On the limits of the use of the terms 'Phyllome' and 'Caulome.'

A SUGGESTION,

BY

F. O. BOWER, D.Sc.,

Regius Professor of Botany in the University of Glasgow.

IN the 'Practical Course of Instruction in Botany,' Part II, page 1, I appended a foot-note to the description of the leafy shoot of *Polytrichum commune*, which runs as follows:—'Though the terms "stem" and "leaf" are used here, it must be distinctly borne in mind that the members thus named, being parts of the oophore generation, are not homologous with, but at most only analogous to the stem and leaf in vascular plants, which are parts of the sporophore generation.' Thinking that this point would be generally admitted, no further explanation was given, and it was with some surprise that I found this passage objected to by certain of my colleagues. Since the point is not universally agreed to, and since this passage stands in a somewhat dogmatic form in a text-book designed for the use of students, the best course will be to state more fully the grounds upon which the statement is based. Moreover, there is at present a wave of what may be called 'morphological scepticism' passing over the minds of many in this country. Some think the distinction of the categories of members is not sufficiently definite; others are inclined to deny that distinctions can be drawn at all; thus the present appears to be an opportune time for the consideration of the basis on which we rest our distinction of the parts of the shoot, viz., stem and leaf, and the limits which may, and I think should, now be placed on the application of

[Annals of Botany, Vol. I. No. II. November 1887.]

those terms. If, in pursuing this subject, I traverse ground which is too familiar for the taste of some, the excuse will be that this is done in the interest of clearness.

Sachs has stated in his Lectures[1] that 'it is impossible to express morphological ideas clearly and exhaustively by means of simple definitions.' Since the definitions cannot be simple, it is all the more necessary to be aware of, and to estimate at their true value in relation to one another, those criteria upon which organographical distinctions are, or have been, based; these will now be considered seriatim, and with special reference to the distinction of the parts of the shoot, viz., axis and leaf.

I. The first basis of distinction of the parts of plants was undoubtedly that of *external form and appearance*, and it is also popularly used to the present day by the lay public, which would call underground stems roots, and the phylloclades of *Ruscus* leaves. It is unnecessary here to show that the external form and appearance of the mature member form an insufficient basis for morphological distinction, since this principle is insisted on in every text-book.

II. Nor is it necessary here to point out, or prove by examples, that *function* is an unsafe guide. It may, however, be noted in passing, that function has been made the chief basis of the system of physiological organography propounded by Professor Sachs in his Lectures; and though he expressly states that his system is not intended to replace purely formal morphology, there can be little doubt that his use of familiar terms in a new sense will tend to obscure their morphological meaning in the minds of many.

III. A method of distinction of members according to the disposition of the tissues in the mature state (the *anatomical method*) is one which has especially met with acceptance in France, where it took its origin and was first developed in the extensive researches of Van Tieghem[2]. This author

[1] Engl. Ed. p. 2.

[2] Recherches sur la Symétrie de Structure des Plantes Vasculaires, in Ann. Sci. Nat., sér. 5, t. xiii.

wrote, with special reference to the leaf[1], as follows: 'We shall show that in the whole series of vascular plants all the bundles of the leaf are in their disposition and orientation placed with reference to a plane which includes the axis of symmetry of the stem and the radius of insertion;' and continues, 'thus while the plant-axis in both parts, viz., root and stem, which compose it, is throughout symmetrical with reference to a line, the appendage is only symmetrical with reference to a plane.' This method of distinction, which its author applied to the solution of various morphological problems in connection with the flower, was taken up and further elaborated, and still more precisely stated by Bertrand[2]; and if the constancy of structure of corresponding members of all vascular plants were greater than it is, the anatomical method might doubtless prove a ready and efficient rule of thumb for distinguishing different categories of members and solving morphological problems. Unfortunately numerous known facts are against this: it will be well to cite a few pregnant exceptions to the rules as above laid down, and these are to be found especially in shoots of peculiar conformation.

