

ON PSEUDODICHOTOMY IN ALOË TRANS- VAALENSIS O. KTZE.

by

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With Tab. I and 5 textfigures.

Aloë transvaalensis O. Ktze. is a widely distributed and very polymorphic species found in the greater part of the Transvaal and in some of the adjacent territories. Its various forms differ inter alia in the colour of the flower, the length of the bracts, the number of branches in the inflorescence, the position of the inflorescence on the rosette, the shape and colour pattern of the leaves, the form of the marginal teeth, and the mode of branching of the vegetative shoot.

The diversity in the way of branching in the latter is all the more remarkable, because the two main types distinguished by Berger¹⁾: the formation of lateral shoots on the older parts and the forking of the stems at their end, two types which according to that author are characteristic for two groups of Aloës of quite different habit, are found here in plants of the same species and sometimes even on the same individual.

Plants in which no branching occurs, and whose rosettes therefore remain always simple, and large clusters of rosettes owing their origin mainly to lateral branching, are much more common than the forked individuals in which we are here chiefly interested. The lateral branches spring from the basal part of the very compact stem (Aloë trans-

¹⁾ A. Berger, Liliaceae-Asphodeloideae-Aloineae in „Das Pflanzenreich" IV, 38, pag. 5.

vaalensis is a „stemless” species) on or somewhat below the level of the soil, and begin their development only after the leaves have been worn off. Their first leaves are scalelike and show the same distichous arrangement as those of the seedlings and the internodes are long, thin and yellowish, bringing the top of the shoot with as little delay as possible from under the shade of the mother plant into the light. The origin of these lateral branches has been studied in detail by Schoute¹⁾ in some other species. It was found that they develop from axillary buds situated on the anodic side of the leaf base, that is to say: somewhat away from the middle in the ascending direction of the genetic spiral. *Aloë transvaalensis* is not a suitable object for a study of this point: I have not been able to find the buds on those parts of the stem where the leaves are still present, and on the wrinkled surface of the older parts the exact position of the leaf scars is not recognisable.

Plants with forked rosettes are not found in such large numbers as the types just mentioned. Nevertheless they are by no means rare. In old plants the bifurcation is moreover often two or three times repeated. Lateral branches are sometimes met with at the same time.

The greater part of these forked rosettes shows an arrangement of the leaves of the same kind as that described by Schoute²⁾ in *Aloë soccotrina*. Along the line where the two branches come together, the oldest leaves are found: in one of the shoots the first one only, in the other shoot the first one and the second one. My curiosity however was roused, when I found two plants with an entirely different arrangement. Of one of these plants photographs are shown in fig. 1. (Tab. . . .) In each of the shoots it is here only the first leaf which turns it back towards the cen

¹⁾ J. C. Schoute, Über die Verästelung bei monokotylen Bäumen, III. Rec. d. trav. botan. Néerl. Vol. XV. 1918, pag. 327.

²⁾ J. C. Schoute, l.c. pag. 310.

tre of the rosette, and there are therefore in these rosettes only two leaves with their backs in contact with each other instead of three as in the other ones. There is however a peculiarity which is still more remarkable: the two branches are symmetrically arranged with regard to a small leaf which is just visible on one side of the fork. It was only natural to suppose that this leaf must have been produced by the shoot just before the bifurcation took place. If that had been true, it would have resembled the angular leaf found by Velenovsky²⁾ in the bifurcated shoots of a great number of Pteridophytes, and by Schoute³⁾ in the forked stems of an Egyptian *Hyphaene*. A closer investigation however revealed that this leaf was not inserted below the two branches, but on the stalk of an inflorescence which, when the photographs were taken, was still hidden between the leaf sheaths. However, before I enter into the details of this study, I will first describe and illustrate the arrangement of the leaves and inflorescences in a rosette in which no forking has taken place.

If a rosette produces yearly only a single inflorescence, the latter may become visible in the centre, and in that case its stalk is always perfectly straight, or it may appear in an excentric position, and then the basal part of the stalk is curved. Not unfrequently more than one inflorescence is produced, and in that event they make their appearance soon after each other, the youngest one as a rule exactly in the centre.

An analysis of a plant with two inflorescences, the youngest one occupying the centre of the rosette, is given in fig. 2. In fig. 2a a transverse section is shown, which has been cut in such a distance above the growing point, that

²⁾ Jos. Velenovsky, Vergleichende Morphologie der Pflanzen. I. Teil. Prag 1905, pag. 242 et seq.

³⁾ J. C. Schoute, Über die Verästelung bei monokotylen Bäumen, II. Rec. d. trav. botan. Néerl. Vol. VI. 1909, pag. 10.

