THE CONCEPTS ON WHICH A MORPHOLOGY OF THE VASCULAR PLANTS SHOULD BE BASED

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It can hardly be denied that the expression "General Plant Morphology", which is so often met with in botanical textbooks, has little or no meaning. A general morphology of the Plant Kingdom would have to occupy itself with those morphological features that are common to all groups of plants, which means that it would have to confine itself to the common features of the cell structure and eventually to such peculiarities as are independent of the uni- or pluricellular structure of the plant body, e.g. its enclosure within a rigid envelop. However, when we realize that there is in this respect no fundamental difference between the common features of plants and animals or, at least, of some groups of animals [1]) it will be clear that the use of the expression "General Plant Morphology" is misleading and should be avoided.

What in most botanical textbooks is understood by "General Morphology" is not a morphology of the whole Plant Kingdom but only of a part of it; however, the delimitation of this part, and this is a most astounding feature, is but seldom explicitly indicated, and, moreover, proves to vary, sometimes even in different chapters of the same work. Most textbook-writers seem to agree that *Algae* and *Fungi* have a morphology of their own, and that the latter should be left to specialists in these fields; they accordingly restrict their attention either to the *Embryophyta*, i.e. the group which comprises the *Bryophyta* and the Vascular Plants, or to the Vascular Plants alone.

Morphology, of course, should deal with a well-defined group, for its object is the investigation of the plan according to which the body of the representatives of the group that has been chosen is constructed, and only in a well-defined group the presence of such a plan is to be

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[1]) This apparently means that the generally accepted division of the organisms in animals and plants is unacceptable, for it is certainly impossible that groups for which no definite set of general differences can be indicated, should be regarded as natural ones, and as it also seems impossible to change their delimitation in such a way that this end could be achieved, the division into two main groups is definitely to be rejected. An acceptable division can be obtained only by recognizing a larger number of main groups.

expected. Now Engler's group *Embryophyta* is undoubtedly a natural, i.e. a well-defined, unit, as the plants that are brought together under this heading appear to agree in important points, viz. in the antithetic alternation of a haploid and a diploid generation, and especially in the structure of the reproductive parts of gametophyte as well as of sporophyte, the common feature being the cellular structure of the wall by which the mass of reproductive cells is surrounded; only in cases of extreme reduction, viz. when the male gametophyte assumes the character of a pollen tube, these cells are wanting. A general morphology of this group of plants would have to confine itself to these features with, perhaps, an excursion into the domain of plant anatomy in order to pay some attention to the less exceptional but still rather characteristic structure of the growing points.

Of the two groups that have been brought together in the *Embryophyta*, that of the Vascular Plants is probably the best-defined one. It is well characterized by the strongly pronounced dominance of the sporophyte over the gametophyte, and by the peculiar internal differentiation that is met with in the vegetative part of the sporophyte. The points of resemblance in the outward form are, as will be discussed further on, of a more or less controversial nature, and are here for this reason omitted. The *Bryophyta* do not impress us in the same measure as a natural unit, for apart from the dependence of the sporophyte upon the gametophyte, the groups that have been brought together under this name, seem to have little in common. The absence of the internal differentiation found in the Vascular Plants is a purely negative character, and therefore of no account, and in the absence of common characters of a more positive nature the possibility that the dependency of the sporophyte on the gametophyte might have developed independently in the various groups, or in some of them, should receive careful consideration. However, as I do not intend to deal with the morphology of these groups, the question whether they are all correctly included in the *Bryophyta* or whether some of them would deserve a more independent position, may here be left out of consideration.

