On the Pitcher of Nepenthes: A study in the Morphology of the Leaf.

BY

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With Plate XVI.

The ordinary method of morphological treatment of leaves is to distinguish from one another those parts, which can in very many cases be obviously recognised in the mature state with the naked eye, viz. the sheath, petiole, and lamina. This distinction of parts is commonly applied both in treating of simple and of branched leaves.

Those who have studied the development of leaves have for the most part followed in the same lines, and have pointed out how, as a rule, the primordial leaf is differentiated at an early period into two parts, viz. the 'foliar base' or sheath, and 'upper leaf' or lamina, while between these parts thus early distinguishable a subsequent process of intercalary growth results in the formation of the petiole. This method of distinction of parts is maintained by most writers on the subject, whether the leaf be a simple or a branched one.

In a paper presented to the Royal Society in 1884, I pointed out that this method of treatment of the leaf is at variance with our treatment of the shoot as a whole: that in thus distinguishing sheath, petiole, and lamina, we lay stress upon the results of intercalary growth, which are regarded as only of

1 On the Comparative Morphology of the Leaf, etc. Phil. Trans.
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minor importance in the treatment of the shoot as a whole; and we put on one side the branching of the leaf, though in treating of the shoot as a whole the time, place, and order of origin of leaves and buds upon the main axis are considered of primary importance, and indeed form the foundation of our morphology of the shoot at large.

Now, the fact that intercalary growth frequently obscures the branching of the leaf, does not appear to me to be a sufficient reason for sacrificing consistency of method; furthermore, a comparative study of the leaves of vascular plants low in the scale appears in no way to justify this sacrifice of consistency. I therefore proposed in the paper above mentioned, that in the morphological treatment of the leaf, the main axis of the leaf exclusive of all its branches should first be recognised, and distinguished as the *phyllopodium*, while the term *pinna* should be retained for the branches of the first order borne upon the phyllopodium. The relations of the parts of the shoot would thus be as follows:

\[
\text{Shoot.} \quad \begin{array}{c}
\text{Axis.} \\
\text{Phyllopodium.}
\end{array} \quad \begin{array}{c}
\text{Leaf.} \\
\text{Pinna.}
\end{array}
\]

The practical difference between the two methods is this:— under the old method, placing the results of intercalary growth in the foremost place, we should, in attempting to solve a problem in foliar morphology, first ask, Where are the limits between sheath, petiole, and lamina? Under the method which I proposed, the first question would be, Does the leaf branch?

Finding that the method worked well in practice in ordinary cases, it was thought well to apply it to a familiar problematical case, viz. the pitcher of *Nepenthes*: the result is to suggest a new view as to its morphology. Previous writers (with the exception of Griffith) have assumed that this most wonderful
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Leaf is a simple, unbranched one, and the main question discussed by them has been, which part corresponds to the petiole, and which to the lamina of ordinary leaves? The chief views which have been advanced as to the morphology of the pitcher of *Nepenthes* are the following:

1. That the lid of the pitcher is the lamina of the leaf, while the rest of the leaf, including the pitcher itself, represents the petiole, which widens below into the broad assimilating expansion and basal sheath; this is the view held by Van Tieghem and by Drude.

2. Goebel, on the other hand, holds that the lid of the pitcher does not represent the whole lamina, but that it is only the upper end of the lamina, of which the pitcher is also a part. He would imagine the pitcher of *Nepenthes* as essentially similar to the bladder of *Utricularia*, and says, 'If we imagine the bladders of the latter greatly enlarged, the lid not folded over the inner margin of the mouth, but closing the wide opening like a lid, we should have the pitcher of *Nepenthes*.' He further regards the tendril as the result of intercalary growth from the upper limit of the petiole, the latter being represented by the broadly-winged basal portion of the leaf.

