to think that it is little more than half a century since the history of the life cycle of a fern was first completed. In some sixty years a vast array of kindred facts has been acquired, and a theoretic structure is being raised upon them which, though still protean, is gradually acquiring some settled form. Never has the advance of morphological thought been more rapid than at present. The support of the facts of alternation from the unexpected quarter of minute cytology has been one of the most striking features in the recent history of our science. The discovery of spermatozoids in the cycads and *Gingkoaceæ* has filled in a gap in the story of evolution which all followers of Hofmeister must have felt. But in no field of morphological research has investigation been more amply rewarded than in paleophytology. The luminous facts derived from fossils are shedding fresh light on obscure problems, such as the origin of the seed habit, and helping us to locate such difficult groups as the *Psilotaceæ* and

Equisetaceæ. When we regard these rapid advances, and truly estimate the influence they bring to bear upon morphological theory, we must surely congratulate ourselves on being devotees to a science which is very actively alive.

But at the same time the detached cynic may find in the methods of plant morphologists, or still more sometimes in their want of method, food for much critical remark. And if he put his finger upon one mental process which more than another has introduced discord, it would, I think, be 'assumption.' It may be that our science is not worse than others in this respect; but I am very sure that arguments based upon ill-founded assumption have put back the progress of morphology more than anything else in our discussions. Any one can find examples for himself in the literature; some of us in our own writings. It remains for us who tread the difficult path of morphological theory to beware lest we neglect those warnings with which its course is so plentifully strewn; for it is just as much the duty of a scientific man to avoid blurring the issues for others by faulty argument, as it is to attempt to make clear to them what he himself believes to have been obscure.

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SCIENTIFIC BOOKS.

The Belgian Antarctic Expedition. Resultats du Voyage du S. Y. Belgica en 1897, 1898, 1899, Zoologie. Nématodes libres. Dr. J. G. DE MAN. April 15, 1904; 51 pp., 4to, pl. i-xi. *Bryozoa*, by A. W. WATERS. February 15, 1904; 114 pp., 4to, pl. i-ix.

The report on the free nematodes considers four fresh-water forms truly Antarctic, and six marine species collected in the Magellanic region, of which, however, one had been originally described from South Georgia. Three of the Antarctic forms are new, one being supposed to belong to a new subgenus (*Plec-*

toides); the other form, a *Dorylaimus*, is too young for determination. The other three belong to the genera *Mononchus* and *Plectus*. This little group has a special interest in being the first known fluviatile forms from the Antarctic continent. All the species are treated at great length and profusely illustrated.

We learn from Water's report that 86 species of Antarctic bryozoa were collected; on one occasion 55 species were obtained at one haul of the tangles. Eleven others from the extralimital subantarctic waters are also considered.

Of the 86 species and varieties of Antarctic origin 57 are new, many of which are very closely related to already known northern forms.

Of the Chilostomata only seven are known from the northern hemisphere, all of which are also known in the fossil state. Three species are cosmopolitan and also Arctic. But little support is given to the 'bipolar' theory by the Bryozoa considered in this paper. The specimens of *Hornera lichenoides*, long since reported as brought from the Antarctic by Sir James Ross, there is much reason to believe did not come from that region, as they agree with Arctic and do not agree with Antarctic specimens of that genus. *Orthopora*, *Cellarinella* and *Systenopora* are described as new genera, all of which are Antarctic. A new species of *Alcyonidium* and seven new *Cyclostomata*, with seven others previously known, and one indeterminate, complete the enumeration.

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SCIENTIFIC JOURNALS AND ARTICLES.

In the *Botanical Gazette*, for September, M. A. Chrysler has written upon 'The development of the central cylinder of Araceæ and Liliaceæ,' developing in these groups the recent stelar theories and reaching the general phylogenetic conclusion that monocotyledons are derived from dicotyledonous ancestors.—D. S. Johnson has given an account of 'The development and relationships of Monoclea,' a Jamaican liverwort.—W. C. Coker has writ-