FASCIATION AND DICHOTOMY [1])

by

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CHAPTER I.

Fasciation.

§ 1. **Introduction.**

The curious phenomenon of malformed band-shaped stems, oc-curring in so many different plants, has drawn the attention of botanists for centuries. In roots the same feature usually escapes observation: but since some cases have been described for aerial roots (W o r s d e l l, 37, p. 68), we do know that roots also may be subject to the same anomaly, in exactly the same form.

In fasciated stems and roots the apex no longer shows the usual paraboloid shape, but is transformed into a cuneiform body with a narrow vegetative ridge.

This is the salient point of difference from all cladodes or other flattened axes like the stems of some lianas, in which the departure from the cylindrical form is brought about by later growth proces-ses, not by the shape of the apex. In the teratological literature this fact has not always been duly recognized, see for instance M o-quin-T a n d o n (19, p. 154). For lianas this view needs no proof as the young stem for a long time remains cylindrical. For cladodes it has been demonstrated by A s k e n a s y (1), by C h u r c h (4, p. 221) and independently again by B i l h u b e r (2, p. 235).

Fasciation is a wide-spread phenomenon, occurring in Pteridophy-tes (P e n z i g 22, p. 561: *Psilotum;* 562: *Lycopodium*), in Gym-nosperms, in Monocotyledons and in Dicotyledons of the most dif-ferent description; M a s t e r s (16, p. 33) records a long list of plants in which it has been observed.

The literature on fasciation being very scattered and, like that on many other teratological topics, being more or less incoherent,

[1]) The main contents of this paper have been read at the XXIXe Vlaamsch Natuur- en Geneeskundig Congres at Gent, April 1936, (28).

we cannot survey a regular progress in our knowledge of the subject; we find rather that some opinions on fasciation have been held alternately, in most cases without a sufficient basis of facts. We shall therefore begin with a statement of the principal facts.

§ 2. Principal facts to be observed in fasciated stems and roots.

a. Typical fasciation. The typical and at the same time by far the most frequent form of fasciation may be described as follows.

A stem or root with a normal cylindrical base gradually broadens and flattens out in its distal parts; the transverse section being extended in one direction, called the sagittal plane by G e o r g e s c u (9, p. 8), the dimension in the perpendicular direction, the transversal plane of G e o r g e s c u, is not altered.

The broadening in the sagittal plane usually continues as long as the organ grows; it may seem to have stopped in parts with a strong intercalary growth like flower petioles or inflorescence shafts. It may even go back again somewhat; this does not pertain however to the vegetative ridge which can only broaden out, but to the adult tissues formed by the apex. This occurs often when owing to bad nutrition the higher parts consist of not fully developed tissues [2]).

In some cases the broadening of the vegetative ridge goes on more quickly than would correspond to the amount of longitudinal growth of the organ; in such cases the vegetative ridge cannot remain straight but forms folds in the transversal plane, in the way of a pleated collar. This form of fasciation has been sometimes called a pleated fasciation; essentially it only represents a mere variation of the typical form.

In some other cases the longitudinal growth being different in the different parts along the sagittal axis, the organ assumes a remarkable curvature in the sagittal plane, giving it a crosier-like form. This effect evidently is due to differences in the parts of the vegetative ridge; we can often state that the parts growing faster in length are thicker in transverse section too. On this mere incidental difference G e o r g e s c u bases his distinction between dorsiventral and bilateral fasciations (9, p. 15) which will not be made here.

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[2]) S t r e i t w o l f reports (29, p. 24) that in his material broadening out of the shoots was observed as frequently as constant breadth or tapering upwards; his material was however not well chosen in so far as the examined parts often were only upper parts of fasciations, e.g. scapes of *Taraxacum* without the radicle rosette.

Frequently the fasciation is accompanied by a splitting of the organ, a fact which is no doubt related to the same unequal distribution of growth vigour over the vegetative ridge; the resulting branches which are all placed in the sagittal plane may be fasciated themselves in the same plane or they may be normally cylindrical.