3. It is to be noted that both these views ignore the fact, long ago demonstrated by Sir J. D. Hooker, that the apex of the lid is not the organic apex of the leaf, but that the latter is to be found in that spur which is constantly present in leaves of mature plants, immediately behind the point of insertion of the lid. Hooker, in the paper above cited, expresses the opinion that 'the pitchers are modifications of a gland situated at the apex of the midrib of the leaf'; he calls the lower flattened and winged part the lamina, and, speaking of the stalk of the pitcher, he says, 'It is a body more or less strictly analogous to the terminal cirrus of the leaf of *Gloriosa* or *Flagellaria*.' He recognised what others who have written later failed to apprehend, that, 'as the pitcher enlarges, the apex,

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1. Traité de botanique, p. 1462.
2. Schenk's Handbuch der Botanik, i. p. 137.
3. Ibid. iii. p. 238.
which points upwards and backwards, elongates at first considerably, and becomes the styliform process at the junction of the lid and the pitcher, and that it 'continues to be the organic apex of the organ.' Further, he figures the peculiar bilobed conformation of the young lid, which leads me to the conclusion now to be put forward. In his Address at Belfast in 1874, he still maintains the view above quoted, and Eichler, in his paper on the leaves of Cephalotus¹, expresses his adherence to it.

Now, it is to be noted that these writers, under the influence of the old method, seek first to homologate the parts of the pitcher to sheath, petiole, and lamina,—parts which depend for their distinction upon the results of intercalary growth; and the question did not present itself to them, whether the leaf be a simple or a branched one. It was, however, a matter of the greatest interest to me to find the following passage written by Dr. Griffith in the year 1837²:—'There can be no doubt but that the pitcher is merely due to a hollowing of the apex of the petiole, or rather tendril. The lamina is of difficult explanation (if it is the lamina of the leaf) from its venation, its emargination, and the prolonged apex of the tendril; it is a compound one, analogous to the leaf of Bauhinia.' It will be seen that, though Griffith had apparently not made observations on the development of the pitcher, his comparison with the leaf of Bauhinia coincides in the main with the view to which study of the development of the leaf has led me.

My first observations were made upon a single bud of Nepenthes, sp. from Kew. These showed that the leaf first arises as a conical body, with the side directed towards the apex of the axis flattened (Fig. 1); the flattened side is soon marked by two longitudinal flanges or wings, while close to the apex a shallow oval depression soon makes its appearance. This is the first trace of the cavity of the pitcher (Fig. 2); above it is the smooth conical apex of the leaf, which is thus far a simple, winged phyllopodium. Subsequently the leaf elongates, the

wings increase, and a two-lobed outgrowth appears above the oval depression (Fig. 3, p); this is the lid of the pitcher, which, growing larger, ultimately covers the mouth of the cavity (Fig. 4). It will be seen in the examples to be described that the clearness of marking of the two lobes varies, even in the same species; but in the larger majority of cases it is clearly seen, and may usually be recognised even in the mature state; it was this that attracted Griffith's attention, and led him to suggest the comparison with Bauhinia.

Now, isolated observations, such as the above, upon the leaves from a single bud, are insufficient to settle the question of first origin of this two-lobed lid, and of its relation to the apex of the leaf. A comparison was therefore made of numerous leaves, in various stages of development, of *N. phyllamphora*, from the Glasgow Garden, and of *N. distillatoria* collected in Ceylon. In both these species the first stages are as above described. In *N. phyllamphora*, the lip of the oval depression becomes straight on the side nearer the apex (Fig. 5, a), while the apex itself becomes broad and flattened (Fig. 5, b). This is the first step in the formation of the lid, though the two lobes are not yet to be recognised; very soon, however, the flattening having increased, the apex (ap) and the two-lobed lid (p) are distinguishable (Fig. 6), becoming more clearly defined as the leaf grows older (Fig. 7). As before, the lid, retaining clearly its two-lobed character, covers over the cavity of the pitcher, while the growth of the apex frequently becomes irregular in this species, resulting in those variously laciniate spurs, which are easily recognised with the naked eye in the mature pitcher (Fig. 8). Meanwhile the part of the phyllopodium below the depression becomes differentiated into the pitcher itself (as Figs. 4, 8) and the basal expanded portion, while the intercalation of the tendril takes place subsequently.

