ON THE FOLIAR ORIGIN OF THE INTERNAL STELAR STRUCTURE OF THE MARATTIACEAE ¹)

by

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§ 1. Introduction.

The peculiar structure of the adult stem in the Marattiaceae has since long drawn the attention of many investigators, and a good deal of work has been devoted to the elucidation of the morphology of the stelar structures in the stem of these ferns.

The papers of Mettenius (12), Kühn (9, 10), Shove (18), Brebner (3), Farmer and Hill (4), Gwynne Vaughan (19, 20), Charles (7), West (21) and Blomquist (2), have made us acquainted in good detail with the arrangement of the vascular parts in the stem of the most important forms of the Marattiaceae.

What perhaps strikes us most in these discriptions is the fact that the adult stems, whatever different structures they may show in the different genera, develop from the same starting point, the solid protostele, and that in their elaboration they follow exactly the same rules, so that the differences between the adult stems in the different forms are chiefly due to a more or less advanced stage in the development.

The course of development may therefore be described

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in general terms for all the Marattiaceae and this may be done as follows.

The starting point of the stelar structure in the sporeling is invariably the solid protostele, as has already been referred to; West (21, p. 377) observed that even in an adventitious bud the protostele was present.

The first leaves have generally simple leaf-traces, and these weak traces do not yet cause gaps in the protostele; only in the adventitious bud investigated by West, earlier stages in the elaboration of the stelar structure were hurried over, and the protestele became at once crescentic above the insertion of the first leaf-trace.

The following leaves have increasing leaf-traces, which soon consist of two lateral strands instead of a single median one; these strands begin to cause gaps in the stele in the same way as in other ferns, and so a normal solenostele or a dictyostele is initiated.

Up to this point the general stelar structure of the Marattiaceae is in no way remarkably different from that of other ferns; it is only when the elaboration of the internal stelar structure begins that a new element is introduced, which is comparatively rare among ferns and which fully deserves our particular interest.

There is however one point in the descriptions of the authors with which I have to deal before I come to the origin of the internal structure, viz. the direction in which the leaf-traces grow.

The authors generally describe the phenomena as if the leaf-traces arose from the stele and developed acropetally into the leaf. In their descriptions the leaf-gap is caused by the outgoing leaf-trace, which takes away a portion of the vascular tissue from the axile strand (Farmer and Hill 4, p. 376); these traces are simple at first, but afterwards as the plant produces stronger leaves they dichotomise in the cortex (Blomquist 2, p. 186) and finally they are given often off separately ab initio (Brebner 3, p. 527); in some species they even leave the stem-stele as six or more separate strands, among which the two main laterals may easily be recognised (West 21, p. 370).

In some cases this way of describing the phenomena is simply metaphorical without any presumption as to the real origin of the structures. In other cases it is clear that the authors are inclined to believe that the leaf-traces are formed acropetally in reality and the expression about the origin of the leaf-gap is considered to be an explanation.

In his paper on *Danaea* Brebner writes about this point: "In all cases the development is described from below upwards, and hence the roots will be spoken of as coming in to the stele, but at the same time it has to be clearly borne in mind that the roots arise from the endodermis (this has not yet been definitively proved) and pass outwards and downwards" (3, p. 525). From this follows at any rate that Brebner is inclined to consider the description as regards the leaf-traces as true.

In previous papers (Schoute 16, p. 317, 17 p. 156) I have tried to prove that the formation of leaf-traces is induced in a basipetal direction, and I am still inclined to adhere to this opinion, which has never been refuted as far as I know.

Direct observation of the development of procambial strands is not sufficient to check its truth, as the first induction of the strand, which is of course invisible, does not necessarily take place in the same order as the subsequently following visible processes of differentiation: the only proof of the basipetal order of the induction is given by the fact that the regularity of the distribution of the leaf-traces often diminishes from the leaf-insertions downward; if the traces were given off from the stele the distribution of these insertions should be quite as regular as or even more regular than the phyllotaxis itself.

If we read the descriptions of the stelar structures of the Marattiaceae from this point of view, there is nothing which does not harmonize with it; there is even one fact which is decidedly in favour of it.

We find namely indicated by West for *Danaea alata* that the two lateral strands of one leaf-trace are usually inserted on the stele at different levels (21, p. 370). This is quite natural if the strands come down from the leaf into the stem: their insertion to the stele may be somewhat different for the two strands, according to the form of the stele.

If the leaf-trace springs from the stele, the origin as two or more strands is already difficult to understand, and the origin at different levels is not easily reconciled to the fact that higher up the two strands are situated in a perfectly symmetrical way in the cortex.

Later on we shall however treat more facts illustrating the truth of the conception of downward growth of the leaf-traces in the Marattiaceae.

One might be inclined to ask: if the traces grow downward, how are we then to understand the formation of the leaf-gaps? To answer this question I may refer to a paper of Posthumus (13) from the Groningen botanical laboratory.

Posthumus, sharing the opinion that leaf-traces are formed in a basipetal way and bringing fresh arguments for that view (l. c. p. 145—148), comes to the conclusion (p. 277—278) that the leaf-traces in Ferns were originally mesarch. The central protoxylem-strand is however accompanied on its adaxial side by a certain amount of parenchyma. If this parenchyma strand is poorly developed, it will form a cylindrical tube in the strand, or, as the protoxylem-strand itself diminishes in strength in downward direction, a funnel of parenchyma.

This funnel is stronger developed in traces of stronger leaves, and in most cases it will reach the stele in its downward course. As this parenchyma must prevent the formation of xylem elements, it will cause a groove in the stem-xylem opposite the leaf-traces, and even a funnel in the stem-xylem. These funnels may unite, thus hollowing the xylem and forming a medulla, or if the stem-xylem was already reduced in its inner parts and a medulla was present, the funnels may form gaps above the insertions of the leaf-traces.

These suppositions have proved to be extremely useful in understanding the complex anatomy of many Fern families, and it seems very probable to me that they may be correct.

I now come to the description of the origin of the internal structure. In all genera the internal system takes its origin from the normal stele, more precisely from the upper margins of the leaf-gaps.

At first it is only a small strand, composed in some cases of phloem only (Brebner 3, p. 534), in others it is a well defined meristele, which runs from the top of a leaf-gap inward.

From our point of view this must be a trace coming from one of the later formed higher leaves, which on being continued downwards abuts on the lower strands and their accompanying parenchyma strands, and which can only pursue its way over the back of these parenchyma strands into the medulla.

In the literature on this subject these strands are described since Mettenius as compensating strands or compensating segments (Ersatzbündel, Ersatzschicht) or sometimes as commissural strands (West 21, p. 369, Blomquist 2, p. 186), or as central strands (Brebner 3, p. 529). The first term conveys the idea that the gap is closed partly at least by the aid of a strand arising from the interior system; and the direct statement that internal strands close leaf-gaps recurs even more than once in the literature (Brebner 3, p. 536; West 21, p. 370, Blomquist 2, p. 186); this idea must of course be abandoned if our view holds good.