In stems typical fasciation is always accompanied by an increase in the number of leaves around the stem: the phyllotaxis at the same time loses its regularity; for illustrations see C h u r c h (4, p. 223) and G e o r g e s c u (9, p. 42—51).

Typical fasciations nearly always occur as rare monstrosities: d e V r i e s succeeded however in showing that the power of producing fasciations every now and then, is transmitted by heredity (33), the well known case of *Celosia cristata* only differing from most other cases by a much higher hereditary percentage. In any case the production of fasciations is dependent to a large extent on nourishment, excessive nutrition favouring their origin.

b. *Radiate fasciation.* Besides the typical fasciation some modified forms are to be observed in rare cases. As the first of these modifications we may cite the radiate fasciation, as yet met with in stems only. The apex does not form a straight ridge in these cases but becomes stellate with three or four arms. The stem accordingly is radiate in transverse section. Examples have been described by d e V r i e s (35, p. 548: *Amarantus speciosus, Digitalis lutea, Celosia cristata*), N e s t l e r (20, *Amarantus*) and W o r s d e l l (37, p. 88: *Primula veris*).

As far as can be made out from the few available data, the other characteristics of this radiate fasciation are identical with those of the typical form.

c. *Ring-fasciation.* Another modification is the ring-fasciation, also only observed in stems; it is a very rare anomaly but in some varieties of *Pisum sativum* it is the normal state and breeds true (C o m p t o n, 5). It has been described for *Peperomia maculosa* by d e V r i e s (32) and for *Veronica longifolia* by N e s t l e r (21). In these cases the stem apex is not converted into a linear apical ridge but it assumes an annular shape; the so formed stem therefore has an infundibular shape, with an internal downward tapering and blindly ending cavity, lined by an internal epidermis.

The outside of the stem in all cases bears, in an irregular phyllotaxis, leaves or bracts, eventually with axillary flowers or inflorescences. The funnel inside may produce them in the same way; the

orientation of these phyllomes and lateral branches is invariably towards the apical ring, not, as would have been the case in an invaginated apex, towards the funnel base. In *Pisum* the inside of the funnel may be entirely devoid of any organs (C o m p t o n, 5) or it may bear them as in other cases.

In its higher parts the funnel usually breaks up into parts, by the same process of splitting as in the typical fasciation.

The stele of these fasciated stems in all cases shows a double vascular ring, an outer ring in normal orientation, connected to the outer leaves, and an inner ring in inverse orientation, without any connection with the outer system, formed in *Peperomia* and in *Veronica* by the leaf-traces of the inner organs, and dying out under the funnel base. In *Pisum,* where the funnel breaks up into crescentic parts with leaves inserted especially at their two ends, the presence of the internal cylinder may be due to the foliar traces of these leaves, in the same way as in the normal distichous *Pisum* stem where the two leaf orthostichies by their extending traces give rise to a closed and normal cylinder.

d. *Connation.* A last group of phenomena, usually taken as fasciations, are the ribbon-shaped stems or roots, due to the fusion or connation of two or more vegetative cones; for connate stems of this kind V i s c h e r (31) makes use of the term syncaulome [3]). The first author to point out the essential contrast between these fusions and other fasciations seems to have been F r a n k (7, p. 233). He observed racemes of Crucifers with an increased number of flowers in an irregular arrangement and found several cases of neighbouring insertions united into a ribbon with longitudinal furrows. Moreover he met with a stem of *Knautia arvensis* where two lateral branches were fused with the main axis.

Of course for those botanists who believe that all fasciations are due to connation, the existence of a separate class of connation fasciations is not acceptable; it has accordingly been denied by J a c o b a s c h (11, p. 131). We may however point out the following differences between true fasciation and connation.

In the first place a connation does not arise like a fasciation as a normal cylindrical organ, but is ribbon-shaped from the beginning. In the second place its anomaly is not progressive but stationary, or it even tends to disappear by a partition of the

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[3]) As the term syncaulome is not to be paralleled by the term synrhizome for fused roots, it is perhaps better to designate all these cases simply as connate stems and connate roots.

ribbon-shaped body into its component parts which then are normal themselves.