Turning now to *N. distillatoria*, the results are in the main similar, the first stages being as before (Figs. 9, 10): the apex becomes flattened as seen in profile (Fig. 10), while the surface-view shows that the cavity is first overarched by a simple flap,
which represents the young lid (Figs. 11 and 13, A). The relation of the lid to the apex, which develops into the spur, is essentially the same as in *N. phyllamphora*, but it is only at a subsequent period that the two-lobed character of the lid becomes apparent (Figs. 14–17). The apex (ap) may in this species remain a simple cone, or it may occasionally assume an irregular form (Fig. 16), as is so frequently the case in *N. phyllamphora*.

It would be desirable to study the development of the pitchers in the first plumular leaves, and especially so after the interesting observations of Sir J. Hooker and subsequently of Prof. Alexander Dickson\(^1\) on such leaves in the mature state. Unfortunately I have been unable to obtain specimens of seedlings in the earliest stages; I owe, however, to the kindness of Messrs. Veitch, of Chelsea, two of the youngest seedlings they could supply of *N. phyllamphora*. One of these had five, the other six expanded leaves; they were not so young as those described and figured by Hooker, though they were of such age that the tendril was not intercalated between the pitcher and the expanded base of the leaf, and the wings were obviously continuous from the base up to the pitcher. In the mature leaves of these young plants the spur was much less clearly to be recognised than in pitchers of more mature plants of this species, while the irregular fringes were larger in proportion than in older specimens; the lids were quite as clearly lobed as is usually the case in mature plants. Examination of the development of the leaves of these seedlings as exhibited in their terminal buds gave practically the same results as those above detailed for older plants, the relation of apex and lid, and the two-lobed character of the latter being quite similar. The evidence from these somewhat advanced seedlings cannot be regarded as conclusive, but as far as it goes it supports the view now to be put forward.

The above facts coincide in all essential points with the observations of Sir J. D. Hooker, and they lead me to the

following conclusion:—That the leaf of *Nepenthes* is not a simple but a branched one; regarding the spur at the back of the lid as the organic apex of the leaf, the lid which arises on its frontal or adaxial face, more or less distinctly below its extreme lip, and with a two-lobed form, may be regarded as representing two coalescent pinnae. The whole leaf would then consist of (1) a phyllopodium, winged throughout its length, terminating in the spur, and developing the pitcher itself as an involution of its upper surface; (2) a pair of pinnae, which show congenital coalescence across the frontal face of the phyllopodium, and constitute the lid of the pitcher.

I see only one other way of interpreting the facts. It might be possible to regard the lid as being truly the apex of the leaf, while the spur might be recognised as an outgrowth of the abaxial or lower surface of the leaf close to its apex, as in the leaf of *Iris*; but against this view is to be set the difficulty of explaining the two-lobed character of the lid while young, its venation, and its emargination when mature without any trace of a central spine at its apex. Moreover, observation of stages of development, such as those shown in Figs. 5–7 and 10–13, though they do not show the point so definitely as might be wished, indicate, I think, plainly enough that the organic apex of the leaf is represented by the spur, while the lid arises on its adaxial surface, though very little below its apex. I therefore think that the latter interpretation of the facts is untenable.