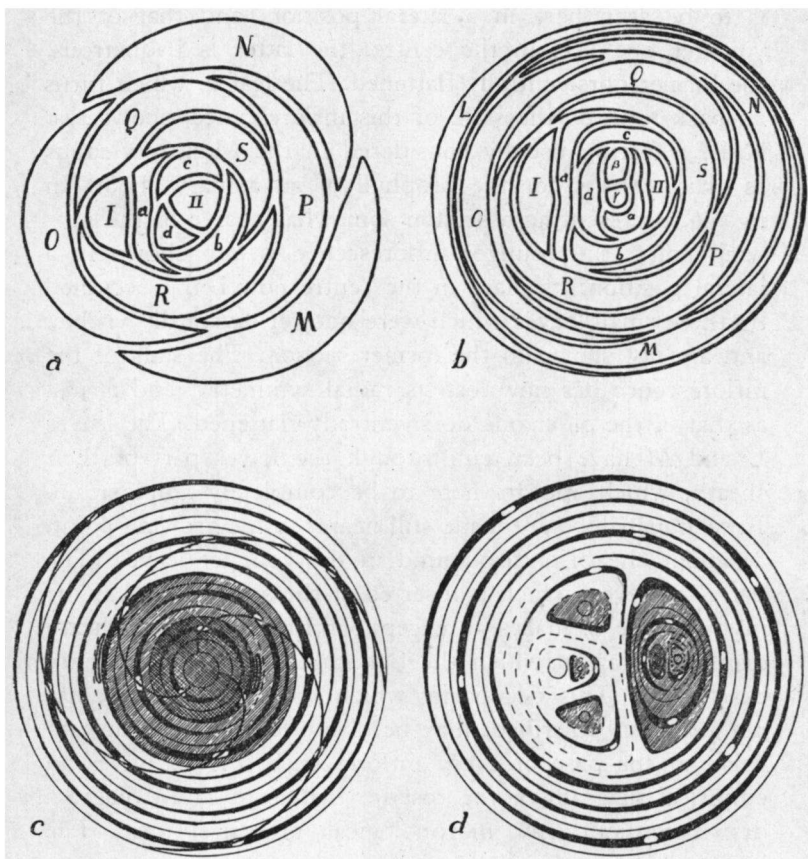


FIG. 2. Analysis of a rosette of *Aloë transvaalensis* O.Ktze. with two inflorescences. *a*, and *b*, sections; in *a*, the stalk of the youngest inflorescence is seen in the centre of the rosette; in *b*, which has been cut somewhat nearer to the growing point, it has shifted already to a lateral position; *c*, empirical diagram; *d*, theoretical diagram.

only those leaves which were already outwardly visible, have been touched. The stalk of the older inflorescence (I) is to be seen here in a lateral position, and that of the younger one (II) in the centre; the latter is triquetrous, the former dorsiventrally flattened. The leaf *a*, which turns its back towards the stalk of this inflorescence, shows two keels, a feature usually considered in the Monocotyledons as characteristic for the prophyll of an axillary shoot. In fig. 2*b*, representing a section somewhat nearer to the growing point, the younger inflorescence is also shown in a lateral position, its place in the centre now being occupied by three small leaves which were not yet outwardly visible, and are not shown in the former section. The stalk of the inflorescence has now lost its radial symmetry, and is just as that of the older one dorsiventrally flattened. The leaves *L* and *M* have been cut through the lower part of their sheath, which appears here to be completely amplexicaul. In sections which are made still nearer to the growing point, a similar sheath is also found in the younger leaves. The leaf *S* however, which is inserted at the same height as the inflorescence *I*, makes an exception. In this leaf the sheath displays a gap in which the flat stalk of the inflorescence exactly fits. This peculiarity which, as far as I know, has not yet been described, may be observed in *Aloë transvaalensis* at the base of every inflorescence. Fig. 2*c* gives an empirical diagram of the rosette, that is to say a diagram drawn without any morphological preconceptions. The leaves are represented by circles with a thickening on the side where the blade is found, the middle of the latter being marked by a white spot. A circle which is completely closed, symbolizes a leaf whose sheath is fully amplexicaul; a dotted part means a gap. The insertion of the inflorescences should have filled these gaps. In order however to show the gaps and the inflorescences at the same time, the latter have been shifted somewhat in the direction of the centre. That

part of the shoot, which begins just above the insertion of the leaf *S* and of the inflorescence *I*, is obliquely shaded, the part above the leaf *d* and the inflorescence *II*, cross shaded. The three spiral lines represent those parastichies, which in the intact plant are the most easily perceptible.

The position of the inflorescences in this diagram 2c, is very peculiar, and seems to be inconsistent with established morphological views. The inflorescences are drawn as axillary branches, but as such they could only belong to the leaves just below those with the open sheath. In that case they would owe their origin to buds which must have made their appearance on the cathodic side of the leaf about 45° from the centre of the axil. This would not in itself be quite impossible: axillary buds in Monocotyledons appear very often in an excentric position. It seems however that they are always shifted towards the anodic side of the leaf, that is to say exactly in the opposite direction.

In order to explain their insertion at the same height as the following leaf of the main shoot, we should have to assume moreover that the basal part of the inflorescence had grown together with the internode following the subtending leaf. As a similar assumption has been accepted already in several other cases, it might here also be acceptable. Another argument against the axillary nature of the inflorescence is the presence of a long internode between its base and its lowest leaf scale, whereas other axillary shoots in the Monocotyledons have only a very short, often indistinct internode below their first leaf: in our *Aloë* the branches of the inflorescence offer a good illustration of this rule. The question however seems to me to be solved beyond dispute by the evidence afforded by a study of those cases where branches arise on both sides of the inflorescence. As these branches are identical in every essential point, there seems to be no other possibility than that they are both axillary structures, and that the inflores-

cence is the continuation of the main shoot. If we accept the same explanation in those cases where beside the inflorescence only a single shoot is found, we arrive at the interpretation laid down in the theoretical diagram, fig. 2*d*, an interpretation which is now universally accepted.