The textbooks that in the part dealing with morphology restrict their attention to the Vascular Plants, pay, as a rule, but little attention to the common features of this group. They base their treatment mostly on the rich material that former generations of botanists have brought together in the study of its most important subdivision, viz. that of the Angiosperms. Historically this is, of course, easily comprehensible, as Linné, Goethe and A.P. de Candolle, the men by whom the foundations of this morphology were laid, were but superficially acquainted with the other groups of Vascular Plants, and as the morphologists of the next period were more attracted by the great diversity displayed by the Angiosperms and by some other groups of Phanerogams than by the comparative uniformity that prevails in the remaining Vascular Plants. From a scientific point of view the neglect of these other groups is to be regarded as most regrettable, for it was not realized in good time that the base on which classical morphology

was built, was too narrow, and that concepts that were developed in the study of this limited domain, and that in the latter had proved most valuable, were not necessarily applicable in the wider field, where, indeed, their introduction has led to much confusion.

However, before entering into the problems that offer themselves to us in the wider field of the Vascular Plants, we will do well to consider the common features of the latter in somewhat greater detail.

In the structure of the gametophyte there are in the Vascular Plants apparently no common features that are not found also among the groups that have been brought together in the *Bryophyta*, and the gametophyte therefore needs no further consideration.

In the highly developed sporophyte, on the other hand, rather striking common characters are met with, of which, as stated above, no equivalent is found in the Bryophytes. This does not apply to the reproductive parts, for here, as in the gametophyte, no common characters seem to be present that are not duplicated in the *Bryophyta*. In the vegetative part, however, the situation is quite different. Here we find in the first place in the internal structure a differentiation of an epidermis provided with stomata of a quite distinct pattern, and of a stele consisting of xylem and phloem elements. Then there is also a differentiation of the outward form, but here the interpretation of the parts to which this differentiation has led, offers, as I hinted at above, considerable difficulties, and what in reality are merely analogous developments have often uncritically been accepted as homologies. However, with regard to one particularity of the outward form, viz. the presence of roots, there can hardly be difference of opinion. Their endogenous origin as well as the presence of the calyptra appear to be sufficient proof of their homology. The morphological identity of the leaves that we observe in the different groups, on the other hand, may seriously be questioned, and if the leaves should prove to be of different morphological value, it can hardly be doubted that the stems of the different groups too will have to be interpreted as analogous structures.

In order to solve this problem in the right way we should attack it by means of the principle on which all morphological conclusions are to be based. This is that all parts of the same rank occupy a definite position with regard to each other, and that deviations from this position are always but spurious and to be explained by means of a few auxiliary hypotheses, of which classical morphology recognized three, viz. abortion, splitting and concrescence. The first two can still be accepted in the original form, but instead of concrescence it seems preferable to introduce the expression "intercalary growth", which describes what is actually observed in cases that so far have been explained by the aid of concrescence, and seems therefore more suitable. This, however, is here a point of minor importance.

The questions we have to solve are therefore 1⁰ what are the main parts of the sporophyte, and 2⁰ what position occupy these parts with regard to each other.

The first question is easily answered. In the sporophyte we find just as in the gametophyte a juxtaposition of a vegetative part and a repro-

ductive part. That the presence of the latter, in the sporophyte as
as in the gametophyte, is a necessary condition, is obvious, for without
the reduction division in the spore-mothercells formed in the repro-
ductive part of the sporophyte, and without the fusion of the sexual cells
originating in the reproductive parts of the gametophyte, the antithetic
alternation of generations could not be maintained. It is true that the
original reproductive part of the sporophyte is occasionally replaced
by one of different morphological value, viz. by one that is derived
from the vegetative part (vegetative reproduction), but as this is
obviously a side-issue, it can not obscure the significance of the original
reproductive part. That the vegetative part too is to be regarded in
the Vascular Plants as an essential component of the sporophyte, need
not be doubted either; the reproductive part is for its food supply
entirely dependent on it. However, even in the *Bryophyta*, where the
sporophyte lives parasitically on the gametophyte, and where the
vegetative part therefore is not needed for the food supply of the repro-
ductive part, it is never entirely suppressed.