Instead of the above terms which are used somewhat vaguely and confusedly, I shall therefore choose the designation "continued leaf-traces".

The course of these continued leaf-traces may be different in different cases. In those stems where the internal system is very weakly developed, a continued leaf-trace may end blindly in the medulla. One single case of this condition is described by Gwynne Vaughan (20, p. 261) for *Archangiopteris*; and Miss Charles describes strands (7, p. 88) of a certain length up to 0.3 mm with blind basal endings in the medulla.

These facts would strongly support our views if we were quite certain that the reverse did not take place: internal strands ending free towards the stem apex. There are some vague indications in the literature that this may be the case [1]); I will revert to this again in the second paragraph.

In most cases however the continued leaf-traces fuse with other vascular tissues, and we may distinguish two cases here.

In stems with a weak internal system the continued leaf-trace generally crosses the medulla and joins up with the normal cylinder on the opposite side above a lower leaf-gap. The strands may occur at some leaf-gaps while

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1) Brebner (3, p. 534) indicates that Farmer and Hill found these blind ends in this way; when we read the paper of Farmer and Hill (4) we find p. 387 the sentence: "It is, however, not very unusual to find some of these rudimentary commissural strands ending blindly in the central parenchyma, a fact which supports the view as to their secondary origin in such cases." That the ends are turned upwards is not directly expressed though it may be inferred from the context.

Another indication is found in the paper of Miss Charles (7, p. 88); her second way of origin of the medullary system may probably pertain to such cases, though the description is not quite clear.

others are devoid of them, in an irregular succession (Charles 7, p. 89). This irregular distribution is exactly what may be expected if the leaf-traces grow basipetally; if they grew acropetally it would be hard to explain.

When the internal system increases in strength, the continued leaf-traces do not cross the medulla, but unite, forming together a protostele just as the first leaf-traces in the sporeling did.

This protostele is soon elaborated as the continued leaf-traces themselves become stronger and stronger. The higher continued leaf-traces become double, just as the leaf-traces in the cortex did (West 21, p. 369, 386); this very remarkable phenomenon becomes quite natural now. It only means that the fusion of the two main lateral bundles of the trace is postponed and takes place in one of the interior systems. The continued leaf-traces soon begin to cause gaps in the internal stele, and so a second dictyostele is built up, resembling in every respect the normal exterior one.

In this stele the same process may be repeated; if the continued leaf-traces extend far enough downward in this second stele, they will abut on lower, earlier formed traces with their accompanying dorsal parenchyma strands, and then turn in into the newly formed medulla to begin with the elaboration of a third system.

In consequence of what has been said above I will call these internal steles simply second, third etc. stele, and the compensating or commissural strands of the authors continued leaf-traces; where needed the portions of them may be indicated as first continuation (between the normal and the second stele) second continuation, etc.

In this account of what is known about the stelar structure of the stem of the Marattiaceae I have not yet mentioned the development of the roots, which are abundantly formed in the stems, and which are formed not only on the outer stele but also on the different internal ones.

The roots are in many cases undoubtedly related to the leaves and their distribution may be rather regular. The idea that the roots might influence the shape of the cauline stelar system presents itself quite naturally; I shall however try to demonstrate that such an influence does not exist and that we need not reckon with the roots in our attempt to understand the cauline stelar structures.

Blomquist (2, p. 188) writes about the young sporophyte of *Angiopteris*: "Each leaf is definitely related to one root"; their relation is described as follows: "In the younger stages each leaf trace is joined to the central strand directly above the insertion of its corresponding root; but in the older stages the leaf trace may be displaced to the right or left of the corresponding root, as the case may be, due to the spiral condition of the central strand."

Other authors mention analogous, but varying conditions; Holle (8, col. 217) found two roots on every leaf-trace in young specimens of *Angiopteris* and Shove (18, p. 506) found in stems of full grown individuals that the roots originate, a few in the outer, the majority in the inner steles. Those roots which arise from meristeles nearer the upper than the under side of the dorsiventral stem make their way to the lower surface through almost the whole thickness of the stem.

Quite another relation between root and cauline structure is mentioned by West (21, p. 369) for *Danaea* and by Gwynne Vaughan for *Archangiopteris* (20, p. 262); in these plants the roots arise from the outer stelar system above a leaf-gap, on the spot where internally a first continuation of a leaf-trace goes inward.

In *Kaulfussia* West found (21, p. 383) that most roots are inserted indiscriminately upon any of the stem meristeles, but usually the second stele bears roots just under the insertion of the first continuation of the leaf-traces.

The relation between leaf-traces and roots therefore is a varying one; but the places from which roots usually arise are those where the descending leaf-traces may be present: the roots may originate just under the insertion of the trace on the first stele, from the first stele where a trace bends inward as continued trace, or from the second stele under the insertion of a continued trace and probably from farther points of the continuation.

It is however clear that the regular shape of the different steles of the cauline system can never be explained by any action from the much more irrugularly distributed roots; the only influence roots may have on the cauline system is that a meristele which forms a root in a very early stage may develop more tracheal elements and may get stronger. West wrote about the inner system of *Danaea* (21, p. 371). "The commissural strand then crosses over towards the upper end of the near leaf-gap above; meanwhile, the number of its vascular elements are considerably augmented by the addition of those of a root-trace."

In my own observations I shall therefore only point to the distribution of the roots as far as required by the above considerations.

After this long introduction I now come to the aim of this paper; I hope to prove that the idea of the basipetal development of leaf-traces is apt to give us a much better idea of the stelar morphology of the Marattiaceae than any other conception.

In order to bring this about I must show that the distribution of the continued leaf-traces is so as might be followed from this conception. In the literature we have some indications that this will be the case, but no sufficient proof.

West gives a figure (21, p. 367) of an internal stelar system of an old specimen of *Danaea*, which shows a great resemblance to the external system of a younger plant. He writes: "An interesting parallel may also be drawn between the leaf-traces and the compensating strands, which respectively pass through an ontogenetic series of stages with a simple single strand, passing through an intermediate condition where the strand forks near its base, and ending with two independent strands which originate, not from the base, but from the lateral margins of their respective gaps." (21, p. 372).

What we have to prove however, is that continued leaf-traces are really found in the places required by our point of view and that the distribution of the gaps in the second stele is such as follows from the phyllotaxis. From the literature this is not to be gathered and that is the reason that I set myself to find this out.

§ 2. Investigation.

The material at my disposal consisted of one single living plant of a *Marattia* sp. from the Groningen botanical Garden. It was cultivated under Nr 11101 as *Marattia pruinosa*, a species not mentioned in Christensen Index filicum [1]).

The stem showed a number of leafbases and four living expanded leaves; it was first roughly sketched from four sides to determine the phyllotaxis.