Adopting then the view that the leaf is a peculiarly developed phyllopodium, bearing two pinnae which show congenital coalescence, it remains to draw comparisons with other leaves. I am not aware that any case exists of such coalescence of pinnae across the frontal or adaxial face of the phyllopodium. It is obvious that Griffith's comparison with the leaf of *Bauhinia* does not exactly fit. There the terminal spine, or true apex of the leaf, lies between the two pinnae, which are sessile upon the phyllopodium, being inserted upon

it by very broad bases; there is, however, in Bauhinia no extension of their growth across the adaxial surface. But if we pass on to stipules (which in many cases are without doubt essentially similar in their nature to pinnae, and may often be regarded as basal pinnae of peculiar character) similar developments are to be found. In the intra-petiolar stipules (e.g. of Melianthus) a coalescence of the two stipules across the adaxial surface of the phyllopodium has taken place, and such examples seem to approach most nearly to the constitution of the lid as above suggested for Nepenthes. It is to be admitted that the emargination of the lid is often very slight, while in early stages of development the lid may appear to be actually entire (Figs. 11, 13); but in this I see no grave ground for doubt of the assumed congenital coalescence. Numerous examples might be cited of congenital coalescence quite as complete as this, where the fact of coalescence is beyond doubt—for instance in the stellate Rubiaceae, and especially in Rubia peregrina, all stages of coalescence of the stipules may be found, from those in which the two stipules of one pair are united at their base, through those united for half their length, to those which show only two terminal teeth, but have two prominent midribs, and finally to such as are absolutely entire at the apex, and have only a single well-marked midrib. In these last the coalescence (which on comparative grounds cannot be doubted) is complete and congenital, and in them we have an example closely similar to the cases shown in Figs. 11 and 13. In the mature lids of pitchers the venation may, as in the above-cited case of Rubia peregrina, show a certain relation to the external form, and on looking over a number of specimens in Kew, it has been seen that, as a rule, where the emargination is distinct the venation is referable to the two lobes; while where the lid is most nearly entire there is frequently a single central rib more clearly marked than the rest. Similar observations may also be made on the coalescent pair of outer perianth-segments in Cypripedium. Other examples might be cited, but sufficient has now been said to show that the lid of the pitcher of Nepenthes presents in its
origin, as well as in its mature structure, characters which justify the conclusion that it is the result of a congenital coalescence of two pinnae.

Turning now to the phyllopodium, that is, the whole leaf exclusive of the pinnae which constitute the lid, the pitcher itself is seen to originate first as an involution of the frontal or adaxial face of it, near to its apex, and the involution begins before the lid makes its appearance. It is brought about by the more active growth in an area surrounding a certain point than at the point itself. In this respect the pitcher of *Nepenthes* corresponds to that of *Sarracenia* or *Utricularia*, while over-growths of a similar order are not uncommon among other plants. Dickson has compared the pitcher to the peculiar funnel-shaped, abnormal leaves of *Croton*, while Goebel has drawn the comparison between pitchers and orbicular leaves, and the pitcher may be regarded as an extreme instance of such slight hollowing of the upper surface as is to be found in such cases as *Hydrocotyle, Tropaeolum*, and *Nelumbium*.

Regarding then the pitcher as the result of involution of the upper surface of the phyllopodium at a point near its apex, it remains to consider the lower portion of the leaf. It has been pointed out in my paper above quoted that in very many cases, and especially in the Ferns, Cycads, and Dicotyledons, the phyllopodium is a winged structure throughout its length, and that those parts of it which may be distinguished when mature, depend for their differentiation upon the different mode of localisation of intercalary growth in them; the parts usually recognised may be termed the hypopodium (or sheath), the mesopodium (or petiole), and the epipodium (or upper portion of the main axis of the leaf exclusive of the pinnae); but in my former paper it was expressly stated (p. 610) that ‘such distinctions are only to be drawn where they are warranted by the exigencies of description.’ In simple sessile leaves it is obviously impossible to distinguish those parts.