In various species of *Juncus* a foliage leaf projects beyond the apparently lateral inflorescence as an elongated conical or nearly cylindrical structure, which shows just above the inflorescence a sheathing base; if transverse sections of this, which is actually a leaf, be examined, those cut through the sheathing portion show an arrangement of the tissues which would fall under Van Tieghem's definition of a leaf; but in the

[1] We need not here refer to the anatomical distinction of stem and root, since we are at present specially concerned with the leaf. It is, however, to be noted that Van Tieghem began his researches on the root, which is much less subject to metamorphosis than stem or leaf, and it might accordingly be expected that its type of structure would be more uniform than theirs; he found but few roots of aberrant structure. His researches on the stem and leaf have, I believe, never been completed, and in his Traité de Botanique he lays no great stress upon the anatomical method of distinction of parts of the shoot. It may perhaps be concluded from this that he has not found the anatomical method apply so readily to the more plastic members of the shoot as it does to the more uniformly constructed root-system.

[2] Archives Botaniques du Nord de la France, 1881.

cylindrical upper portion the structure is symmetrical round a central point, and even corresponds in detail to that of the axis below the inflorescence. Accordingly the upper portion of the leaf would, on anatomical grounds, fall under the definition of an axis. Thus one and the same member, which on other grounds is regarded as a leaf, shows in its lower portion those anatomical characters which are ascribed to the leaf, in its upper portion those ascribed to the axis[1]. The tubular leaves of species of *Allium* present similar difficulties, the sheathing lower portion conforming to the foliage type, while the tubular upper portion has the vascular bundles corresponding in position and arrangement to the type of the stem. Again, in the ensiform leaves of *Iris*, *Tofieldia*, etc., and the phyllodes of certain *Acacias*, it would be impossible to tell from the transverse section alone, and judging by the arrangement and orientation of the bundles, whether the member were a leaf or an axis.

The exact converse of the case of *Juncus* or *Allium* is shown in the phylloclades of *Ruscus androgynus*[2]. If transverse sections be cut at the base of the phylloclade, the arrangement and orientation of the vascular bundles is according to Van Tieghem's type for an axis, being symmetrical with reference to a central line; but if sections be cut successively further from the base, it will be seen that the arrangement and orientation of the bundles gradually passes over into Van Tieghem's type for the leaf. As Professor Dickson has pointed out, the phylloclade undergoes a twist at the base, so that the morphologically lower surface is directed upwards, and this actually upper surface bears no stomata, though they are to be found in large numbers on the morphologically upper but downward directed surface; all the vascular bundles have their xylem directed upwards, i.e. towards the morphologically lower surface. In passing from the base where the

[1] This example has been cited by Goebel as showing that the distinction of members on anatomical grounds is untenable. Vergl. Entw., p. 128.

[2] The structure of these is described by Professor Dickson (Foliage Leaves in *Ruscus androgynus*) in Trans. Bot. Soc. Edin., vol. xvi.

arrangement is characteristic of the stem, to the upper expanded portion where the structure of tissues and orientation of bundles is throughout characteristically foliar, the bundles first separate into groups, each group having as its centre a relatively large bundle, which is so placed that the xylem is directed towards that surface (the morphologically lower) which is ultimately directed upwards, and the smaller irregularly arranged bundles then coalesce with the larger one. Thus we have here the converse case of a member, which on other grounds would be recognised as an axis, showing in its lower portion an axial type of internal structure, which gradually changes in its upper portion to that laid down by Van Tieghem as characteristically foliar.

Though other examples might be adduced, these will suffice to show that morphological distinctions of the parts of the shoot cannot be based on the disposition or orientation of the vascular bundles: equally insecure would be conclusions based upon their number, as is obvious when it is remembered that scale-leaves are often without vascular bundles at all, and that the cotyledon of *Lycopodium* may show a similar simplicity of structure[1]; also the case of the genus *Gnetum* may be cited, in which I have already shown[2] that in one species (*G. africanum*) the central bundle, which is present in other species, is absent, though there is no corresponding difference of configuration. And lastly, observations on the point of fusion of vascular bundles from one member with those of another give only uncertain ground for morphological conclusions, since we know that in cases where there is no question of morphological character the fusions may take place at very irregular points (e.g. the shoot of *Helianthus*).

From the examples above quoted (and they might be greatly added to) it appears that observations of the arrangement, orientation, number, or point of fusion of vascular bundles constitute an insufficient foundation for the solution

[1] Treub, Ann. Jard. Bot. Buit. vol. iv. p. 134, in *L. cernuum*. Goebel, in Bot. Zeit., 1887, in *L. inundatum*.