This proved to be a regular Fibonacci one with left-handed genetic spiral; the four living leaves, counted from the lowest visible scar, were the numbers 23—26. After determining this, I removed the leaf bases from the stem, and partly sectioned the remaining part, which was of the form and shape of a duck-egg. The sections were cut without any imbedding, in a fresh state; the object was

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[1]) The lack of venulae recurrentes and of acuminate apices of leaflets, further the surface which was nowhere pruinose, and the presence of paleae on the rhachis made sure that it was not *Angiopteris pruinosa* Kze; the general habit induces me to believe that it was probably a form of *Marattia fraxinea* Sm. As yet the species has not formed fructifications in our garden.

fixed in a specially manufactured clasp of a Shanze microtome, and with the ordinary microtome razor 42 sections of 250 μ were obtained.

Section 1 contained only leaves, as it was cut over the apex of the stem, in sections 2—6 the leafbases became more and more contiguous, those of the peripherical leaves first, the central ones last; the stem apex was evidently slightly hollowed as in many monocotyledons. Sections 7—42 showed the stem itself. After these 42 sections 13 others of 350 μ were cut; the bigger parts of the stem requiring somewhat thicker sections. As the stem had then been cut halfway farther sectioning got more and difficult.

The sections, some of which were not quite whole, were drawn at low magnification ($\times 2^1/_2$) with a camera lucida and with the aid of a glass from spectacles; camera, magnifying glass and section all being fixed to one and the same stand.

From these drawings I give part in reproduction in the figures 1 and 2; Fig. 1 contains sections 54—50. In every drawing the black areas represent the xylem parts of the meristeles; the phloem surrounding these xylem parts is left white. The numerous roots are represented by three concentric lines; the outermost and the inner one include the cortex, the middle one divides the cortex in an outer and inner part. This rather arbitrary way of indicating the roots was only chosen to avoid confusion between roots and meristeles in the drawings.

At the low magnification used in drawing it was not always possible to distinguish between the xylem of the meristeles and the steles of the roots. Where roots spring from the meristeles their stele is therefore also given in black as long as the rootstele was continuous with the meristele.

In section 54 we see no less than six of such insertions of roots, three on the outer ring of meristeles and three on the inner ring.

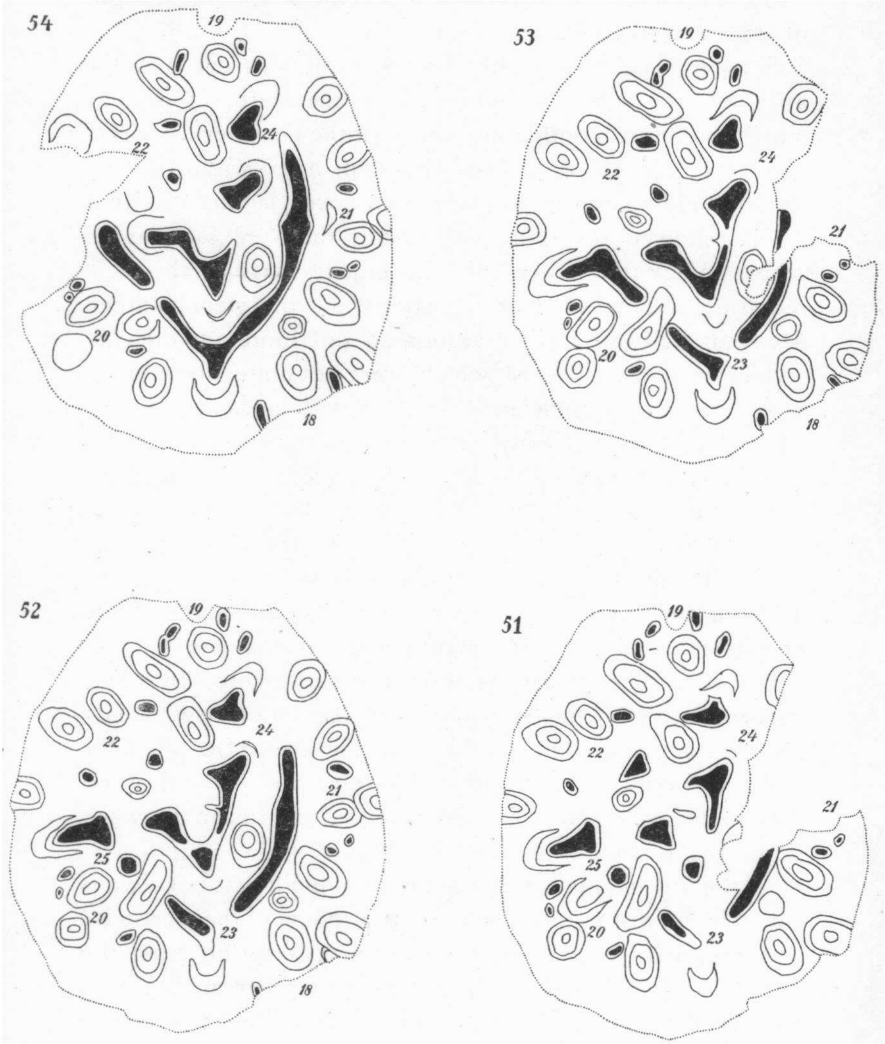

Fig. 1. Marattia sp. Four consecutive sections of stem, $^5/_4$ nat. size.

At first sight the distribution of the meristeles seems to be rather irregular; closer examination however, soon reveals a great degree of regularity.

In section 54 the lowest leaf-trace is that of leaf 18, of which two strands are to be seen right side under, on the edge of the section. That these two strands really belonged to the trace of leaf 18 could easily be inferred from the comparison of the section with the unsectioned part of the stem, where the scar of leaf 18 was only partly cut away. In the same way the traces of 19 and 20 were determined; we see that both consist of three strands, viz. one to the right and two to the left.

The two strands of 18 were only one half of the trace; both the right and the left trace were double in the plant, and only the inner strands were contained in the section.

From this regular succession of traces 18—20 we may continue in the same spiral; we soon recognise 21, with three strands, like 19 and 20, and trace 22, which is only partly present in section 54, but in a whole state in 53. Here both left and right strand are single: as trace 22 is cut nearer to its insertion than trace 18 which is placed lower, we conceive that the traces are all rather equal and that the two right strands first unite to a single one, then the two left strands, and that the leaf-trace is simplified in its downward course in this way to two equal lateral strands. This idea is confirmed by following the same traces in the higher sections; 19 has four strands in section 51, 20 in section 46.