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1 The tubers of orchids, and of *Phylloglossum*, and inferior ovaries; these, however, involve the actual apex, while here it is not the apex which is arrested in its growth, but the point of arrest is at some little distance below it.
Now, because certain modes of localisation of growth in the developing leaves are common, and since accordingly in large and complicated leaves the parts above distinguished usually have a certain conformation, it does not follow that this should always be the case. But the attempt made by most writers to homologate the parts of such a peculiarly developed leaf as that of *Nepenthes* with the parts of leaves of the usual type, implies the assumption that it is possible to make the distinction in every case, and that the parts thus recognised are in some recondite way different from one another. In the absence of evidence that *Nepenthes* is descended from ancestors with a normal petiole, which in this plant became widened into its well-known expanded base, it will be well, I think, to give up the attempt to homologate the parts of this phyllopodium with those of the ordinary type. It was the unnatural extension of a generalisation, based on wide but not universal experience, to all cases, that ruined the spiral theory of Braun and Schimper; and in the case of the leaf the extension of the notion of transverse limitation must have like results. While we note that a distinction of petiole and lamina, as parts having usually a definite relation of form and position, is applicable to a large proportion of leaves, let us beware of assuming that the parts of all leaves, however peculiar their form, are referable to such a type.

To meet the difficulty of want of uniformity in different leaves, and especially in cases such as that now under discussion, it is, I think, important to fix the attention upon the phyllopodium throughout its length. It is, as a rule, a structure which is traversed by two longitudinal wings; such wings, or longitudinally directed flanges, are to be found in a very large proportion of leaves, from the lowest Ferns to the Dicotyledons, and, though not universal, the prevalence of this winged character is a much more constant and important phenomenon than those on which the distinction of sheath, petiole, and

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1 Drude and Goebel both attempt to define limits of petiole and lamina in *Nepenthes*. 
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lamina are based. These wings are early recognisable in the developing leaf, and are usually present on its adaxial face; they are the seat of important subsequent growths; their most prominent mode of development is the formation of the lateral flaps of the simple lamina; or upon each of them may arise in longitudinal series the pinnae, which may remain rudimentary, and show congenital coalescence (as in leaves with serrate margins), or the pinnae may develop separately from one another (as in the truly pinnate leaf). The prevalence of these wings from the Ferns upwards, and the influence of their existence upon the ultimate conformation of leaves, makes it appear to me to be important to recognise their presence more fully than is usual; the recognition of the phyllopodium, as usually a winged structure, seems to me to lead to a better insight into the real nature of the leaf than the usual custom of drawing at once the transverse limitations of sheath, petiole, and lamina.

The phyllopodium, thus recognised, is susceptible of various development throughout its length, according to the varying balance of transverse and longitudinal growth. Where the transverse growth is relatively great, and the longitudinal less, the result is such a development as that which we usually term a lamina. Where the longitudinal growth is in the ascendant the result is what we call a petiole. Beyond the fact that these differences of localisation obtain respectively in those two parts, and that the petiole is intercalated at a relatively late period, there seems to me to be no essential or recondite

1 This expression of opinion is diametrically opposed to that of K. Reiche (Ber. d. D. Bot. Ges., 1888, p. 328), who remarks as the result of the observation of winged stems and decurrent leaves of certain Phanerogams as follows:—‘Dass die Flügel an pflanzlichen Organen aus geringen, morphologische Charaktere darstellenden Bildungen hervorgegangen seien.’ This conclusion is based on a narrow comparison. The author does not refer to any vascular Cryptogams or Cycads, and generalises from observations on a few stems to ‘plant-organs’ generally. Now the morphological importance of characters depends upon their prevalence through large groups, and the prevalence of a more or less clearly winged character in the leaf from the Ferns upwards is accordingly a character of morphological importance; certainly its importance in the leaf is not to be set aside because it is not prevalent or constant in the stem.
difference between petiole and lamina. Further, if this be the case, there is no need to assume that their order of succession on the phyllopodium shall be always the same: it is quite possible to imagine the balance of intercalary growth characteristic of what we call the lamina to be localised near to the base of the phyllopodium, while the intercalation of a part, comparable as regards its development to the petiole, may take place higher up; and this is exactly what takes place in *Nepenthes*, for the tendril-like prolongation is intercalated at the point marked (x) in Figs. 4 and 14. I would not go so far as to suggest the application of the term petiole to the tendril, and lamina to the expanded portion at the base, as this would be a use of established terms in a forced sense. It is, I think, preferable to drop the attempt to homologate the parts of all leaves to the usual plan as leading to unnatural comparisons, recognising, however, that the peculiar mode of development of the winged phyllopodium in *Nepenthes* shows in inverted order those characters which lead to the distinction of the parts usually termed petiole and lamina in ordinary leaves. It seems to me to throw no more light upon the morphology of the leaf of *Nepenthes* to call the basal expanded portion the petiole than it does to attempt to distinguish petiole and lamina in an absolutely sessile leaf: in other words, the terms petiole and lamina are to be used only in a descriptive sense, and it is not to be assumed that because such parts are commonly to be distinguished in leaves of complicated form, therefore the parts of all complicated leaves are referable to such a classification. In order to justify the use of the term petiole for the basal expansion of the leaf of *Nepenthes* it would be necessary to demonstrate that this plant was descended from a typically petiolate ancestor, and that the petiole had actually become transformed to the condition in which we see it; but such evidence is not forthcoming at present.