[2] Phil. Trans., 1884, Part ii. p. 599.

of morphological problems, and it will be noted that the anatomical method breaks down most conspicuously at the very points where questions of the nature of members arise, that is, where there is some marked peculiarity of external conformation. But it is not necessary on this account to throw anatomical evidence entirely on one side; it may be taken advantage of as collateral evidence to support a view based on other and firmer ground; still, since it is plain that the internal structure follows in great measure the modifications of external form and function, observations in this direction can never acquire first-rate morphological importance[1].

IV. Passing now from the consideration of the mature member, upon the characters of which it is found impossible to base a consistent distinction of members of different categories, to their origin and development, we may consider how observations on these points have been, or are used as a basis of classification of members. It was Schleiden who first laid special stress on development as the basis of morphology[2]; and though his proposed distinction of axis and leaf *according to the duration of apical growth* is not now found sufficient, his service to the science in turning attention to development should not be underrated. His definition is as follows[3]:—'So ist also das Blatt die aus der Grundlage der Pflanze, der im Wachsthum und daher morphologisch unbeschränkten Axe, hervorgehende, im Wachsthum und daher morphologisch beschränkte Form; unter diesen Begriff fallen alle Blattorgane, und alle Axen sind ausgeschlossen.' Though this distinction holds for the large majority of cases, still since stems of limited growth are known to exist (e.g. *Welwitschia*, species of *Streptocarpus*, the receptacle of Compositae, various

[1] Hofmeister, All. Morph., p. 415, states broadly, 'Uebereinstimmungen oder Differenzen der äusseren Form, des inneren Baues, der Function sind nicht Maassgebend für die Deutung eines gegebenen Gebildes als Achse, Blatt, oder Haar.' He does not, however, give examples from vascular plants, which would bear out this statement as regards the internal structure.

[2] Grundzüge der Wiss. Botanik, p. 20: 'Die Grundlage für alle specielle botanische Morphologie ist die Entwickelungsgeschichte.'

[3] Grundzüge, p. 172.

thorns, etc.), while leaves have not unfrequently a very extensive and apparently unlimited apical growth (e.g. *Lygodium*, *Gleichenia*, etc.), this distinction between axis and leaf cannot be maintained. Nevertheless, the fact that the leaf is usually limited in its apical growth is to be noted as one of the distinctive though variable characters of the leaf.

V. According to the number of layers of meristem which give rise to them respectively, a general difference may be traced between leaves and lateral axes. Upon the value of this evidence it will be best to quote from Warming, who has made such fine and extensive observations in this direction[1]. He writes: 'It is impossible to separate phyllomes and caulomes by constant morphological and genetic characters. We have seen in the second part that they arise from the same peripheral tissue, but at slightly different depths: the leaves spring generally from the first and third layers of the periblem, the weaker leaves, such as the bracts in many inflorescences, even from the first layer only; stems hardly ever originate in the first layer, but most frequently in the third or fourth. This character has its importance, and may often serve as a criterion for determining the nature of an organ of doubtful morphological character . . . . but of course it must not be regarded as an absolute index, which should always be decisive. I think we should rather consider it as a circumstance which is intimately connected with the size of the organs and the space which they require: the more vigorous they are, and the more permanent the rôle which they are destined to play, the more space they require and the deeper is their origin in the axis; since caulomes, by reason of their biological rôle, almost always require more space and vigour, they also originate at a greater depth.'

VI. We may next consider the criteria of *relative time and place of origin*, these being adopted by Hofmeister as his basis of distinction of lateral axis, leaf, and hair[2]: he

[1] Recherches sur la ramification des Phanerogames, in Forgreningsforhold, French résumé, p. xvii.