In fig. 2*d* the branches of the first order are obliquely shaded, those of the second order cross shaded, the shaded areas on the right hand of the figure corresponding to those of fig. 2*c*. To the left of this shaded portion the inflorescence *I* is shown with three of its bracts each of them subtending a branch. To the right of the cross shaded area the inflorescence *II* makes its appearance with two bracts. It will be seen that the arrangement of the bracts on the stalk of the inflorescence is identical with that of the leaves in the axillary shoot which is to take part in the formation of the sympodium. On the branches of the inflorescence, which begin with a very characteristic two-keeled prophyll¹⁾ however the arrangement of the bracts is not quite identical with that on the main stalk, the direction of the genetic spiral in the former being independent from that in the latter. If we assume that the prophyll of the axillary shoot which forms the continuation of the rosette, stands with its centre in the median plane just

¹⁾ A study of the direction in which the convolutive leaves of several Gramineae are rolled up in the main shoot and its lateral branches, has lead me formerly to defend the view that the twokeeled prophyll in these plants and therefore probably also in the other Monocotyledons, owes its peculiar shape to the coalescence of two leaves. (Rec. d. trav. botan. Néerl. Vol. XII, 1915, pag. 31 et seq.). I am no longer of this opinion, not so much, because the arrangement is not always, as Guillaud (Bulletin d. l. Soc. Linn. d. Normandie, 7e Serie, t. VII. 1924, pag. 69) has pointed out, as regular as it has been depicted in my article, (which would to my mind not invalidate my conclusions), but because my arguments don't exclude the possibility of the univalent nature of the prophyll, and as this interpretation seems to be simpler, it should be preferred.

opposite the subtending leaf, we come to the conclusion that the bud from which this axillary shoot has sprung, must have made its appearance about 45° from the centre of the axil in the direction of the next leaf, that is to say on the anodic side of the subtending leaf. As has been pointed out already by Schoute¹⁾, it is this peculiarity which explains the absence of irregularities in the genetic spiral of the sympodium: the angle of divergence between the first leaf of the axillary shoot and its subtending leaf, which is at the same time the last leaf of the preceding part of the sympodium, becomes in this way the same as the angle of divergence between two successive leaves belonging to the same part of the shoot.

A few words may be added here about the development of the inflorescence and the shape of its stalk. Its primordium is at first radially symmetric and this symmetry is retained in those parts which are differentiated first, that is to say in the portion which bears the flowers and in the upper part of the stalk (*II* in fig. 2a). As soon however as the primordium is pushed aside by the first leaf of the axillary shoot, it loses its radial symmetry and becomes dorsiventral (*I* in fig. 2a and *I* and *II* in fig. 2b). Its behaviour shows therefore a marked resemblance to that of a leaf. The latter occupies in these plants at first also a central or an almost central position on the top of the meristematic cone, and is during that time also more or less radially symmetric. When it has to make place for a new leaf, it becomes dorsiventrally flattened. Subsequently it tends to surround the younger leaf by an extension of its margins. The primordium of the inflorescence and that of the leaf in whose axil the sympodium will be continued, belong in this respect more or less together. When the inflorescence is pushed aside by the first leaf of the axillary

¹⁾ J. C. Schoute, Über die Verästelung bei monokotylen Bäumen, III. Rec. d. trav. Néerl. Vol. XV. 1918, pag. 304.

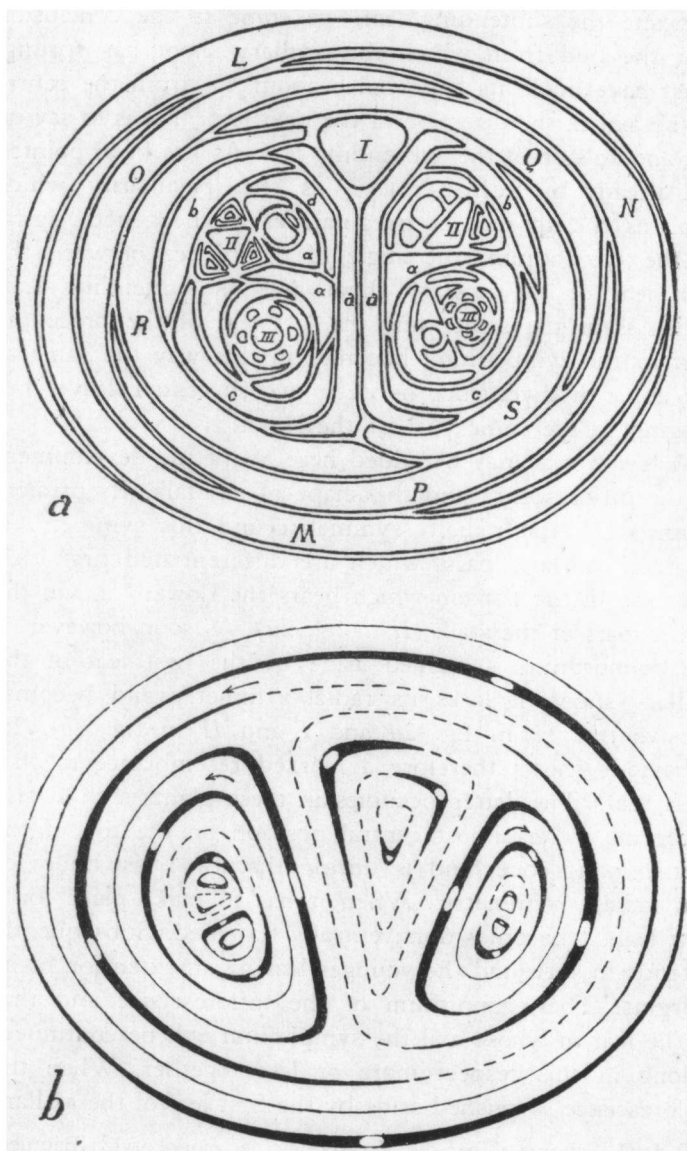


FIG. 3. Analysis of the plant shown in fig. 1. (Tab. I)
a, section; b, diagram.

shoot, it moves towards a spot just face to face with the subtending leaf, and as it goes to occupy a place in the same height as the latter, it prevents the complete closure of its marginal extensions. This explains that only a single scar is left, when in the end both the inflorescence and the leaf are thrown off.