The question what position the two main parts of the sporophyte,
viz. the reproductive part and the vegetative part, occupy with regard
to each other, is not so easily answered. Actually there is a considerable
degree of diversity in the local relation between the two parts in the
various groups of Vascular Plants. In the first place there is a great
variability in the number of the reproductive parts. Sometimes there
are but a few of them, but as a rule they are very numerous, and then
they are either more or less evenly scattered over definite portions of
the vegetative part, or they are arranged in groups that are more or less
evenly scattered. When their number is small, the vegetative part
proves to be divided into more or less equivalent branches, which
bear the reproductive parts at their top, but such a terminal position
of the reproductive parts is never met with in the groups where their
number is very large. Now, from the standpoint of idealistic morpho-
logy it is irrelevant what arrangement we choose as our norm, but
once we have made our choice, we will have to show that the other
modes of arrangement can be derived from this norm by the aid of one
or more of the auxiliary hypotheses that we have mentioned above, and,
if necessary, of one or more additional ones.

The two norms that seem to deserve special consideration, are
1^0 the sparsely branched sporophyte whose subequal ramifications end
in a single reproductive part, the situation that is met with in the
Psilophytopsida (*Psilophytales*), and 2^0 the sporophyte with numerous
reproductive parts occupying lateral positions on the vegetative part
or eventually on the latter's ramifications.

The first of these two norms would seem to deserve preference,
because it assumes a comparatively simple structure of the sporophyte,
which, moreover, would differ but slightly from that of the *Bryophyta*.
Apart from its independence of the gametophyte and its larger dimen-
sions its main difference from the latter would be its division in a few
subequal branches. This division is generally, although apparently
on insufficient grounds, assumed to be a dichotomy, but even if it

could be proved that this is the correct interpretation, its significance should not be overrated, for the circumstance that this type of branching would be characteristic for the simply constructed sporophyte of the *Psilophytopsida*, would not necessarily mean that it is everywhere in the Vascular Plants the first step in the differentiation of the outward form. This conclusion is certainly not justified, for it is just as plausible to assume that the differentiation of the outward form may have started in the other groups of Vascular Plants by means of another type of enlargement, viz. by the development of lateral excrescences. This, at any rate, seems to be the simplest interpretation of the situation that is met with in the other groups. I know, of course, quite well that in one of these groups, viz. in the *Lycopsida*, dichotomy is the normal mode of branching, but it is not this kind of branching with which we are here concerned. This kind is to be regarded as a later phase in the development of the sporophyte; the first step is the differentiation of the lateral appendages of the originally simple axis. These lateral appendages are, of course, the so-called leaves.

The assumption that the development of the lateral mode of ramification was entirely independent of that of the dichotomous one, is on the other hand not necessary either. If the branches of the dichotomy are sufficiently unequal, the stronger one may push the weaker one aside, and placing itself in the continuation of the unbranched part, it may form with the latter a sympode. If this process was repeated a few times, the resulting sympode would be indistinguishable from a central axis provided with more or less equidistant lateral branches.

However, whether we assume that the lateral branching developed in the way described in the preceding paragraph, or that it developed independently, the first stage would have been a more or less pyramidal sporophyte with reproductive parts not only at the end of the axis but also at the end of all the lateral branches. The next step would be that the reproductive part at the end of the axis remained in abeyance, and that the latter continued its growth, producing ever more lateral branches.

A similar division of labour as took place between the axis and the lateral branches and which led to the suppression of the reproductive part at the top of the axis, may have led to the sterilisation of part of the lateral branches. The task to provide food for the growth of the sporophyte may have been restricted to some of the lateral branches, which assumed a flattened form, and which, eventually, may have reached greater dimensions, but lost the power to produce a reproductive part, whereas the lateral branches that retained this faculty, may on the other hand have shrunk. In this way the situation may have arisen that we find in the *Sphenopsida*.