[2] Allgemeine Morphologie, p. 411.

wrote as follows: 'Lateral axes, leaves, and hairs, arrange themselves as regards the time and place of their appearance according to their rank. New lateral axes rise from the surface of the growing-point earlier, and nearer to its apex than the youngest rudiments of leaves.' Against this is to be set the statement of Sachs[1]: 'I constantly find in vegetative shoots and many inflorescences of Phanerogams young leaves above the youngest axillary buds.' This question has also been treated at length by Warming[2], who has shown that though in the vegetative shoot the leaf as a rule precedes the axillary bud, in many inflorescences the bud may precede its subtending leaf, or the subtending leaf may be entirely absent. Again, Goebel's observations[3] on 'dorsiventral inflorescences' and on 'intercalary growing-points' indicate, together with the above, that relative time and place of origin will not serve as a safe criterion of distinction of axis and leaf. In fact we arrive at the conclusion put forward by various writers, that all the above-mentioned characters have only a relative value as applied to the distinction of axis and leaf, all of them being limited by exceptions: in other words, organic nature is not limited by strict rules, and a perfectly natural system of morphology of the shoot cannot be based on narrow definitions.

The difficulty of defining and distinguishing stem and leaf is in itself to be regarded as a strong justification of their designation under the common term 'shoot,' which Sachs has adopted in his Lectures as the correlative of the 'root.' Accepting this idea of the shoot as a whole, one is apt to doubt, in view of the difficulty of their definition, whether there be any essential difference between axis and leaf; and this question is closely connected with the idea of a possible 'terminal leaf:' if there be any recognisable difference then the terminal leaf is at least a possibility. Now Sachs'

[1] Textbook, 1st English edition, p. 154, footnote.

[2] Forgreningsforhold, pp. viii–xi.

[3] Ueber die Verzweigung dorsiventrale Sprosse. Also Vergl. Entwickelungsgeschichte.

well-known definition of stem and leaf is as follows[1]: 'Stem (Caulome) is merely that which bears leaves; Leaf (Phyllome) is only that which is produced on an axial structure in the manner described in paragraphs 1–7:' and he proceeds to say 'that which is common to all leaves is their relation to the stem.' How then about the possible so-called 'terminal leaf'? can such a thing exist? On this point Goebel has written a remarkable passage which runs as follows[2]: 'Terminal leaves are unknown in the vegetative region, though this is but a statement of experience, which would be put aside by the first well-grounded exception; and doubtless a foliage-leaf would remain a foliage-leaf, even if it arose in a terminal position on the growing-point, but therewith the last developmental distinction between stem and leaf would disappear.' This implies that some other basis of distinction would remain, by which the leaf might still be recognised as leaf when terminal, and not merely as a development of the axis, which it would be according to Sachs' definition. What then is that distinction? The distinction, which Goebel would here recognise as overriding Sachs' definition, is one based on comparison of nearly allied forms (a phylogenetic distinction), or possibly of successive members of the same individual. If then the possibility of a 'terminal leaf' be admitted[3], the definition of Sachs appears to be an arbitrary one, and is not to be accepted as final. However, no actually 'terminal leaf,' in the sense above indicated, has been observed. What we require at present is a suitable nomenclature for what is actually seen in nature, and that based upon the definition of Sachs is the best hitherto proposed.

[1] Textbook, 1st English edition, p. 136.

[2] Vergleichende Entwickelungsgeschichte, p. 184.

[3] Compare Warming, l. c., p. xviii. Also Eichler, Blüthendiagramme, p. 48. This question would appear to have lost much of its interest and importance to those who accept Goebel's view of the sporangium as a member 'sui generis.' Beneath it, however, as indicated in the passage from Goebel above quoted, there lies a morphological principle, which is certain to acquire greater importance in the future.

Thus, there is another factor in the morphological problem beyond those above-mentioned, viz. the use of a comparison of closely allied forms, the results of which are accepted by some as overriding conclusions based on other grounds; and whether or not, in the present state of our knowledge, we are justified in regarding such comparison as of first-rate importance, we must take into account this which may be called the 'phylogenetic factor.' An ideal system of morphology of the shoot, which should recognise the true homologies of all members, their origin, and metamorphoses, would be one based on a full knowledge of phylogeny, and what there is of arbitrariness in Sachs' distinction is to be looked upon as a concession to the incompleteness of our knowledge on this point. How incomplete is our information and how uncertain our view, especially with regard to the descent of the Phanerogams, all must be aware. But though our knowledge in this direction is at present far too scanty to form a general basis for an exclusively phylogenetic system of classification of members, there are certain points in the whole series of plants at which it is certainly sufficient for drawing a broad distinction. We recognise that at various points in the series of plants 'parallel developments' have taken place. If our morphology is ever to have a phylogenetic basis, we shall do well not only to admit the fact of these parallel developments having taken place, but, where such a course will conduce to clearness of conception, distinguish them from one another in our nomenclature. It will be well to begin upon what is certainly the most clearly ascertained, as it is also the most prominent example of parallel development in the vegetable kingdom, viz. the foliar differentiation of the shoot in the sporophore, as well as in the oophore generation[1].