The leaf-traces thus being quite regular, the same has still to be shown for the dictyosteles. In the first stele we have in section 54 one very great meristele, occupying nearly half of the ring and two smaller ones on both sides. For the rest of the ring it is not quite clear at first sight which strands belong to the outer dictyostele and which do not. If we look for this part at section 53,

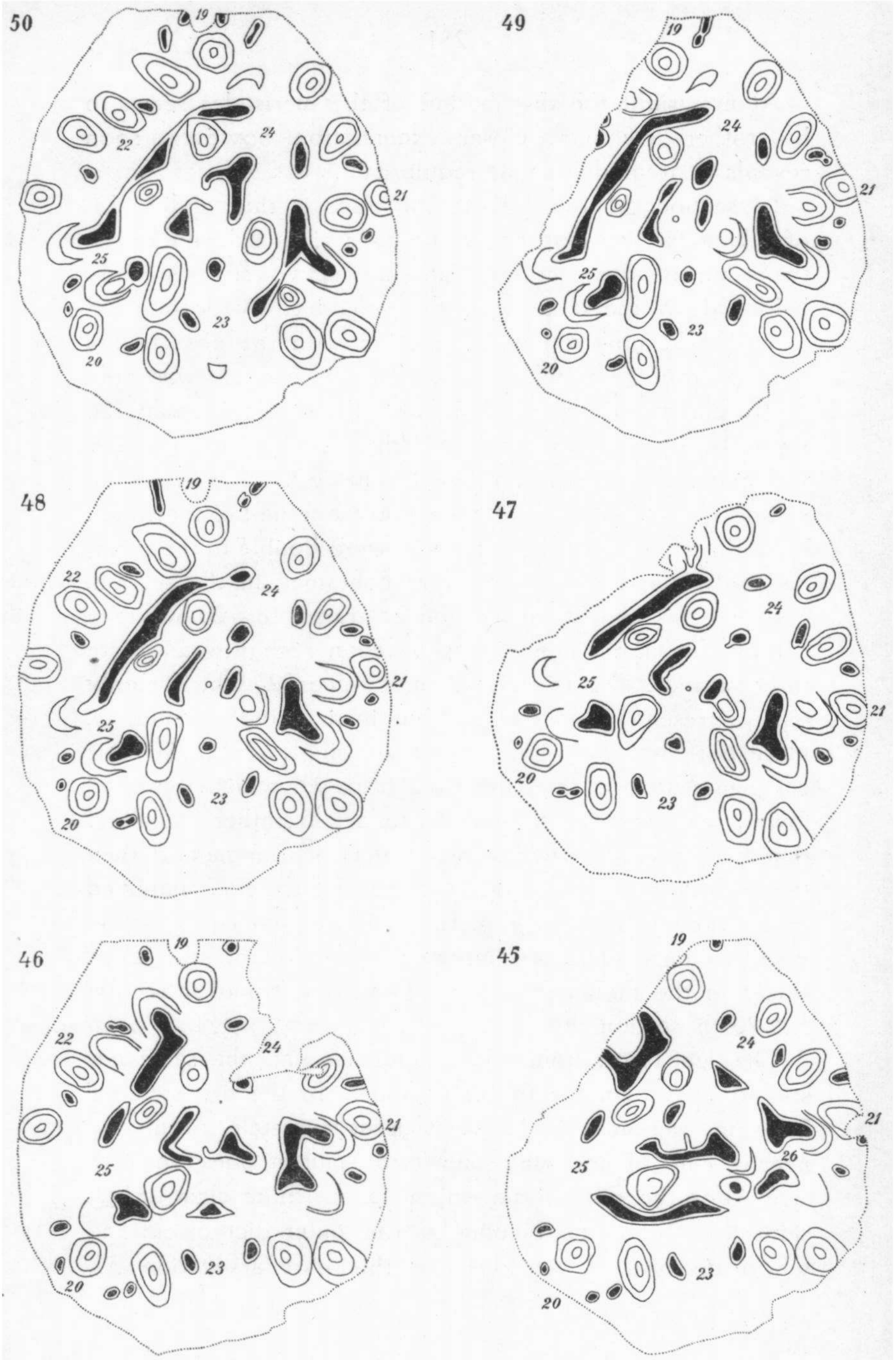

Fig. 2. Marattia sp. Six consecutive sections of stem, $^{5}/_{4}$ nat. size.

which is whole there, we see that the two strands of leaf-trace 22 have approached to the ring and that a third strand is situated between them, but much more towards the internal system.

We shall see that this last one is the continued trace of a higher leaf, which is making its way from the first to the second stele.

To make this clear we must go somewhat higher in the stem, to section 50 in fig. 2. Here the external ring is closed in the neighbourhood of leaf-trace 22, but the xylem is already divided into three parts, one situated just between the two strands of trace 22; in 49 and 48 the xylem is uninterrupted there. In 50 the three xylem strands are still united by phloem-parts, in 51 these have disappeared. So the middle part is separated; this strand moves to the internal system, and in 54 it has done about half the way.

First, however, I am going to describe the outer stele. In section 50 we see clearly how in the first dictyostele two gaps are formed just at the places inward of the two strands of trace 22. These traces will unite to the first stele in the so formed gaps. To observe this union we should have had lower sections than section 54; we may however just as well look for this on the strands of the higher leaves which are cut in our sections much nearer to, or even at their insertions.

Leaf-trace 23 which consists of two lateral strands in sections 49—38 and of four strands in 36 is shown in section 50 just when its right strand unites to the stele, the left still being free. The continued leaf-trace which has shifted to the internal system is quite clear and still free from the second dictyostele. Leaf-trace 24 is also on the right side attached to the first system; the continued trace inside of it has already united to the second system.

Leaf-trace 25 is still more advanced in section 50; its left trace is united to the external system, and the gap between its two strands is going to be closed; if we follow this gap downwards we see it closing in section 53.

As the continued trace inwards of trace 25 in section 50 is no more discernible, we should go upwards to section 44 to see it in free state.

As the examination of such series of drawings requires a good deal of mental energy, most authors on this topic have constructed models in wax, a most useful though laborious means of elucidating the complex structures. These models however have one disadvantage: they are not easily reproduced in a paper. Most photos of these models ar far from clear to the reader, and especially the distribution of the leaf-gaps in two successive steles is difficult to discern.

I have therefore tried another, easier way of representing the stelar structures, which gives a better survey, though in many respects it is not equal to modelling in wax: I have figured both dictyosteles as cut open after a longitudinal line and unrolled.

Fig. 3 represents the outer dictyostele; as the dictyostele itself was conical, the figure is fan-shaped.

From a given centrum 46 concentric arcs of circles were drawn, every one intended to represent the dictyostele from one of the sections 10 — 55 [1]). On every arc I noted where the gaps were and where the meristeles; these

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[1]) As the dictyostele in section 10 was 2 cm in circumference, and in 55 7,2 cm. the inmost circle was drawn so much nearer to the centrum than the outer one that their circumferences got the required relation; the 44 circles between them were distributed according to the thickness of the sections, the conditions being chosen in that way that the distance of the circles in the drawing was ten times the thickness of the sections. As the dictyostele tapered rather regularly upwards, the lengths of the intermediate circles were rather good to scale. From this set of circles I took such a sector that the arcs represented the dictyostele of the section at the same 10-fold magnification as the distance of the circles was enlarged. In this way the form of the gaps in the drawing became pretty true to scale. Fig. 3 gives the original drawing in 1/3 diminuation.

points being united the figure was nearly completed. I had only to fill in some places where the sections where hurt, more over I marked the centres of the insertion of the roots on the dictyostele with a cross.

In the gaps numbers were placed corresponding to the number of the leaf the trace of which was inserted in the gap.

In the sections it was rather arbitrary whether an incoming trace or a departing continued trace should be counted with the dictyostele or not. The places where a trace was taken up into the dictyostele or where it was considered to leave the stele were rendered by an elliptical figure, as if the strand had been cut off there.