Besides the cases reported by F r a n k other instances have been described in literature.

D e l p i n o describes numerous cases of abnormal axillary shoots in the axils of so-called doubled leaves in *Olea europaea* (6, p. 206). These doubled leaves no doubt were themselves due to the development of two leaf primordia in an unusually close vicinity, so that their areas partly overlapped (S c h o u t e, 26, p. 242). In many cases the axillary buds were partly fused in such a way that the resulting branch was ribbon-shaped, with or without a furrow in the median plane; higher up these shoots might dichotomize in the transversal plane, forming two normal shoots.

In the second place we may cite the axillary buds in the cotyledon axils of *Phaseolus*, described amongst others by G e o r g e s c u (9). After decapitation of the epicotyl and the primary axillary buds from the cotyledons, a series of descendingly serial buds in the cotyledon axils develops by intercalary growth (9, p. 21, 56), in the form of a ribbon-shaped stem, with a series of separate vegetative cones at the top. These cones higher up produce normal branches.

In the third place neighbouring scapes of *Taraxacum officinale* may fuse in various ways. As however true fasciation occurs too in *Taraxacum*, yielding monstrosities of a superficial likeness to these connations, an investigation of the whole plant in any case is needed, and the often separately picked monstrous scapes are not sufficient material for their study.

As W y d l e r already reports (38, p. 553), *Taraxacum* is a biaxial plant, the main axis ending in a terminal head and the florets forming the second kind of axis; the more external foliage leaves bear similar branches with a larger or smaller number of basal foliage leaves, whereas the branches from the innermost leaves may be devoid of foliage leaves, giving rise to an inflorescence scape only.

In such cases where the vegetative axis of the plant is typically fasciated, the terminal scape of course is in the same condition, attaining a breadth of 1—3, up to 5 cm (d e V r i e s 34, p. 321); as d e V r i e s remarks l.c. „sind die verbänderten Blütenstiele von unten herauf breit und flach, und nicht, wie gewöhnliche verbänderte Zweige, unten stielrund und sich nach oben allmählig abflachend. Es rührt dieses daher, dass die Fasciation, ganz ähnlich wie bei *Crepis*, bereits in der Rosette entstanden ist". We might add that the intercalary growth of the scape is the reason why

the scape does not broaden out upwards. From my own obser-
vations I can report that in these typically fasciated scapes no
other parts are to be found inside the flattened tube, in contrast
with the conditions to be described presently for the connate scapes.

Connations in *Taraxacum* arise by the fusion of a number of
more or less collateral scapes, formed in the axils of a whorl of
foliage leaves. When the fusion is complete this must yield two
concentric tubes, the outer one with the epidermis outside and a
normal vascular cylinder, the inner one with a vascular cylinder
in inverse orientation and the epidermis inside; both tubes at
the sides facing each other being lined by the irregularly delimited
medullary parenchyma.

At their distal end the tubes together bear the annular common
receptacle which is surrounded by an external as well an internal
involucre.

Such cases indeed have been described by M i c h e l i s (17, 18),
a specimen described by V i s c h e r (31) differing only by the fact
that the outer and inner tubes were not separated by an annular
cavity, but that the medullary tissue was present everywhere
between the two vascular cylinders of which the inner showed
an inverse orientation.

In cases of less complete fusion the boundary between the con-
stituent inflorescences may still be discernible, in the form of
traces of radial septa between the two tubes: a fine specimen
with traces of four septa and terminated by four separate well
developed heads has been described and figured by R e i c h a r d t
(23).

Inside the connate scape of course other organs may be found,
in the first place the terminal inflorescence. In the specimen
described by R e i c h a r d t the terminal scape was somewhat
stunted in growth, shorter and reduced to a slender stalk with
only some hairs at the top; moreover it was fused to the surroun-
ding tube, so that the latter only in its apical part surrounded
a central cavity.