In some cases there is a discontinuity in the development of the inflorescence and then the leaves of the axillary shoot may become visible first. Under these circumstances the inflorescence makes its appearance in a lateral position. When on the other hand the leaves of the axillary shoot lag behind in their development, the inflorescence appears in the centre of the rosette.

If we try now an analysis of the forked plant shown in fig. 1, (Tab. I) we will find there on the whole the same features as in the simple rosettes. Fig. 3 gives a section and a diagram of this plant. The section has been cut below the insertion of the small leaf whose deceptive resemblance to an angular leaf became the starting point of this investigation. The shoot on which it was inserted, was an inflorescence. It is marked in the drawing with the Roman cipher *I*. The two new rosettes are symmetrically arranged with regard to this inflorescence. Their first leaves turn their back towards each other, and are each provided with two keels. Otherwise there is no difference between them and an ordinary leaf. Each of these branches ends again in an inflorescence (*II*). The inflorescence on the left is shown with three bracts each subtending a branch. At the insertion of this inflorescence, the bifurcation of the rosette has been repeated, and one of the branches ends again in an inflorescence (*III*). The inflorescence *II* on the right is shown with two bracts subtending branches. The lower one of these branches has been cut through above the insertion of the prophyll. At the base of this inflorescence only a single branch is formed, which ends in its turn in

the inflorescence *III*, at the base of which there is again a single branch. The rosette on the right hand therefore remains simple: it has the ordinary sympodial structure.

In each of the main branches the first leaf is marked with the letter *a*, in the branches of the next order with the corresponding letter of the Greek alphabet. The leaf *a* on the left presents four keels, that on the right three. A similar difference is also found between the first leaves of the younger pair of branches. This variability in number, is doubtless an indication that the keels are here not of the same importance, morphologically and probably also functionally, as in the prophylls of the branches on the inflorescence, where their number is always two.

The diagram shows that here again an open sheath is found in each leaf subtending an axillary shoot. It shows also very clearly that the branching of this plant is a case of pseudodichotomy arising in the same way as elsewhere in the Liliaceae. If we compare it with the bifurcation of *Aloë soccotrina*, described by Schoute¹⁾, we will find nevertheless some difference. The first three leaves of the two branches are here namely in an almost perfectly symmetric position, whereas in Schoute's plant this is not so. The first leaf of the lower branch is in that plant as has been mentioned already, not only in contact with the first but also with the second leaf of the higher branch. There is still another point of difference. In Schoute's specimen the lower branch was antidromous and the upper one homodromous with the main shoot: here it is the opposite. The antidromy of the inflorescence itself, is perhaps an anomaly: irregularities in the arrangement of the bracts are by no means rare. If we assume that the primordia of the two leaves *a* were already formed before the second bract appeared, the latter might have found no

¹⁾ J. C. Schoute, l.c. pag. 310, fig. 23.

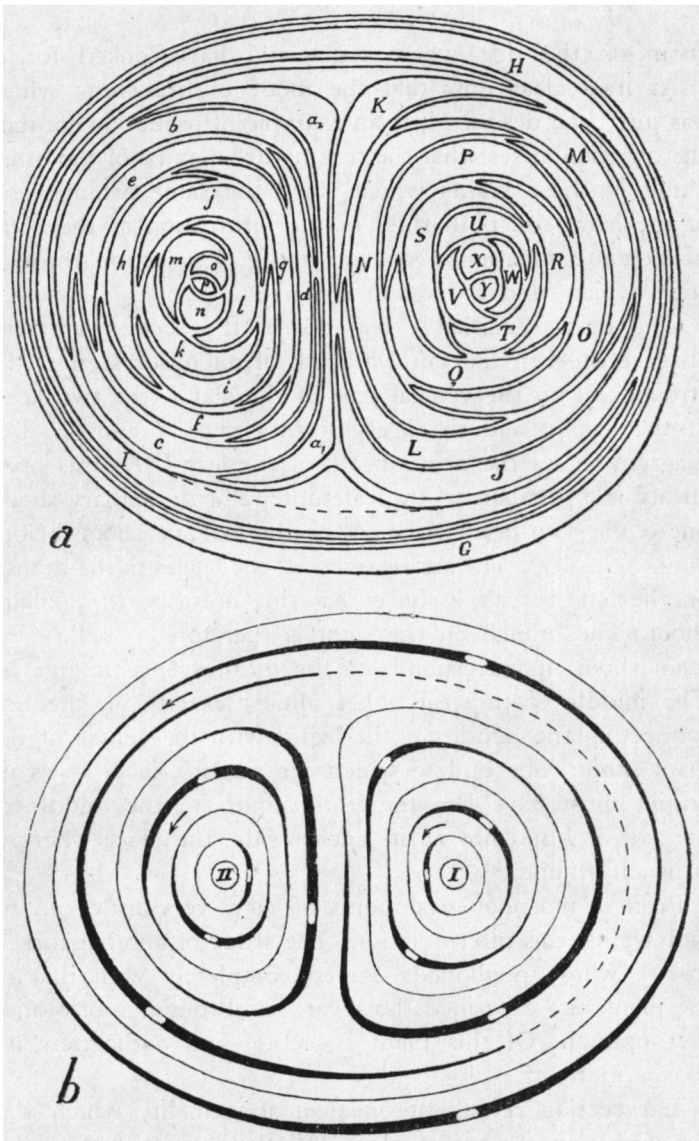


FIG. 4. Analysis of a forked rosette of *Aloë transvaalensis* O.Ktze. in which no trace of an inflorescence could be detected. *a*, section; *b*, diagram.

room on the side where we would have looked for it.