The most conspicuous feature in the figure is that every leaf-gap has two wings. The two lateral strands of the leaf-trace have apparently each a dorsal parenchyma strand which prevents the formation of vascular tissue.

The gaps are otherwise of remarkably varying shapes; the insertion of the right strand is often on a somewhat higher level than that of the left one (e.g. in 23, 24, 25, 27), in 26 the reverse is the case. In 28 the left strand is hardly simple at the insertion; its two components are still discernible.

All this is quite in accordance with the facts found by previous authors, and more over with the view that the leaf-traces are developed basipetally.

The phyllotaxis af the gaps is quite regular, as regular as that of the leaves. The most conspicuous parastichies are the binary, the ternary and the quinary ones; every gap has therefore six adjacent other gaps.

The continued leaf-traces all leave the dictyostele just between the two incoming lateral strands. If we ask from which leaves the continued traces come, we have not much choice; it can hardly be any other than that of leaf n + 5. So in gap 27 the inward running strand must be that of leaf 32, the two lateral strands of it having united in their downward course. The only other possible explanation would be that it is the right strand of n + 5, combined with the left strand of n + 8. The union of two traces of different leaves, which are formed at different times is not very probable, and as we think of the above mentioned cases described by West of double continued traces, or continued traces which unite during their free course, it becomes still more improbable, as in those cases the two strands were quite equal.

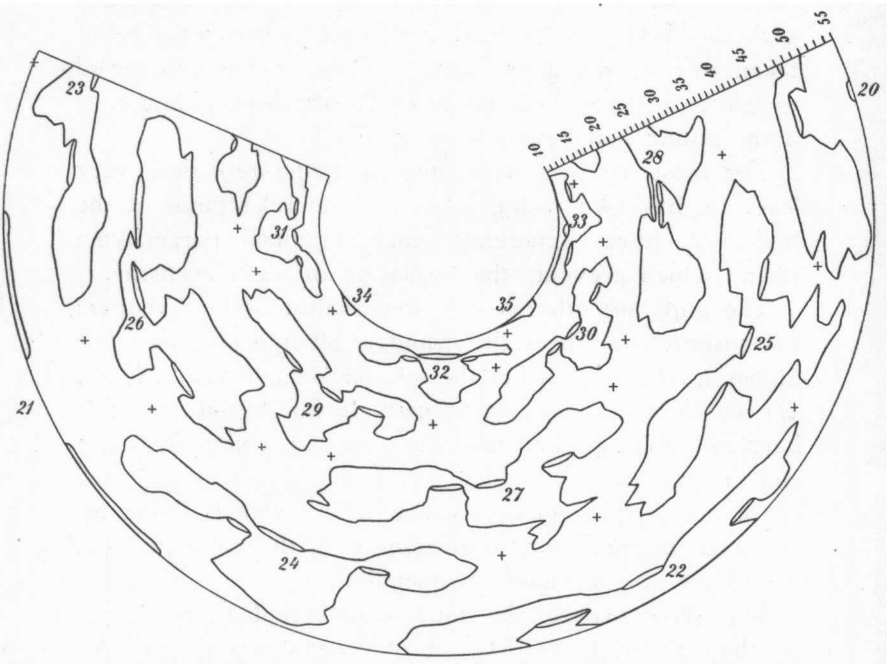

Fig. 3. Marattia sp. Outer dictyostele of stem as cut open and unrolled. Crosses represent centres of root-insections. Numbers in the leaf-gaps are those of the leaf to which the incoming leaf-trace belongs; numbers at right edge of figure are numbers of sections.

If we take it for granted that the inward running strand is the trace of leaf n + 5, we see that the place where this strand runs inward e. g. in gap 27 is not quite below the place where the leaf-trace 32 came in, but that it has shifted to the right. The same relation is to be seen in all other traces; the explanation may be the following. At the time that the trace of leaf 32 was formed, those of 29 and 30 already existed. The trace of 32 in growing downward has been forced to go between the two parenchyma strands of 29 and 30, which afterwards are represented by the gaps 29 and 30. Thus it is already partly shifted to the right, in consequence of the phyllotaxis. For 29 is nearer to 32 than 30, as the secondary divergence of a ternary parastichy $\triangle_3$ is smaller than $\triangle_2$.

Furtheron it abuts on the previously formed leaf-trace of 27 and its gap; as we have two cushionlike parenchyma strands on the backs of the two lateral traces there, it can only follow the gutterlike depression between them, and run inward.

In our drawing the position of the roots has been indicated by crosses as we have mentioned. Their irregular distribution is conspicuous; most leaf-traces have two of them, one in relation to the left and one to the right strand. But 28 has only one, to the left; and the height of insertion is irregular. In all the leaf-traces the right root is inserted higher than the left root; the difference is sometimes hardly to be measured (trace 27) in other cases extraordinary great (trace 32).

In the same way a figure has been drawn for the second dictyostele which is given here as figure 4. We see a set of gaps in the same way as in the outer dictyostele, but now they are all simple, and devoid of wings. In these gaps numbers have been placed in accordance to the views expressed above. If we consider the continued trace 32, which left the first dictyostele in leafgap 27, we get it back in the second as causing a new, simple gap which now bears the number 32.

The distribution of the gaps in this second stele is after quite the same phyllotaxis; two right-handed and three left-handed parastichies are easily recognized. Yet there is a difference in the mutual position of the gaps: owing to the much smaller size of the second stele the quinary parastichies are no longer "contact" parastichies, to use this term in a modified sense, but the adjacent gaps of gap n are n—1, n+1, n—2, n+2, n—3 and n+3.

The figure, however, shows with absolute clearness that for the rest the distribution of the gaps in the second stele is the same as that in the first, and that every gap in the first is represented by a corresponding one in the second. To show this was the principal aim of my investigation, as explained.

In the second stele there were also roots springing from the meristeles; our figure shows that their distribution is quite analogous to that in the first. Every root springs from the stele somewhat under the place where a conti-

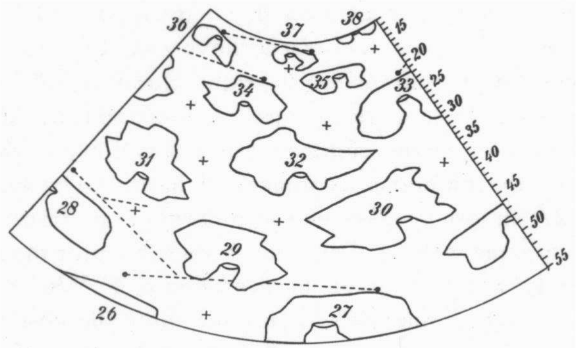

Fig. 4. Marattia sp. Second dictyostele of stem as cut open and unrolled. Black points represent the spots where the strands of the third system communicate with the second dictyostele; dotted lines represent strands of third system running through the medulla. Numbers in the leaf-gaps are those of the incoming continued leaf-traces.

nued leaf-trace has united to it, and reversely every continued leaf-trace, in its downward course in the second stele, bears a root. The one of trace 30 was inserted very low, so that its centre lay under the last section. It is therefore not indicated in figure 4, yet it was present, and to be seen in figure 1, in sections 54 and 53 at the left side of the internal stele.