The situation found in the *Lycopsida* might have arisen in a similar way; a further reduction of the branches ending in the reproductive part might have led to their complete disappearance; in this way the reproductive parts would have become sessile on the main axis. However, the circumstance that they are found in the axil of the sterile appendages, the "leaves", gives this explanation a somewhat strained

look. It would mean that the fertile and sterile branches were originally arranged in pairs, a fertile branch always just above a sterile one. To explain this curious arrangement it seems more plausible to assume either a splitting of the original lateral branches accompanied by a division of labour between the upper and the lower product of this splitting, and followed by a reduction of the upper one with as result a sessile reproductive part, or else the development of a lateral branch near the top of the original one, after which the lateral branch would take over the nutritive function, and growing in size would overtop the reproductive part; subsequent reduction of the part from which "leaf" and sporangium arise, would result in the situation that is actually observed. A similar development might also be assumed for the *Sphenopsida*, where sometimes the relation between the stalked reproductive part and the leaflike lateral appendages appears to be the same as that found in the *Lycopsida* between the sessile reproductive part and the subtending sterile appendages. The difficulties that we encounter in trying to connect the situation found in the *Lycopsida* and *Sphenopsida* with that prevailing in the *Psilophytopsida* accentuates the width of the gulf by which these groups are separated. In fact, it can not be said that the study of this aberrant group of fossil plants has shed much light on the morphology of the other Vascular Plants.

The situation found in the small group of genera formed by *Botrychium* and its allies, for which on account of its isolated position among the Vascular Plants a separate class *Botrychiopsida* should be created, may, as pointed out by Bower, be derived from that found in the *Lycopsida* by assuming a greater differentiation, and a reduction in number, of the lateral appendages of the vegetative part accompanied by a splitting of the reproductive part into a large number of "sporangia" arranged in a spike-like or thyrsoid complex.

In how far the situation found in the genera *Salvinia* and *Azolla* and that met with in *Marsilia* and its allies may be understood by comparing them with the situation observed in the preceding groups, is difficult to decide. The taxonomic position of these two groups of genera too is doubtless sufficiently isolated to justify our view that they should be regarded as distinct classes, for which the names *Salviniopsida* and *Marsiliopsida* may be used. Their inclusion in the *Filicales* and the assumption of an affinity with the in almost every respect fundamentally different *Hymenophyllaceae* and *Schizaeaceae* on account of a superficial resemblance in the structure of the "sporangia" and in the case of *Salvinia* and *Azolla* in the structure of the "sori", is so naive that one wonders how it could have been so widely accepted. In both classes the reproductive parts are split up in a number of "sporangia", a situation that we have met already in the *Botrychiopsida*, and the way in which in both classes these groups of "sporangia" are attached to a leaflike part also reminds us of the *Botrychiopsida*. Therefore it would be best to place these two classes in the vicinity of the latter. The difference in the structure of the wall of the "sporangia" is doubtless important, but its value should not be overrated. Thin walls are in sporangia not necessarily homologous structures.

The position of the reproductive parts in the *Pteropsida*, a class which I wish to restrict to the *Filicales*, seems at first sight entirely different, and is indeed difficult to explain. The structure of the "synangia" of the eusporangiate *Filicales* and the arrangement of the "sporangia" in "sori" in the leptosporangiate representatives of this group, although at first sight also rather strange, offer no great difficulties. The "synangia" find their counterpart in *Isoëtes*, which is best included in the *Lycopsida*, and the splitting of the reproductive part into a number of separate "sporangia" is met also in the *Botrychiopsida*, the *Salviniopsida* and the *Marsiliopsida*. For the position of the "synangia" and "sori" on the underside of what generally are called the "leaves" of the fern, there is in the groups that we have discussed so far, no exact counterpart. However, the circumstance that the reproductive parts occupy in all these groups a definite position with regard to a central "axis", may perhaps be taken as a hint that in this direction a solution of the problem may be found. The axis on which the so-called "leaves" are inserted, may be discarded as entirely unsuited, but in the rachis of the leaf we find an axis with regard to which the reproductive parts are indeed more or less symmetrically arranged. However, if we assume that this rachis is comparable to the central axis of the sporophyte in the *Lycopsida* and *Sphenopsida* or eventually to those parts of this axis on which the reproductive parts are found, then the so-called "leaf" of the fern must be comparable to that portion of the sporophyte of the *Lycopsida* and *Sphenopsida* on which the sporangia are borne. This conclusion, however, can not be regarded as acceptable unless we are able to answer the two following questions: 1^0 how is it to be explained that the reproductive parts are not found along the rachis itself but in some distance from the latter on the underside of the dorsiventral lamina, and 2^0 how is it that the "leaves" are so utterly different in outward form from the axial part from which they arise?