As it is clear now that the mode of branching which has just been described, is an example of pseudodichotomy, the question arises what the true nature may be of the branching in those plants which show the same arrangement of the leaves on both sides of the bifurcation as the plant of Schoute mentioned above. In fig. 4 a section through such a plant and a diagram are given.

The most remarkable features of the section are: the absence of even the faintest trace of an inflorescence, the strong keel on the ventral face of the leaf *I*, the two keels of the leaf *a*, and the keels of the leaves *J* and *K*. The diagram shows the open sheath of the leaf *I*. As this open sheath is a peculiarity of a leaf subtending an axillary shoot, one of the two branches must be the axillary shoot belonging to this leaf. The arrangement of the leaves in the branch on the left, reveals at once that this must be the axillary shoot. The branch on the right is therefore in reality the main shoot: it corresponds to the inflorescence in fig. 2*d*. The middle of the leaf *a* lies almost exactly on the line connecting the middle of the leaf *I* with the centre of the main shoot. The bud to which the axillary shoot owes its origin, must have lain therefore almost in the middle of the axil of *I* and not on its anodic side, the place where it is usually found.

From a morphological point of view very little can be said against this interpretation. The study of another forked rosette whose phyllotaxis agreed completely with that of the plant just described, however, has brought me to another opinion. Of this plant a section and a diagram are shown in fig. 5.

The section reveals at once an abnormality which was not visible in the intact plant. All the leaves of the main shoot which are shown here, as well as those of the branches, form continuous bands winding themselves in slowly

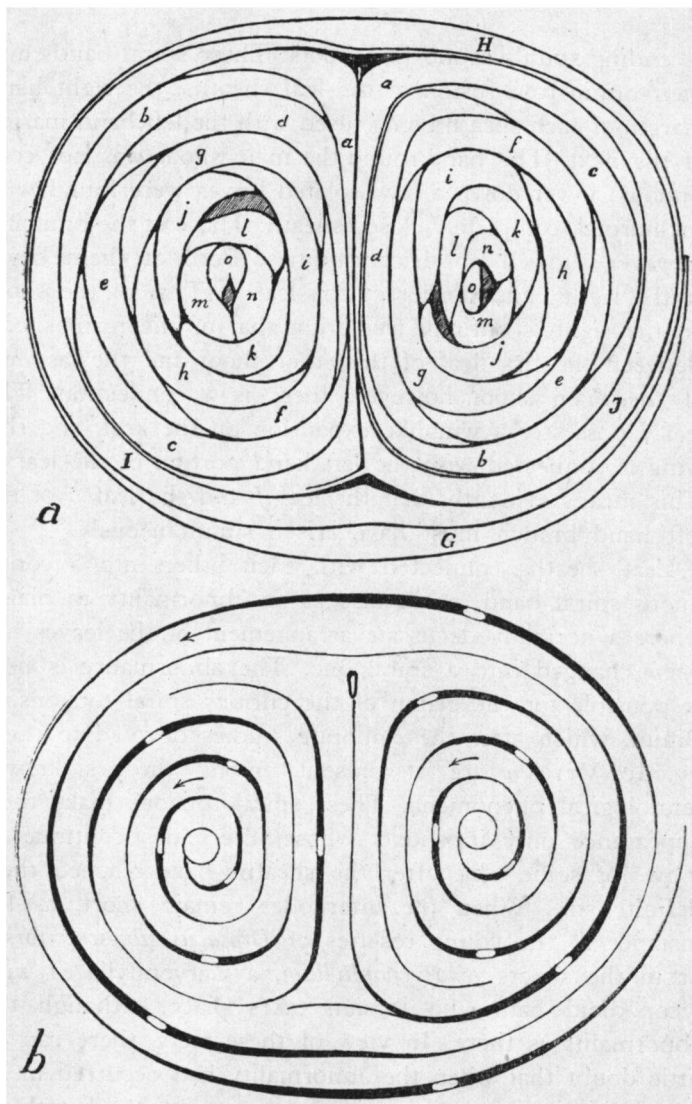


Fig. 5. Analysis of a forked rosette of *Aloë transvaalensis* O.Ktze. with an abortive inflorescence between the branches. The sheaths of the leaves form in this plant continuous spiral bands round the shoots. *a*, section; *b*, diagram.

ascending spirals round the shoots. These spiral bands owe their origin to a fusion of the leaf sheaths, the right hand margin of each sheath being fused with the left hand margin of the next. The band round the main shoot was not continuous: lower down a few isolated leaves were found with the normal, completely closed sheath. Those of the branches however showed no discontinuities. Both of them begin at the right hand border of the leaf *a*. That of the shoot on the right is entirely free from that of the main shoot. Between the first leaf of the other shoot and the last leaf of the main shoot however, there is a connection. The leaf *J* possesses a winglike expansion on the keel, and this wing is connected with the left hand portion of the leaf *a*. This means evidently that the leaf *J* and the leaf *a* of the left hand branch must have arisen simultaneously.