The difference of height in insertion is here still more striking than in the first stele; the root of trace 37 is inserted very high, that of trace 34 very low, between the gaps 31 and 32.

If we compare these ways of insertion with those found in the literature (see p. 276) we have here most relations described by the authors: one root to a leaf-trace, just under its insertion (gap 37 in the second stele), one root lower down (gap 34 ibidem), one root, not under the middle of a leaf-trace, but lateral (leaf-trace 28 in the first stele), two lateral roots to a leaf-trace (the other leaf-traces in the first stele). All these cases may be comprised in one description: the roots arise on the continuation of the leaf-traces in the different steles.

We therefore get a strong impression that the leaf-traces are not only where we see them as leaf-traces or as continued leaf-traces, but also in the dictyosteles where they are united to large parts of adjacent vascular tissues.

In our sections there were also some strands of a beginning third system. As this third system deserves our full attention, I have tried to determine the course of its meristeles as accurately as the thick sections permitted; in the higher parts the tiny strands were only discernible after boiling the sections, so that the starch grains were dissolved.

The sections contained five internal meristeles, all of which are represented in fig. 4 with dotted lines.

As these strands did not yet form a stele, a figure of the third system could not be drawn in the same way as those of the outer two; I have therefore only noted as black points the places where these strands left the second stele and where they were attached.

Four of the five strands clearly arose from the upper margin of a gap viz. of the gaps denoted as 37, 34, 28 and 27; with the fifth I will deal presently. Only the one of gap 28 originated in the middle of the gap, the three others sprang from the right part of their gap.

If we try to make out where these strands come from, our opinion being that they are continued leaf-traces, we must come to the conclusion that they come from leaf n+3. For leaf n+5 is here more remote, and its strand, in passing between n+2 and n+1, would rather abut on the left side of the gap, and surely not on the right half.

Besides, as in the first dictyostele it was probably trace n+5 which run to the second dictyostele at gap n, in the second dictyostele, where the mutual position of the gaps is another, it is strand n+3 which is in the analogous position.

There is still another argument, in favour of this view.

In our plant, the expanded leaves bore the numbers 23—26. Between them the leaves 27—31 could easily be distinguished in the object, and in the highest sections e. g. in section 6, the traces of leaves 32—40 were also clearly seen. The traces of still higher leaves might have been there, but I could not see them with any certainty. As the highest strand of the third system came from leaf-gap 37 in the second stele, this strand must be, according to our supposition, the second continuation of leaf-trace 40. As this one was the last one clearly developed in the cortex of the stem, it is not unnatural that its second continuation was found. If it was the continuation of the trace of a higher leaf it would be more strange, that the leaf-trace itself would be less clear than its continuation.

Of the four strands mentioned, three crossed the medulla straightway and attached themselves to the upper margin of the next leaf-gap: only the strand from gap 28, which may therefore be the second continuation of leaf-trace 31, attached to the second continuation of leaf-trace 30.

In our fig. 4 the course of the strands of the third system could not be represented in the right way; I have, however, represented them for clearness' sake, by dotted lines along the conical dictyostele [1]).

This condition, that the inner strands may unite to a lower leaf-gap margin or may fuse together, is in accordance with what has been found by Miss Charles and other investigators, as reported above.

One of the strands, which run from leafgap 34 to 33, was only well developed in its lower half, the upper half being much thinner and devoid of xylem; the strand was apparently very poorly developed there and only its lower half had been strengthened by the contact with the second system.

I have still to mention the fifth strand of the third system. This one was only present in the sections as the lower half of a strand which had come from gap 28, as indicated in our figure 4.

As section 44 which would have contained the upper half was seriously damaged there, the upper half might have been present in the plant, but lost in the sections. The analogy with the strand from leaf-gap 34 however suggests the possibility that the strand, having been duly induced, would have wholly aborted in its upper half.

For a theory that the bundles are formed basipetally these two strands with a well developed basal part and a

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[1]) A better representation would be obtained if the drawing was cut out and the right and left side united, so that the figure actually assumed the form of a cone; the strands of the third system could then be represented by threads, spanned across the inner space.

badly developed or perhaps a wanting apical part, may seem to form a serious difficulty. We should expect only blind downward endings from the theory; now we found in the literature that there are indications of blind upwards endings.

According to my opinion, however, we must not attach too much importance to the fact whether a certain strand is well developed, poorly developed or aborted. In leaves of Dicotyledons we may sometimes observe that some of the smallest veinlets have considerable parts without either phloem or xylem. Yet these parts unite the parts where the xylem is represented only by a single vascular tracheid: meristeles are apparently capable of extreme reduction. Now it is very probable that the stimulus causing the formation of a vascular strand may be transmitted farther than the actual differentiation afterwards goes. Blind ends of vascular strands may arise, when an induced strand is partly differentiated and partly not, and it need not always be the first induced part that differentiates.

Even if it were proved afterwards that the internal strands of the Marattiaceae may end blindly both downwards and upwards, which has not been done as yet, then I should only be inclined to infer that the direction of the propagation of the stimulus which induced the strands is not to be made out from this.

This direction is made out in another way: the regularity of the third system being much less than that of the leaves, we can only conclude that the regularity of the third system is a weakened consequence of the regularity of the phyllotaxis.

Here we see that three internal strands unite to the second stele, two to other internal strands; for basipetal strands this is quite natural, in acropetal it would be incomprehensible.

There is still one point that must be discussed here: why the internal strands should have a strong tendency to unite to the dictyostele at the top of a lower leaf-gap. This was not only the case here, but also in other plants, described in the literature.

I shall not pretend that I can give a full explanation of this fact. Yet we may take the following into account. As every meristele of the Marattiaceae seems to have a dorsal strand of parenchyma, preventing the formation of vascular tissue, we may expect that the whole inner side of a dictyostele is probably very unappropriated for the attachment of a lower end of a meristele. Meristeles generally unite with their sides; in the dictyosteles of Marattia the only sides of the meristeles are the margins of the leaf-gaps. Through these gaps the parenchyma strands of the leaf-traces pass; we may therefore conceive that the only part, fit for the union with an internal meristele may be the top margin of a leaf-gap. It might be of some interest in this respect to look for a Marattiacea, where the last dictyostele would have accessory gaps other than leaf-gaps, and then to determine how the internal strands would behave.

§ 3. The relation between leaf-traces and the stele.

In § 2 I hope I have given evidence for the thesis that the leaf-traces are decurrent not only in the normal outer dictyostele but also in the "compensating strands" and in the inner dictyosteles.

The question may now rise whether the whole of the stelar structure of the stem is composed of leaf-traces, or if a distinction must be made between two different elements in the constitution of the stelar structures. The distinction between common strands and cauline strands is familiar to all botanists since the time of de Bary; the common strands are those which belong to leaf and stem, the cauline are restricted in their course to the stem; and we could try to apply this distinction here in this way that the common strands would be the continued leaf-traces and the stripes of the dictyosteles where these leaf-traces seem to pass and where roots may arise, whereas the cauline strands would be the remainder of the dictyosteles.