In some other specimens described by M i c h e l i s, the central
scape was complete and free. Finally, in the specimen described
by V i s c h e r, inside the connate scapes no less than twelve
normal and free scapes were present, intermixed with some normal
foliage leaves which no doubt were subtending phyllomes. As
however the monstrous scape was unfortunately severed from
the plant by the amateur finder, a morphological analysis was
impossible.

In any case it is clear that here the whorl ·of connate inflores-

cences had not been formed by the axillary buds from the highest foliage leaves, but from more external ones, including in this way not only the terminal scape but moreover a number of lateral inflorescences with their subtending leaves.

Penzig supposes (22, p. 525) that in such cases the terminal vegetative cone of the stem, after having produced the hollow fasciated scape, may keep the meristematic condition and resume its growth; this view is only quoted here as a specimen of the confusion caused by rash conclusions without a previous morphological analysis.

Finally an example of connate roots. In *Tecoma radicans,* accurately described and figured by F r a n k e (8), the production of adventitious roots is strictly localized on the stem, the roots being formed at and under the nodes in four groups, diagonally placed with respect to the leaf pair.

Every group consists of four, sometimes five, orthostichies, every orthostichy containing up to 40 roots. The roots of one orthostichy are strongly connate: in the beginning a common longitudinal vegetative ridge is formed in the outer part of the cambium (?), the ridge soon forming a number of separate vegetative cones. A common calyptra in the beginning covers the whole orthostichy, and epidermis and cortex are common to all; the steles however from the beginning are distinct. The roots of adjoining orthostichies may locally show mutual connations, but only of a lower degree.

In their further growth the roots gradually separate without any further particular phenomena.

From these examples it will be clear that connation may indeed form abnormal stems and roots showing a certain likeness to fasciations. In view of the difference between the two groups of phenomena N e s t l e r proposes (20, p. 346) to exclude connation from the conception of fasciation and to limit the use of the term fasciation to the gradually expanding case. This proposition will be followed here, the more as in the next paragraph its theoretical basis will be found to be correct.

§ 3. **Possible explanations of fasciation and connation.**

a. *Typical fasciation.* Leaving for a while the radiate and the annular fasciation out of the discussion we may say that the explanation of the typical fasciation usually has been sought in two directions, that of the growing together of several organs, of connation therefore, and that of the broadening of a single

vegetative cone by growth in one diameter only. Incidentally other explanations have been given which may be dealt with first.

Delpino ascribed fasciation (6, p. 218) to an insufficient growth of the medullary tissue, in consequence of an augmentation of the number of leaves by chorisis. Against this view we may not only remark that those stems in which the medulla always forms a large lysigenous cavity may be fasciated just as well as others *(Taraxacum,* scape), but moreover the whole view is untenable, because the fasciated condition is already present in the vegetative ridge in which a medulla has not yet been formed.

Worsdell declared (36, p. 74) that fasciation is „the resultant of the more or less equal conflict waged between two opposed tendencies or forces, viz.: that which, on the one hand, induces integrity, and that which, on the other, induces plurality of parts".

In his handbook Worsdell elaborates this view and presents it under the name of pleiotomy-theory; fasciation now is brought directly into line with twin-formation and with dichotomy. Worsdell summarizes the paragraph by saying that the gradual expansion in one diameter „is due to the tendency on the part of the shoot to dichotomize, this being equally balanced and neutralized at every moment by the opposite tendency, viz., that to cohere as a unity; this alone is the vera causa of the ribbon-growth with which we are so familiar" (37, p. 94).

In our second chapter we shall discuss the relation between fasciation and dichotomy; our conclusion will be that such a relation is not to be assumed. Moreover the whole so-called explanation by two supposed tendencies is hardly more than a paraphrase of the observed conditions, and falls short of being an explanation.

So we may return to the two opposed explanations, that by fusion and that by expansion.