Leaf sheaths connected with each other into a continuous spiral band, occur also as an abnormality in plants where a normally decussate arrangement of the leaves has been changed into a spiral one. The abnormality is here responsible for the origin of the curious spiral torsions of Braun, which after the elaborate studies devoted to them by de Vries¹⁾ are at present among the best known teratological phenomena. These spiral torsions make their appearance only in shoots whose internodes continue to grow for some time after the sheaths have reached their definite size. When the internodes remain short, as for instance in the young rosettes of *Dipsacus silvestris torsus* or in the shoots of *Pycnophyllum*, a Caryophyllacea with lycopodioid habit, no torsion takes place, although the abnormality is there. In view of these facts, there can be little doubt that when the abnormality had occurred in an Aloë with internodes growing out to a greater length, it

¹⁾ Hugo de Vries, Monographie der Zwangsdrehungen. Pringsheim's Jahrbücher. Bd. XXIII, pag. 14 et seq.

would have resulted in a true spiral torsion. So far however the latter have only been described in plants which in the normal condition have decussate leaves.

The arrows in the diagram mark the direction of the genetic spiral, as the latter is usually understood: as the spiral connecting the middles of the leaf insertions in the shortest way possible. In a case like the one before us, it is seen at once that we might better define it as a spiral band of tissue beginning at or near the top of the growing point and giving rise, at regular intervals, to the primordia of the leaves. In our abnormal *Aloë* it is this spiral which becomes visible in the continuous band of leaf sheaths not the genetic spiral of orthodox morphology. The angle of divergence would therefore not be somewhere in the neighbourhood of 120° , but in the neighbourhood of 240° .

More important from our present point of view however is the fact that the section reveals the presence of five inflorescences of which the oldest one is completely aborted, and the two youngest show already signs of decay. Only the two inflorescences between the leaves *i*, *j*, and *l* present a healthy aspect. The presence of an inflorescence between the two shoots makes it at once clear, that they are both axillary structures. Although the arrangement of the leaves in one of the shoots is different from that in the plant of fig. 3, the morphological value of the branches in both plants is nevertheless the same. The abortion of the inflorescence at a very early date, gives the highest leaf of the main shoot in the plant of fig. 5 the opportunity for a further extension of its left hand border, and this explains why the primordium of the first leaf of the axillary shoot has also been shifted to the left. There must have been moreover a very important difference in the point of time at which the various leaves made their appearance. We have seen already that in the plant of fig. 5 the highest leaf of the main shoot and the first leaf of the shoot in the

axil of the preceding leaf, must have arisen simultaneously. It is not impossible that the very early development of the axillary shoot had in this case something to do with the abortion of the inflorescence. In the plant of fig. 3 the almost exact symmetry of the two leaves *a* must doubtless be taken as an expression of their simultaneous origin. It is therefore impossible that the highest leaf of the main shoot and the first leaf of the shoot in the axil of the preceding leaf, came here into being at the same time.

Above I expressed the opinion that a very early development of an axillary shoot might exercise an influence on the development of the inflorescence. We might view this influence perhaps in the following way: If the axillary branch develops too soon, the inflorescence is either killed or converted in a vegetative shoot. The latter interpretation is the one by which I tried to explain the structure of the plant shown in fig 4, before I knew of the existence of forked rosettes with abortive inflorescences; the former the one which seems now more plausible. As far as I can see, there is however only one point in the arrangement of the parts in the plant of fig. 4, which is somewhat unfavourable to the former interpretation. If we assume that the axillary shoot has arisen in the axil between the leaf *I* and the shoot on the right, it must have sprung from a bud in the centre of the axil, which is somewhat uncommon in the *Aloës* where the buds are always found in some distance from the middle on the anodic side. If the shoot had arisen however in the same way as the corresponding shoot in fig. 5 in the axil between the leaf *I* and the place where the inflorescence might have made its appearance, it would really have sprung from a bud on the anodic side of the leaf. On the other hand we should be very careful with the assumption of entirely suppressed inflorescences. If in an unbranched stem an inflorescence was entirely suppressed, the sympodium would not be discernible from a monopodium:

it would be possible therefore to interpret every stem as a complex sympodium, whose components might even be single internodes.

The consideration of the possibility that an important part may have disappeared completely, drew my attention again to the case of *Hyphaene*, the palm whose dichotomous

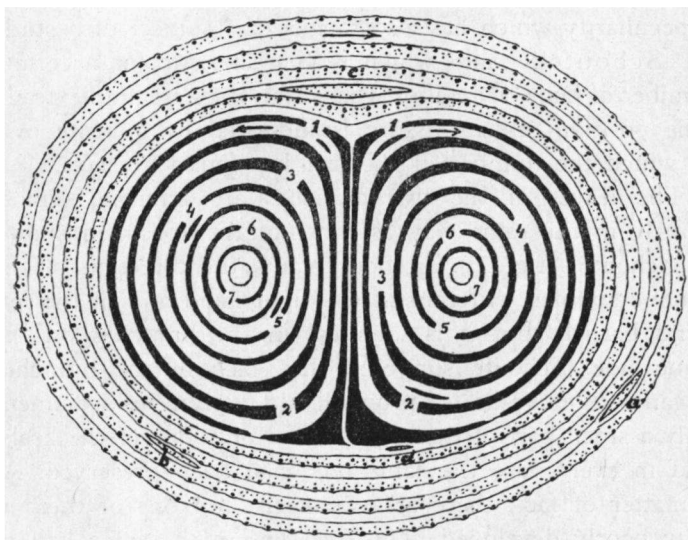


FIG. 6. Diagram of a forked stem of *Hyphaene coriacea* Gaertn.