The dorsiventrality of the branch system on which the reproductive parts are inserted, and the difference in outward form between this branch system and the axis from which it arises, is after all not so very extra-ordinary, for a similar difference is found in some *Selaginella* species (e.g. *S. lepidophylla* and *S. imbricata*), where leaf-like branch systems arise from an in this case sympodial axis. The dorsiventrality of these branch systems assures in combination with their slanting position a better use of the incident light. The second question therefore does not seem to cause much difficulty.

The answer to the first question is not so easily found. It may be formulated also in this way: how can we explain the transition from a structure like the leaflike branch-system of the *Selaginella* species with the reproductive parts in the axil of the leaf-like lateral excrescences of the branches to a fern "leaf" with the reproductive parts on the underside? To explain this we should have to assume in the first place a reversion of the relative position of the reproductive part and the subtending lateral excrescence, and then the interpolation of a growth zone between the place where they are attached to the axis and the axis itself. The reversion may have been brought about by a twisting

of the primordium from which both the reproductive part and the lateral outgrowth to which it is joined, are developed. Seen in connection with the development of the dorsiventral structure, it would appear to be the most useful device to exploit the benefits of the latter to their full extent.

The explanation given in the preceding paragraph may seem to be rather far-fetched, and it might at first sight seem more plausible to assume that what we have before us in the so-called "leaf" of the ferns is no derivative situation, but an original one. However, this would not solve our difficulties, for in that case we would be compelled to derive the situation found in the *Lycopsida* and *Sphenopsida* from that in the "leaves" of the ferns, and this would require just as strained assumptions. The difficulties apparently arise from the great width of the gulf by which the *Pteropsida* are separated from the *Lycopsida* and the *Sphenopsida*.

In the *Cycadopsida*, a group that is usually included in the Phanerogams but which should be kept apart, the situation seems to be very similar to that found in the *Pteropsida*. In the vegetative part of the sporophyte a higher degree of differentiation has been achieved, the "leaves" on which the reproductive parts are inserted being reduced to scales, and the latter collected in "cones".

In the true *Phanerogamae* the situation is not so easily interpreted. The reproductive parts in which the pollen grains or microspores are produced, are borne on stalks that may resemble scale-like leaves, and are for this reason usually interpreted as leaves. The correctness of this interpretation, however, is difficult or even impossible to prove, as axillary buds, the parts by whose presence the leaves in this group are recognized, are always lacking. The morphological value of the parts by which the megasporangia or ovules are carried, is just as difficult to determine, although formerly, when our conclusions were exclusively based on the situation observed in the *Angiospermae*, it seemed absolutely certain that they were to be interpreted as leaves; in the latter group the resemblance between the parts on which the ovules are borne, the so-called carpels, and ordinary leaves is sometimes very striking. At any rate, even if it should appear that the stamens and carpels of the Phanerogams are not fully homologous with the leaves of the *Pteropsida*, it seems reasonable to assume that at least the carpels of the Angiosperms with their often fairly numerous ovules will have arisen in a similar way as the "leaves" of the *Pteropsida*, and if this applies to the carpel, there is good reason to assume that it will apply to the stamen too.

In the preceding paragraph I have expressed some doubt with regard to the existence of a full homology between the stamens and carpels of the *Phanerogamae* and the "leaves" on which in the *Pteropsida* the reproductive parts are borne. If we assume for a moment that the stamens and carpels of the *Phanerogamae* are homologous with the ordinary leaves of these plants, then the question may be formulated also in this way: are the leaves of the *Phanerogamae* homologous with the parts to which in the *Pteropsida* this name is applied?