The fusion theory was held by Maior in 1655 (15) and by Linné in 1751 (14), but without any arguments. The first to argue it seems to have been Hincks (10), who opposed Moquin—Tandon's arguments on behalf of the expansion theory. Hinck's argumentation has been reproduced in full by Masters (16, p. 29); yet it is so poor that only one remark from it may be quoted here. It is that Moquin—Tandon was wrong in contending that fusion of two stems could never be complete and that in any case the two medullary canals could never fuse entirely, so that a fusion product should always be recognizable from its anatomy. Here Hincks no doubt is quite right: such a fusion may quite well be so complete as to include

the formation of one single stele with an elliptic transverse section. This truth however is no argument for the thesis that all fasciations always must be due to fusion.

Perhaps the best defence of the fusion theory has been given by J a c o b a s c h (11) who starts from the description of a fasciated branch of *Acer pseudoplatanus* the apex of which had been cut away and whose branches consequently had strongly developed, partly in a fasciated form. In this material J a c o-b a s c h observed several connations of lateral axes and connations of branches with their laterals.

It is however clear that such cases do not prove anything for other fasciations. The morphological analysis of the complex, the indication of subtending phyllomes and of the number and place of origin of the constituent branches, possible in the object described by J a c o b a s c h, is absolutely impossible in the case of typical fasciations.

Summarizing we may say that the evidence for the fusion theory is of no value.

Turning now to the alternate view of expansion in one diameter as the cause of fasciation I might start from the discussion of M o q u i n—T a n d o n's argumentation: the earlier works of J a e g e r (12) and S c h i e w e k (25) were not at my disposal and from their review by S t r e i t w o l f (29, p. 8) their arguments do not seem to have been of much importance.

M o q u i n—T a n d o n (19, p. 151) does not give any direct arguments for the expansion theory but arrives at it by exclusion, the fusion having to be rejected. Moreover his grouping together of cladodes and fasciations, already alluded to above, shows that M o q u i n—T a n d o n did not understand the real nature of these phenomena.

N e s t l e r believed that a decision between the two opposed theories might be reached from the investigation of the growing shoot or root apex: in the case of fusion he supposed the vegetative ridge to contain a number of vegetative cones or of apical cells, corresponding to the number of fused organs (20, p. 369, 370). And as he did not find such a division into vegetative cones or apical cells, but found that the vegetative ridge in several cases was of a continuous homogeneous structure, he thought to have given proof of the expansion theory, adding however that the way in which this growth in one diameter is brought about remains in the dark (20, p. 458).

In my opinion N e s t l e r's starting point is wrong. In a fusion product the apex may be quite homogeneous, when the fusion takes

place early enough; N e s t l e r's result therefore does not settle the question.

The last paper to be discussed is that by S t r e i t w o l f, who for the first time brings a real argument for the expansion theory (29, p. 26). He points out namely that a normal cylindrical shoot may broaden out into a fasciation, without any indication in its phyllotaxis of a transition between the normal and the fasciated part. An attempt to explain the one diameter growth S t r e i t- w o l f does not make, however.

So we may say that up to the present time we have only reached the result that typical fasciation is brought about by an unusual growth of the vegetative apex, in one diameter. To say that the expansion theory has been proved is saying rather too much. For the result hardly exceeds a correct description of the outward appearance, without even a beginning of an explanation.

Yet, the evident unity of the phenomena, occurring in so many and such different plants, makes the problem very tempting, and on some reflection the solution even does not seem so very difficult. In order to explain this, we have to consider first what conditions obtain in the normal vegetative cone.

In any vegetative cone we may be sure that there is a central part in which no organs have been induced as yet, a neutral part, containing in many cases a great number of cells, a few or one, or not even a whole cell in others. The last condition is realized when organs are induced or even differentiated in the apical cell, as for instance in many *Sphacelariales*. In this central part, or first 'zone as I shall call it, the most characteristic processes of the vegetative cone are going on; the zone by growth produces new parts of the surrounding zone and always concentrates its powers.

Outside the first zone we have the second zone, in which the different organs are induced, without any visible differentiation. In the stem the places of leaves are determined, in the root the vascular strands are induced.