[1] While the terms 'root' and 'shoot' may be accepted, as correlative terms, in the general sense proposed by Sachs, and as including the corresponding parts of oophore and sporophore generations, it must be clearly borne in mind that the differentiation of such parts must have arisen in the two generations in just as independent a manner as the further differentiation of the shoot into axis and leaf; but there would be no sufficient advantage in marking this by a change of terminology to justify disturbing terms which have met with general acceptance in their

The evidence that such a parallel differentiation of the shoot has actually taken place is of the strongest possible kind, and is based primarily upon the researches of Hofmeister, by whom it was first demonstrated that the Moss-plant corresponds in its position in the life-cycle not to the Fern-plant, but to the Fern-prothallus. Taking first the sporophore generation in such a series of forms as *Coleochaete*, *Anthoceros*, *Phylloglossum*, a Fern, and a Phanerogam, we should in them see broadly indicated the rise of the sporophore generation; it is true the series is defective, the gap between the non-foliar sporophore of *Anthoceros* and the foliar one of *Phylloglossum* or of a Fern is a wide one; but there can be no reasonable room for doubt that the differentiation of the shoot into caulome and phyllome was a gradual one, though the intermediate forms have dropped out of existence. This view is strongly supported by analogy of the oophore; here, in such a series of types as *Pellia*, *Blasia*, a leafy *Jungermannia*, and a Moss, we have illustrated a similar but quite distinct differentiation of the shoot of the oophore generation; the two processes of differentiation, taking place at different points in the life-cycle, must necessarily have progressed independently of one another, and all the knowledge we possess of the plants concerned confirms this view[1]. Accordingly, notwithstanding the apparent similarity in external conformation, the 'leaf' in the oophore is not the lineal descendant of the leaf in the sporophore: thus we can only recognise the parts of the shoot in the sporophore and oophore generations as morphologically *analogous* to one another; the two are 'homoplastic,' but not morphologically homologous. This being so, I think it is desirable in the interests of clearness

present sense. The same may be said of the terms stem and leaf, which may still be accepted in a general sense as applicable to corresponding parts of oophore or sporophore generation.

[1] The notable fact of the similarity in external conformation of the oophore and young sporophore in *Lycopodium cernuum* and *inundatum* presents no obstacle to this view: it would appear that the differentiation had taken place both in oophore and sporophore, but still the process of differentiation might have been independent in the two generations.

and especially on behalf of students, that this conclusion should appear on the face of our terminology; the enclosure of the words 'leaf' and 'stem' in inverted commas, when applied to the oophore generation, is but an impotent distinguishing mark. I would therefore propose that the terms phyllome and caulome be reserved for those parts of the sporophore generation which are usually so called, thus retaining those terms in their original sense; while the terms 'phyllidium' and 'caulidium' might serve for the analogous developments in the oophore generation. Such a distinction of terms has been habitual in regard to the roots, the term 'root' (rhizome), in the sense adopted by Sachs in his Text-book, being applied to the true root of the sporophore, while the terms 'rhizoid,' 'rhizine' (or perhaps better 'rhizidium'), express the analogous and functionally similar parts in the oophore[1].

I am aware that objection will be raised to this proposal on the ground that it will be impossible to distinguish all parallel or morphologically analogous developments by distinct terms: thus, if we admit that heterospory has arisen at more than one point in the Vascular Cryptogams, it is at present unnecessary to distinguish the different sporangia in heterosporous Ferns, fossil Equisetums, and Lycopods by distinct terms: this is obvious. But it is, as far as I can see, no objection to the adoption of distinctive terms in what is the most prominent case of parallel development in the whole series of plants, or in other cases also where such a course would be conducive to clearness[2].