That I put the *Phanerogamae* first in formulating the question raised in the preceding paragraph, is no accident. When they spoke of leaves, botanists thought originally of Phanerogams only, and when they afterwards extended the use of the term to ferns, they simply did not realize that it might here be misapplied. In classical morphology the leaf is defined as a lateral appendage of the stem with a bud, or eventually a shoot, in its axil. This definition is applicable only to Phanerogams, and even here it does not apply to all the parts that are usually designated as leaves, for the perianth lobes, the stamens and the carpels are never provided with buds in their axil; if the last-named parts therefore are regarded as leaves, we have to assume that the buds have aborted; this, of course, is possible. In the *Pteropsida*, however, buds are never present in the axils of the parts to which the name leaf is applied. In some distance of the latter we find the meristem patches that eventually may develop into new shoots, but the localisation of these patches is not always the same, and it is, moreover, questionable whether these entirely undifferentiated groups of cells may be homologized with the buds of the Phanerogams. In view of the totally different way in which the branches of the *Pteropsida* are formed, it seems impossible to regard them as fully homologous with the branches of the Phanerogams, and if the branches are not fully homologous, it is hardly to be expected that the leaves will be. It is rather unfortunate that in the *Cycadopsida* the mode of branching seems to be unknown. Branched stems are in this group very rare, but as the cones are usually terminal, the stems will often be sympodial, and it ought to be possible to determine the position of the bud by which the shoot is produced that will form the next member of the sympode. The results of such a study might throw new light on the affinities of this group of plants.

In the preceding considerations we have as much as possible avoided the use of the terms "stem" and "leaf". If it is true that the leaves of the *Phanerogamae*, the group in which the term "leaf" first obtained a morphological definition, are not fully homologous with the "leaves" of the ferns, and that the latter are not comparable to the "leaves" of the *Lycopsida* and *Sphenopsida* but to the whole leafy shoot of the latter, it will have to be admitted that the Phanerogams are the only group in which this term has rightly been applied, and that its use in the morphology of the other groups must necessarily lead to confusion. If it is applied at all in these groups we should realize that we do not use it in a morphological sense, but in an organographical, i.e. a functional or ecological, one.

In the *Phanerogamae* the division of the vegetative part of the sporophyte in stem and leaves has in the past proved its usefulness in the efforts to master the great diversity of detail in the plan according to which this part of the sporophyte is built. In recent times attempts have been made to replace this admittedly purely idealistic division by schemes in which the plant is regarded as consisting of a succession of identical units. The latter may consist either of a leaf with the internode at the top of which it is inserted, or else of a leaf with the sector

of the stem that extends in a downward direction to the first leaf belonging to the same vertical row. So long as these "phytonic" theories are confined to the Phanerogams, there is very little against them, but their application should not be extended to other groups of Vascular Plants, for as neither the "stem" nor the "leaves" can be regarded in the various groups as homologous parts, the combination of such a "leaf" with a portion of such a "stem" can not be homologous either. Whether these views are to be accepted in the Phanerogams instead of the classical dualistic interpretation, will depend in the first place on their adaptability to the purposes for which such an interpretation is intended, and in this respect there can, in my opinion, be no great difference between them, for if they are accepted, the next step will be that the unit is divided in a leaf, which is to be defined in the same way as before, and in a stem piece.