branching has been studied by Schoute¹). As I had at my disposition a forked stem piece of another *Hyphaenë*, namely of *Hyphaene coriacea* Gaertn., I resolved to test the general validity of his conclusions on this object. On the two branches of this piece all the leaves were still present, and on the main shoot, where they had been thrown off, it was not difficult to determine their position, because the scars left by them and by the axillary inflorescences

¹) J. C. Schoute. Über die Verästelung bei monokotylen Bäumen, II. Rec. d. trav. botan. Néerl. Vol. VI, 1909.

were still plainly visible. In fig. 6 a diagram of the arrangement of the leaves and the inflorescences is given. The scars are indicated schematically by their outline and by the marks of the vascular strands. The heavy black lines show the insertion of those leaves and inflorescences as were actually present. The middle of the leaf sheath is easily recognisable by the position of the median fissure, a peculiarity which has also formed the subject of a study by Schoute¹⁾, and which is characteristic for a certain number of fanleaved palms whose leaf bases are amplexicaul. The position of this fissure is indicated by a white oval in which the number of the leaf has found a place.

The leaves of the two branches are arranged almost exactly in the same way as those of the specimen shown in Schoute's fig. 3²⁾. In both plants the direction of the genetic spiral is different in the right hand and in the left hand branch, but it is identical in the branches on the same side. Schoute supposed that each of the branches began with a two-keeled prophyll, although in his specimens only a small part of these leaves and only one of the keels, and in every case the same one, had been preserved. As a matter of fact, there are two keels, but one of them is only poorly developed. This keel lies in the same half of the leaf sheath as the strong one, but very near to the place where the median fissure will appear. When the latter begins to show itself, it follows the curving of the leaf sheath apparently without increasing its resistance in a marked way. Apart from the keels on the sheath these first leaves differ in no wise from the other ones. In the axil of several leaves a more or less rudimentary inflorescence

¹⁾ J. C. Schoute, Sur la fissure médiane de la gaine foliaire de quelques palmiers Ann. d. jardin botan. d. Buitenzorg, 2. Série, Vol. XIV, pag. 57.

²⁾ J. C. Schoute, Über die Verästelung bei monokotylen Bäumen, II. Rec. d. trav. botan. Néerl. Vol. VI, 1909, fig. 3.

is found. As these inflorescences arise almost exactly in the middle of the axil, they are visible through the median fissure of the sheath.

So far there is no difference of any importance with the stempieces studied by Schoute. In the arrangement of the leaves below the fork however, there appears a rather important variation.

The last leaf of the main shoot (*d*) has an axillary bud which is not found just below the point where the two strong keels meet each other (the place occupied by it in Schoute's specimens), but somewhat to the right. It was apparently rudimentary. The preceding leaf has in its axil a very large scar. As a matter of fact, this is by far the largest scar which I have found on this stem piece. It lies exactly beneath the place where the two branches join each other. In Schoute's specimens this scar occupied a position more to the right.

That the two branches in his specimens occupied with respect to the highest leaf of the main shoot symmetrical positions, was for Schoute the reason to regard the mode of branching in these plants as an example of true dichotomy. He expressed his opinion in the following words¹⁾: „Nur bei Hyphaene haben wir den ersten Fall einer echten Dichotomie bei den Phanerogamen, wo die morphologischen Verhältnisse ganz von denjenigen der seitlichen Verzweigung abweichen, dagegen mit demjenigen, was wir bei den dichotomen Kryptogamen fanden, durch das Auftreten eines „Angularblattes“ deutlich übereinstimmen“. Velenovsky²⁾ accepts this view, and adds: „Aus alledem vermag man nun den Schluss zu ziehen, dass die alte kryptogamische Dichotomie ihre Nachklänge noch unter den Phanerogamen hat, wenn dieselben auch nur als Ausnahmen oder als abnorme Fälle in die Erscheinung treten.“

¹⁾ J. C. Schoute, l.c. pag. 21.

²⁾ Jos. Velenovsky, Vergleichende Morphologie der Pflanzen. IV. Teil. Prag 1913, pag. 113.

This conclusion of Velenovsky however does not follow explicitly from the data brought together by Schoute. The latter lays stress on the similarity of the mode of branching observed in *Hyphaene* with that of the dichotomous Pteridophytes, but he does not express an opinion on the question whether this is to be taken as an analogy or a homology. Velenovsky however takes the latter for granted. In view of the fact that the gametophyte of various Bryophyta shows also a dichotomy characterized by the presence of an angular „leaf”, which of course cannot be homologous with the angular leaf of a plant with true leaves, it seems to me that there is also no sufficient ground to defend this homology here. The circumstance that in the Lycopodiales and Filicales dichotomy is the only mode of branching, whereas in *Hyphaene* dichotomous and lateral branching occur side to side with each other, is also unfavourable to this view.

If there might be a mechanical cause for a definite arrangement of the leaves in those cases where a bifurcation of the growing point takes place, there would be no reason why the same arrangement might not have arisen independently in various kinds of plants. According to Schoute¹⁾ the true dichotomy owes its origin to the event that „bei der Gabelung des Stammes kein Austreiben von Seitensprossen stattfindet, sondern dass der Vegetationspunkt des Stammes sich in zwei gesonderte Vegetationspunkte spaltet”. If we accept this definition, we will also have to regard as true dichotomy the splitting of a fasciated shoot in two equal branches. The latter of course is only a special case of the more general splitting up in a greater number of more or less unequal branches, and it is therefore certainly in no way related to the dichotomy of the Lycopodiales and Filicales.