Posthumus (13, p. 277) generally distinguishes between stem-xylem and leaftrace-xylem in Ferns; the stem-xylem is e. g. clearly to be seen in the fossil Osmundaceae with a solid central xylem.

This stem-xylem is perforated by the leaf-traces and their accompanying parenchyma strands; besides the central part of the xylem may be reduced itself. In this way the different stelar structures of the Ferns arise.

In a recent paper (14, p. 102) he puts his views in the following way. From a descriptive point of view the distinction between leaftrace-xylem and stem-xylem is fully justified: the course of differentiation is different in both, the place of the protoxylem is not the same.

Whether the stem-xylem is derived from the leaftrace-xylem, is not to be made out; either case is as likely as the other.

The first of these two sentences of Posthumus is quite clear; if there are differences between two parts of the xylem, these parts deserve a separate description.

The second sentence will, as we hope, sooner or later loose its validity; perhaps criteria may be found. For as we have several instances of Ferns with a solid central xylem, we may ask whether a corresponding xylem was already existent in the ancestors before there where leaf-traces, in the way of what *Rhynia* shows, or whether such a stem-xylem has never existed in the ancestors or has in any case disappeared in the offspring.

To prove either of these views will not be easy; that it is hopeless is doubtful. To my opinion in the Marattiaceae there is a rather strong indication that the stelar structure is only built up from leaf-traces and that there are no remnants of old cauline strands whatever.

To make this clear we have to remember the following. The idea of a stem-xylem, as advocated by Posthumus, starts from a solid xylem strand to which foliar traces are united. By the development of leafgaps and by the disappearance of the central part of the stem-xylem the dictyostele is formed. The whole form of a normal solenostele or dictyostele may be satisfactorily explained in this way; the parts uniting the foliar traces are the remnants of the stem-xylem. If however, a second stele is formed in Marattiaceae, it has exactly the same form and hence we must suppose that in the second stele the foliar traces are also united by stem-xylem; the original stem-xylem therefore will not be medullated in the usual way, but only a central part and a cylindrical part between the two steles will have disappeared. And this phenomenon must become more and more complicated when the continued leaf-traces form more steles. This is apparently a very complicated hypothesis and it is much simpler to suppose that the leaf-traces have the tendency to enlarge, where they may come into connection with other leaf-traces: this is repeated in the same way in every stele and so the uniting vascular parts are formed.

Wholly different views on the relation of foliar traces and cauline strands and on the stelar morphology of the Marattiaceae in general have been developed by Campbell.

Campbell has repeatedly investigated sporelings of Eusporangiate ferns (5, 6); afterwards similar research has been carried out in his laboratory by Baas Becking (1). The outcome of these studies was that the stele of the sporeling is built up from leaf-traces only, and that there is no cauline part whatever in the stele of young plants.

So up to this point our results are quite in accordance with theirs. The internal system of the Marattiaceae is, however, described by them as strictly cauline; reasons for this assumption are not given. It is unnecessary to say that I can not support this opinion.

Neither can I share the view that the stelar theory is not to be reconciled with the facts as revealed by a study of the Eusporangiatae (6, p. 304).

This opinion is based on the false notion that the stele of the stem should contain or even should consist of purely cauline strands in the sense of de Bary. In Angiospermae we may say that the vascular tissue of the stem always consist of leaf-traces only, the existance of cauline strands, of which de Bary cited several instances, being wholly fictitious. Yet the assumption of a stele is a very useful one; out of the leaf-traces and the surrounding parenchyma tissues the stele is built up as an entity of higher order.

Campbell writes on the Marattiaceae (5 p. 213): "Without exception, for a considerable time at least, the vascular system of the sporophyte is composed exclusively of tissue belonging to the leaves and roots, the stem apex playing no part in the building up of the vascular skeleton."

The last part of the sentence is only true so far that there are no cauline strands to be seen between the highest leaf-traces and the apex; this has been proved quite clearly by Campbell himself. But that the stem apex does not play a part cannot be granted as the apex forms the meristematic tissue in which the new leaves with their leaf-traces originate.

Baas Becking reminds in this connection (1, p. 335) of the phyllopodium theory of Delpino and remarks that the embryological evidence is mainly in favour of the phytonic view (1, p. 334); his idea is evidently that the stele of the stem is unimportant or does not exist as the stem itself does not constitute an independent part of the plant body.

I am still inclined to believe that the phyton conception is not among the successful ideas in plant morphology;

if it held true the leaves should multiply by a kind of propagation, which should be regulated in such a way that the laws of phyllotaxis would be kept; how this would be brought about is not easy to explain, and the anatomical evidence which reveals us the presence of an apical meristem, in the young sporophytes of Marattiaceae even with an apical cell, is decidedly not favourable to such conceptions.

It is only in the youngest sporophytes where the first leaf assumes a terminal position, as in many Monocotyledons, that the origin of a leaf from another leaf is simulated.

Campbell summarizes his views on the stelar structure of the Eusporangiatae as follows (6, p. 314): "The "dictyostele" of Ophioglossum and most Marattiales is in no sense a monostele. The „foliar gaps" are not breaks in a single tubular stele, but are merely spaces between the coalescent leaf-traces, and the pith is part of the ground tissue included within the cylindrical network formed by the united bundles derived from the leaves."

This description is wholly erroneous; if it were right the stem of the Eusporangiatae would be built up like the stem of the seed plants (confer Posthumus, 13) but from the works of Mettenius and the other authors cited in the introduction, it is quite clear that, as also follows from my own investigation, the leaf-gaps in the outer dictyostele of the Marattiaceae are true leaf-gaps as in all other Ferns, i. e. breaks in the tubular stele caused by the insertion of leaf-traces; the new element in the present paper being that the analogous gaps in the inner systems too are true leaf-gaps.

§ 4. Comparison of the internal stelar structure of the Marattiaceae with that of other ferns.

Among the ferns with internal structure there is one group which is so much akin to the Marattiaceae that they are placed by nearly all investigators in the same order

Marattiales, viz. the *Psaronii* sp. [1]. It is therefore of interest to compare the internal structure of *Psaronius* with that of the Marattiaceae and to see if our views hold good for *Psaronius* too.

The most detailed description of the *Psaronius* stelar structure is given by Rudolph (15), and this description is even much more suitable for our purpose than any of the recent Marattiaceae, as the relation between the different steles and the connecting vascular strands is made perfectly clear. Rudolph writes (15, p. 178): "Die Blattspurstränge würden also, nach diesem Verhalten zu schliessen, als einfache Stränge aus dem Innern des Stammes kommen und in radial schiefem und tangential geradem Verlauf nach aufwärts ziehen, hiebei würden sie mit jedem der in radialen Reihen und konzentrischen Kreisen stehenden Bundel, die sie auf ihrem Wege treffen und die offenbar der Achse parallel laufen, seitlich verschmelzen, würden eine Zeitlang in den von diesen gebildeten Zylindern verlaufen und an der Bildung derselben teilnehmen, weiter oben sich wieder loslösen, in den nächsten Zylinder eintreten u.s.f. und schliesslich nach der Anastomose mit den peripheren Stelen, durch die Arme derselben erweitert, als fertige Blattbündel austreten."