However, to be quite fair with regard to these "phytonic" views, we will do well to realize that the juxtaposition stem—leaves overemphasizes the importance of the stem, and that this juxtaposition has more than once led to misconceptions. In works on plant anatomy the growing point by whose activity the continuation of the stem is secured and new leaves are evolved, is usually designated as the growing point of the stem. Further, when the first rudiments of the leaves become visible at some distance from the top, the naked top portion is described as part of the stem. However, when we realize that the main part of the stem is formed by the internodes, we will have to admit that at least this part of the stem is not represented at all in the growing point. Moreover, that the leaves would arise at some distance from the top, viz. at the point where their primordia first become visible, is a gratuitous assumption. In the embryo of the *Monocotyledones* the single cotyledon is produced in a terminal position, and at the top of the embryo of a Dicotyledonous plant similarly two cotyledons are formed, and only after the latter have reached a certain size, the top becomes the starting point of a new development; the original position of the two cotyledons therefore might be described as jointly-terminal. In the *Monocotyledones*, moreover, the leaves immediately following the cotyledon are also occupying at first a terminal position, and where in the full-grown plant the leaves end in spines, as in *Aloë*, *Sanseviera*, *Agave*, the perfect radial symmetry of the top portion of these spines still bears witness to the originally terminal position of the leaf primordium, just as the dorsiventrality of the subsequently developed parts of the leaf may be accepted as proof that these parts were formed after the leaf primordium had shifted to a lateral position. The development of a new leaf primordium from one side of the old one is responsible for a shifting of the latter in the opposite direction. The stem, on the other hand, owes its origin to the expansion of the basal parts of these leaf primordia, and its subsequent development to the evolution of intercalary growth zones in this meristematic cell mass. A critical analysis of the processes that take place in the growing point therefore stresses the significance of the leaves, and favours a "phytonic" interpretation. That this has mostly been overlooked, may be due to the

circumstance that most anatomists were led astray by the study of the easily accessible growing points of *Hippuris* and *Elodea*, which to a superficial observer suggest the presence of a stem with, at a considerable distance from the top, the first signs of leaf development. This impression is entirely false. The core of such a growing point may be regarded as belonging to the stem, but there is certainly no reason whatever to see in the superficial layer at the top anything but the as yet undifferentiated stratum from which the leaves will arise. The first sign of internodes is noticed at a point that is even much farther removed from the top than the point at which the first leaf primordia become visible. In the ferns, on the other hand, there is good reason to believe that the "leaves" originate in a lateral position, and this might be another reason to deny their full homology with the leaves of the Phanerogams.

Above we have referred to a difference in position of the buds in the Phanerogams and of the meristematic patches from which in the ferns eventually new shoots may arise. The position the new shoots occupy in regard to the old ones, is doubtless not only here but everywhere in the Vascular Plants a point of morphological importance. Nevertheless it can not be regarded as equal in importance to the study of the position the reproductive parts occupy in relation to the vegetative part, for the division of the sporophyte in a vegetative and a reproductive part is a feature that is found in all *Embryophyta*, and for this reason these parts must occupy in the general plan of this group a definite position with regard to each other, of which eventual deviations are to be explained by the aid of auxiliary hypotheses, but the branching of the vegetative part is evidently confined to one of the subdivisions of this group, viz. to the Vascular Plants, and as it evidently arose in most groups only after the vegetative part had reached a considerable degree of differentiation, it seems reasonable to assume that it will have developed independently in the various groups.

Before entering into this subject I should like to make a few remarks on the use of the term "branching". In discussing the primary differentiation of the vegetative part I have used it, instead of a better one, for those processes which lead to an enlargement of this part by the production of the kind of appendages that, on account of a functional similarity, are usually designated as "leaves", but which, as we have seen, may possess a quite different morphological value. However, as a rule the use of the term is confined to such processes of enlargement in which the new-formed parts are a more or less faithful replica of the original one, and in this sense we will use it in the following considerations.

The kind of branching defined in the preceding paragraph may take place in two ways. It may be due to a splitting of the growing point into two more or less equal or, rarely, distinctly unequal parts, but the branches may also arise from groups of meristem cells that are set aside for this purpose at some distance from the apex of the growing point, and that for some time remain dormant. In the first case we speak of dichotomy, in the second case of lateral branching.