¹⁾ J. C. Schoute, Über die Verästelung bei monokotylen Bäumen, II. Rec. d. trav. botan. néerl. Vol. VI, 1909, pag. 4.

The occurrence of such an arrangement as has been described here in *Hyphaene coriacea*, where no angular leaf is found, along with that described by Schoute in his *Hyphaene spec.*, seems to prove beyond doubt that the resemblance of this mode of branching with the true dichotomy of the Lycopodiales and Filicales is only superficial. When we compare these two kinds of arrangement in *Hyphaene* with each other, we must come to the conclusion that the bifurcation must be due in both cases to a change in the form of the growing point which from circular in outline became elliptic, the short axis of the ellipse lying between the highest two leaves. A similar change as a matter of fact must also have preceded the bifurcation in those plants of *Aloë transvaalensis* where the inflorescence between the branches became abortive. If it is therefore not comparable to the mode of branching of this *Aloë*, it has probably no morphological significance at all, and it might perhaps be regarded as a very regular, hereditary fasciation. But before we accept this conclusion, we will have to consider first the possibility already alluded to, that it might be after all only a disguised form of lateral branching.

The various possibilities have already been discussed by Schoute¹⁾. One of the branches might be the continuation of the main shoot, or both of them might be axillary shoots. If we consider one of the branches as the continuation of the main shoot, the other one must be taken as an axillary shoot of the highest leaf. In the axil of this leaf however there is an inflorescence. The vegetative axillary shoot and this inflorescence would have sprung therefore from collateral buds. This is in itself not at all impossible. The arrangement of the leaves round the branches makes this supposition however improbable. As the

¹⁾ J. C. Schoute, l.c. pag. 8.

angle of divergence between the leaves of *Hyphaene* is almost the same as that between the leaves of *Aloë transvaalensis*, and as the highest leaves on the main shoot occupy in our specimen of *Hyphaene* almost the same position as in the *Aloë* of which an analysis is given in our fig. 4, we should expect in both cases nearly the same arrangement of the leaves on the branches. In both branches of *Hyphaene* the position of the leaves 1 and 2 is however on the contrary quite different from that of the corresponding leaves on the branches of our *Aloë*. If both branches were axillary shoots, we should expect a similar arrangement of the leaves as in fig. 5, where it is however, as we have seen already, essentially the same as in fig. 4. This supposition is therefore also improbable. We will have to accept therefore Schoute's conclusion that the mode of branching to which in *Hyphaene* the bifurcation of the stems is due, is not comparable to the lateral branching which we find elsewhere in the Seedplants. As an angular leaf however is not always present, it is not allowed to homologize it with the dichotomy of the *Lycopodiales* and the *Filicales*. For the time being we will have to regard it as a phenomenon sui generis.

Summary.

In *Aloë transvaalensis* O. Ktze there are two, perhaps even three types of pseudodichotomy. The presence of the first type is correlated with the normal development of a terminal inflorescence, that of the second one with the more or less complete abortion of the latter. In these two types both branches are axillary shoots. Where no trace of an inflorescence can be detected, one of the branches may be regarded also as the continuation of the main shoot, and that case would represent then the third type. As there is however no difference in the arrangement of the leaves

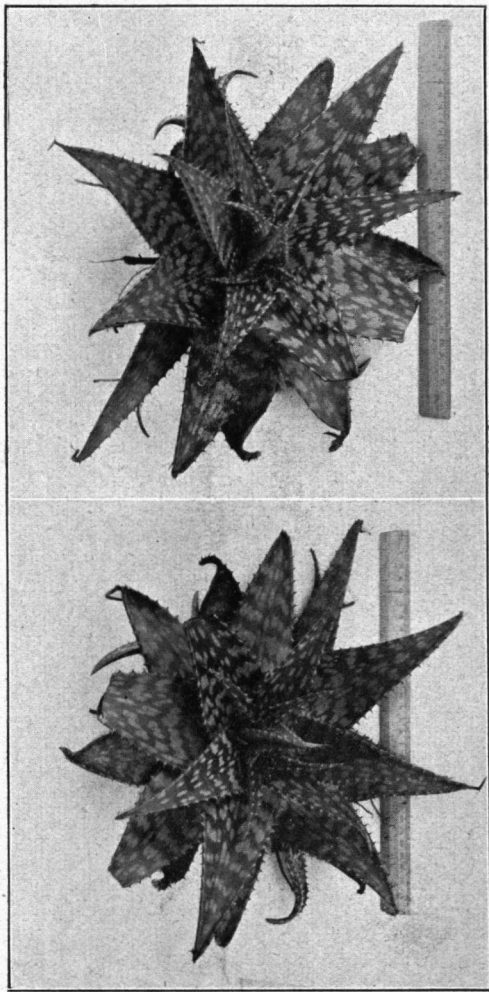


FIG. 1. Photographs of a forked rosette of *Aloë transvaalensis* O.Ktze. revealing the presence of small leaf on one side of the fork.

between the second and the third type, it is probably better to consider them as identical.

In one plant a curious anomaly has been found, consisting in a fusion of the leaf sheaths into a continuous band which winds itself spirally round the stem. This anomaly makes it probable that the angle of divergence between the leaves in these plants is not somewhere in the neighbourhood of 120° , but in the neighborhood of 240° .

A dichotomously branched stem piece of *Hyphaene coriacea* Gaertn. has been studied, and it has been found that there was in this case no angular leaf, so that from the point of view of the morphologist the dichotomy of *Hyphaene* cannot be identical with that of the Lycopodiales and Filicales, although it is, nevertheless, probably a true dichotomy.