[1] It is in connection with the term 'rhizoid' that Professor Sachs has most conspicuously thrown overboard a distinction of terms which conveys the idea of want of homology in functionally similar parts. The avowed object of removing the cause of that 'prejudice against descriptive Botany still frequently existing even in scientific circles' can hardly be accepted as sufficient to justify the sacrifice of clearness of conception. Compare Lectures, p. 35.

[2] There can be few morphologists who have not felt the impropriety of designating by the same term the true leaf or phyllome of the higher plants and such members as the so-called leaves of *Nitella* or *Caulerpa*, the limited lateral branches of Florideae, the amphigastria of *Marchantia*, none of which can have been lineally connected with the true leaf of the sporophore: such members would fall under the term phyllidia, and thus be distinguished from the true sporophoric phyllome. It is true the analogies are at times extremely close, as that of the phyllidium of

Again, it may be urged that if this distinction, based on a want of homology, be marked by a difference of terms, the student will conclude that all those developments which are termed 'phyllome' or 'caulome' are lineally connected, and likewise all those called 'phyllidium' and 'caulidium': this difficulty would, however, be due to a process of defective reasoning from which the student must take care to guard himself. The fact is that it is not clearly desirable that every recognised case of want of homology of homoplastic members should be distinguished by definite terms, nor is our knowledge sufficient as yet to justify an extensive use of phylogeny in checking the nomenclature of morphology, even if it were desirable.

Again, it may be argued that observations of apogamy and apospory show that the two alternating generations are not so distinct from one another as has been supposed. This objection is virtually answered in another place[1], where the opinion is expressed that such observations as those of apospory do not indicate a reversion bearing a deep morphological meaning, but are rather to be regarded as mere sports.

In thus proposing to recognise more fully the fact of parallel development in the terminology of the science no new principle is made use of: it is merely intended to bring generally accepted conclusions into greater prominence, so as to obtain a clearer view. It is, however, a move exactly in the opposite direction to that recently made by Prof. Sachs. In his Lectures on the Physiology of Plants he brings together under a common name homoplastic organs of radically different origins[2]. Though this system of physiological organography is an undoubted advantage to the physiologist, who, in pursuing his special line of study, will necessarily centre his attention on the individual rather than on the race, the use of the old terms in a new sense, which disregards such conclusions as are based

Fissidens to the phyllome of *Iris* or *Narthecium*; but it is exactly in these cases that it is most necessary to keep clearly before the mind the fact that these members are not lineally related, but are only analogous to one another.

[1] Trans. Linn. Soc. vol. ii. p. 322. [2] Annals of Botany, vol. i. p. 84.

on a phylogenetic view, is little short of a disaster to comparative morphology. Notwithstanding Prof. Sachs' disavowal[1] of any wish to supersede or exclude purely formal comparison, the adoption of terms which have already a more or less definite morphological meaning in a different and still less definite physiological sense must result in confusion in the minds of students. Here again the regret may be expressed that in adopting a new point of view, in itself of the greatest value, a correspondingly new series of terms was not introduced. In morphology the phylogenetic factor is certain to become of constantly increasing importance as the effect of the hypothesis of evolution takes form in a sounder view of the relationship of the main groups of living plants: it is only to be expected that, as the sum of known facts increases, morphological distinctions based upon phylogenetic view will be more clearly recognised. The suggestion embodied in this paper, to limit the terms 'phyllome' and 'caulome' to the sporophore generation, is intended as a step in this direction. We should thus arrive at the following classification of vegetative members :—

I. Shoot { Stem { Phyllidium (oophore). / Phyllome (sporophore). / Leaf { Caulidium (oophore). / Caulome (sporophore).

II. Root . . . { Rhizidium or Rhizoid } (oophore). / Rhizome or true root } (sporophore).

The terms shoot and root, stem and leaf, would thus be used in a general sense, being applicable to the corresponding parts in both oophore and sporophore indiscriminately; the terms phyllome, caulome, and rhizome would, however, be applied only to the parts of the sporophore, while the terms phyllidium, caulidium, rhizoid or rhizidium would be reserved for the corresponding parts of the oophore.

[1] Lectures, p. 72.