Dichotomy is the typical mode of branching in the *Lycopsida*. Here the equivalence of the two branches is reflected in their symmetrical position with regard to the uppermost "leaf" of the axis from which they arise; this "leaf" appears to be inserted just below the fork. In this typical form dichotomy appears to be confined to the *Lycopsida*, and here it is the only mode of branching. A forking of the stem occurs, however, also in the leafless *Psilophytopsida*, where, however, it is not certain that it is a true dichotomy, and further, by way of exception, in some Phanerogams. In this class it has been observed as a regular feature in some species of the palm genus *Hyphaene*, and as a monstrosity in some other *Monocotyledones* (*Fritillaria meleagris*, *Tulipa*). In the *Hyphaene* species investigated by SCHOUTE (Rec. d. trav. bot. Néerl. 6: 1. 1909) the uppermost leaf below the fork was found to occupy the same position as the corresponding "leaf" in the *Lycopsida*, but in another *Hyphaene* species which I myself could study (Rec. d. trav. bot. Néerl. 25A: 75. 1928), this position was occupied by the highest leaf but one, so that the position of the uppermost leaf below the fork can not be regarded as constant. This seems to accentuate the more or less accidental character of this type of branching in this genus, where I regarded it (l.c. p. 79) as a "very regular, hereditary fasciation", comparable to the forking occasionally observed in fasciated stems of *Fritillaria meleagris* and *Tulipa*, and therefore of minor importance. It should furthermore not be overlooked that it is in these species of *Hyphaene* by no means, as in the *Lycopsida*, the only mode of branching, for the inflorescences develop from axillary buds.

In the *Sphenopsida* the branching is always lateral, but the position of the branches with regard to the "leaves" differs from that observed in the *Pteropsida* and in the *Phanerogamae*, for they are found to alternate with them. This entirely different arrangement doubtless points to an independent development.

The differences in the origin of the lateral branches in the *Pteropsida* and the *Phanerogamae* have already been mentioned.

The ideas set forth in the preceding pages might have been expressed also in a phylogenetic form. We might have started e.g. from the *Bryophyta* with their simple sporophyte provided with a single terminal reproductive part. From such a type the *Psilophytopsida* might have sprung, where we find forked stems with a reproductive part at the end of the ramifications. The next step might have led to the *Sphenopsida*, where the terminal reproductive part has been suppressed, but where the function of the latter has been taken over by the reproductive parts at the end of the ramifications of the vegetative part, of which a large part has been modified into "leaves". Further reduction of the lateral excrescences ending in reproductive parts would have led to the situation found in the *Lycopsida*. A concrescence of all the lateral parts would have produced the "leaf" of the *Pteropsida*, and from the situation found in the latter we might have passed on to the *Cycadopsida* and the *Phanerogamae*.

This phylogenetic system has, like all the other ones that have been

proposed, several weak points, of which I will mention but one, viz. the assumption that the starting point should be found in the *Bryophyta*. We might just as well have chosen the fern leaf as our starting-point, i.e. a vegetative part provided with a considerable number of reproductive parts that are more or less evenly scattered over its whole surface. This would have had the advantage that we would have started from a sporophyte that was built according to the same plan as the gametophyte, where we find as a rule a large number of reproductive parts (antheridia and archegonia) scattered over the vegetative part. Starting from this point we would have recognized in the situation met with in the *Bryophyta* one of extreme reduction. In the absence of decisive fossil evidence—and there is very little hope that the latter will ever be forthcoming—, such a view could be defended just as well.

In idealistic morphology it is of no great importance from which point we start, as it confines itself to establishing homologies and distinguishing between various modifications of the homologous parts. In the Vascular Plants the latter prove to be of greater importance than the homologies themselves, which means that a morphology of the various classes is more promising than one of the whole group. However, before engaging in a morphology of one of these groups, one should be quite clear with regard to the meaning of the terms that are to be used. One of the aims of this paper is to show that such terms as "leaf" and "stem" should be avoided, as the parts to which they have so far been applied in the different groups, are of entirely different morphological value.