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[1] A strong indication for the near relation between *Psaronius* and Marattiaceae is given by the multicellular root hairs, a unique feature among Ferns. Solms-Laubach who first explained the peculiar origin of the root-traversed pseudo-cortex as formed by a strong development of multicellular hairs from the stem surface and from the roots, wrote (11, p. 755): „ebenso ist die Erzeugung von mehrzelligen Füllgewebshaaren, an den wurzelbürtigen Systemen wenigstens, eine Besonderheit der Psaronien, da man hier doch einfache Wurzelhaare erwarten würde. Unter den lebenden Farnen ist bis jetzt nichts ähnliches bekannt, an einem von mir eingesehenen Cyatheaceenstamm waren nur einfache Wurzelhaare zu finden."

Campbell describes however multicellular root-hairs of *Danaea* (5, p. 179) and *Kaulfussia* (ibid. p. 187); this peculiar correspondence has not yet been pointed at as far as I know.

From this description it follows with absolute clearness that the gaps in the second stele were caused by the continued leaf-traces which run down from the top of the gaps in the first stele, etc.

In other fern families there are, however, also scattered species with internal structure; if we put together what is written about by Mettenius (12), Gwynne Vaughan (19, p. 698) and Posthumus (13, p. 202) we find that the phenomenon is discernable in at least four other families, viz. in the *Cyatheaceae* (in each of the three subfamilies: *Dicksoniae*, Gwynne Vaughan p. 701, *Thyrsopterideae*, and *Cyatheae*, Posthumus p. 258); *Polypodiaceae* (in five of the nine subfamilies, *Aspidieae: Dipteris coniugata*, Posthumus p. 217, *Davallieae: Saccoloma* and *Dennsteadtia*, Posthumus p. 219 and 224, *Asplenieae*: *Polybotrya*, Posthumus p. 232, *Pterideae*: *Pteris*, Posthumus p. 240, *Acrosticheae: Chrysodium*, Posthumus p. 247); *Parkeriaceae* (*Ceratopteris*, Mettenius p. 531), *Matoniaceae*, *(Matonia*, Gwynne Vaughan p. 703).

It is not within the scope of the present paper to investigate the origin of the stelar structure of these many ferns. If however we read the above cited authors, we get a strong impression that in all these cases the internal systems are nothing else but continued leaf-traces.

Gwynne Vaughan came to the conclusion (19, p. 704) that in all ferns the internal system is an accessory development, to be derived from the ordinary stelar cylinder by the progressive elaboration of a local thickening of the xylem-ring at the leaf-gap margin. As in our view the internal system begins with the abutting of higher leaf-traces on the lower leaf-gaps and the continuation of these traces inward, the description of Gwynne Vaughan fits well in our conception.

Posthumus distinguishes between three different ways of origin of the internal stelar structure (13 p. 202). The first is the one described by Gwynne Vaughan; the second way is that two lateral parts of the leaf-trace free themselves from the main body, and instead of uniting with the normal stele, they run in through the leaf-gap into the pith. The third way is essentially the same as the second, with this difference that the inward running strands were already free in the petiole.

It is clear that these varieties may be explained in the same way as the first mode. The leaf-trace itself is composed of a great number of minor strands decurrent from the different parts of the leaf. In many forms all these strands have united in the petiole and the resulting strand enters into the stele as a unity. In other ferns the composing strands have not yet united, and in the Cyatheae a number of them form an internal system in the stelar structure of the petiole.

The leaf-gap margin has not sufficient room for the insertion of all the strands, and part of them is forced by the parenchyma strands of other strands to bend inward and to run into the medulla.

We may therefore presume that a detailed investigation will prove that in other ferns with internal stelar structures the origin of these structures will be the same as in the Marattiaceae. The peculiar distribution of the phenomenon in so many remote groups is quite natural according to this theory, as the leaf-traces may be more or less decurrent even in closely related plants.

§ 5. Summary and conclusions.

1. The conception that the stimulus determining the course of a leaf-trace is transmitted in the stem in a basipetal direction, might explain the peculiar complicated stelar structure of the Marattiacean stem. The facts recorded in the literature all point to that direction; one of the most important deficits in our knowledge was that it had not yet been made out whether the gaps in the inner

steles are to be found at those places where they must occur according to that view.

In the present paper the proof is given that in one single stem of a *Marattia* sp. (*fraxinea?*) the distribution of the gaps in the second dictyostele and the distribution of the strands of the third system were as they should be from that point of view. The basipetal development of leaf-traces is thus confirmed.

2. Leaf-traces consisting of two separate lateral strands cause a two-topped gap at their insertion in the stele; after the fusion of the two strands the same leaf-trace causes a simple gap: the form of the gap gives an image of the parenchyma strand which lies at the dorsal side of the leaf-trace strand.

3. The gradual elaboration of the stelar structure in the individual stems of the Marattiaceae is the natural outcome of the development of stronger leaves with more robust leaf-traces. The stelar type of the Marattiaceae is therefore essentially the same as that in other ferns; not only in the young individuals with one single stele, but in the adult ones too it is only a variation of the normal monostely.

4. The close relation between *Psaronius* and the Marattiaceae as shown by Rudolph is corroborated by the present investigation, as the correspondence in structure of the different steles, which Rudolph established in *Psaronius* is here demonstrated to exist in Marattia too.

5. The origin of the internal structures in other fern families is probably the same as in the Marattiaceae; what is found in literature on that topic points decidedly to that direction. In some of these ferns the leaf-trace is only partly inserted in the normal stele, while part of it runs directly into the medulla. This must be explained in this way that the leaf-trace, owing to its complication, is not able to form a single strand or one single tangential row

of strands, which may enter into the stele as a simple part of it, but that it forms at least two rows of strands; the outer may unite to the stele, the inner will run inward on the dorsal parenchyma of the outer row. Further investigation from this point of view of these ferns is desirable to check the correctness of this opinion.

6. Campbell came to the conclusion that the stelar theory cannot be reconciled with the facts as revealed by a study of the Eusporangiatae. This conclusion is based upon the misunderstanding that a stem stele should be independent of the leaf-traces, and that the leaf-traces should be subsidiary structures of it. If the idea of the stele is taken in this way there would not be a single plant with a stele among the seed plants, and among the Pteridophytes they would be rare. On the contrary, the stele is generally composed wholly of the lower ends of the leaf-traces; the stele is mostly only a higher unit formed by them.

7. The distinction between stem-xylem and leaftrace-xylem as made by Posthumus is to be accepted as a way of describing stelar structures. Whether it has a phylogenetic sense is not yet certain; the conditions in the Marattiaceae do not point to that direction.

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Groningen, July 1926.

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