The above attempt to apply the method of treatment of the leaf, advocated in 1884, to a most problematical case has had the result of eliciting a new view of its morphology. The attempt has also shown that the method, which I believe to
be in accordance with our treatment of the shoot as a whole, is applicable to the most difficult cases. It is obviously an elastic method, and in this respect it accords with the morphological spirit of the time; it is generally recognised that in their adaptation to special physiological requirements plants are susceptible of the most varied development, and that this does not follow a rigid type. This is admitted as regards the arrangement of leaves on the shoot, in the branching of the shoot, and in the development of the nodes and internodes. It is time that, in considering the leaf, which is the most plastic of all members, a similar elasticity of method should be adopted, and the assumption that in complicated leaves the parts are necessarily referable to sheath, petiole, and lamina should be recognised as being based on insecure foundations.

December, 1888.
DESCRIPTION OF FIGURES IN PLATE XVI.

Illustrating Professor F. O. Bower's paper on the leaf of *Nepenthes*.

*Nepenthes*, sp.: Figs. 1–4.

Fig. 1. Apex of young leaf, *a*, with young leaf, *b*, seen in profile. \( \times 36 \).

Fig. 2. Next older leaf of the same bud seen in full face; *c*, cavity; *w*, wings. \( \times 36 \).

Fig. 3. An older leaf with the lid, *\ell*, already present; *a\ell*, apical spur. \( \times 36 \).

Fig. 4. A leaf still older; *as*, the part which forms the pitcher; *xx*, the point of origin of the tendril. \( \times 20 \).

Figs. 5–8, *Nepenthes phyllanphora*.

Fig. 5. Apex of stem, and young leaf; *A* as seen full face; *B* in profile. \( \times 36 \).

Fig. 6. A somewhat older leaf; *ap*, apical spur; *\ell*, lid; *c*, cavity. \( \times 36 \).

Fig. 7. Another leaf slightly older. \( \times 36 \).

Fig. 8. A much more advanced leaf, showing irregular growth of the apex, *ap*. \( \times 18 \).

Figs. 9–17, *Nepenthes distillatoria*.

Fig. 9. Young leaf in full face. \( \times 36 \).

Fig. 10. Young leaf in profile. \( \times 36 \).

Fig. 11. Apical portion of an older leaf in full face. \( \times 36 \).

Fig. 12. do. do. in profile. \( \times 36 \).

Fig. 13. do. do. in full face and in profile, somewhat older. \( \times 36 \).

Fig. 14. A leaf more advanced; lettering as before. \( \times 36 \).

Figs. 15–16. Leaves in which the lid has covered in the cavity of the pitcher. Fig. 16 shows irregular development of the apical spur. \( \times 36 \).

Fig. 17. An older leaf of the same, showing very clearly the two-lobed character of the lid of the pitcher. \( \times 36 \).
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