Outside the presumably rather narrow second zone, a broad third zone follows in which the induced parts begin to differentiate; in this zone the leaf primordia, the leaf-traces and the root strands become visible.

The parts of all three zones grow in three dimensions; the zones themselves keep their places only by the constant transition of parts from one zone to the next. The growth of the three zones together finds its expression in the form of the apex, a form which is well known to be different for different plants, and even for

stems of the same plant, when these stems have different plastics. In any case however the growth of any zone must be such as to harmonize with that in the others; if not, the form of the vegetative cone changes, or perhaps even the coherence of the parts will be impaired.

Now we may further assume that in stout vigorous stems the first zone is larger than in weak stems. This is demonstrated by the fact that the phyllotaxis in stems of different vigour usually differs, and that these differences are always such that the number of leaf parastichies in the stronger stems is higher. A larger first zone of course must be surrounded by a wider ring of second zone. In this wider ring, more space being available for organ induction, higher leaf parastichy numbers (or in the root higher vascular strand numbers) are to be expected.

Fasciation being generally recognized to be furthered by excessive nutrition, it may begin with an unusually large first zone, consequently shortly afterwards an unusual high number of surrounding organs in zone three. In most cases nothing extraordinary will follow on this state of things, all zones growing in due proportion and only producing an uncommonly vigorous shoot or root.

In some cases however a disharmony may be the effect, especially when the zones one and two are occupying an unusually large part of the apex slope, so that for zone three the opportunity of widening, i.e. of tangential growth, is limited. When such a tangential growth nevertheless follows in the usual proportion, a tangential tension will be the effect.

Such a tension may have the following consequences: the ring zone of young organs, becoming wider than corresponds to the amount of inner tissues, may remain annular and distend the inner tissues. In other cases it may become elliptical, or in still other cases it may become folded in some pleats; what will happen will largely depend on the spatial relations and the consistency of the different tissues.

It is my aim to demonstrate that these different cases successively must give rise to the ring-fasciation, to the typical fasciation and to the radiate fasciation; I shall begin with our present topic, the typical fasciation as the result of an elliptical third zone.

In such a case, even when the ellipse only has a small excentricity, we may easily conceive that, for those organs which are situated at the ends of the long axis, the opportunity for tangential growth has increased, so that the tension here will be diminished or removed. For the organs at the ends of the short axis on the

contrary the tangential growth finds less room than ever. So the tangential tension will be increased there, and it will extend the inner zones, i.e. zone two and zone one.

The result will be that at the flat side of the ellipse zone two will grow longer, and will give rise to an augmented number of new organs; these in their turn will grow tangentially when arrived in zone three, and so on. In the stem this will not only lead towards an increasing number of leaf parastichies, but moreover to a loss of regularity of the phyllotaxis, as the new parastichies are inserted at the flat sides only.

The vegetative cone being converted in such a way into a vegetative ridge, splitting into separate parts may easily ensue; as soon as the tangential tension is not quite evenly distributed along the vegetative ridge the first zone of the latter may get local thickenings and thinner places which soon, by the transgression of parts to zone two, may lead towards a splitting of the whole fasciation.

After the views enounced here, the typical fasciation is nothing but a dilatation phenomenon, a passive transverse extension of the central area of the vegetative cone. This theory not only satisfactorily explains for the first time the external morphological phenomena of the typical fasciation, but moreover it is corroborated by the results of the anatomical investigations as instituted by several authors (see G e o r g e s c u, 9, p. 52). In all cases the histological differentiation in fasciated organs appeared to be the same as in normal parts, the only difference being found in the amount of the tissues produced.

An instructive series of transverse sections through a fasciated shoot of *Celosia cristata* is given by G e o r g e s c u ; it is reproduced here as fig. 1.

A is the highest section; all cells in it are isodiametric, as may be expected in a meristem, even under dilatation, when the cell divisions are frequent. In B and C the leaf primordia are to be observed, in D and E the sections pass through the leaf-traces. The fact I wish to point out especially is that in E the medullary cells are elongated in the sagittal plane. As medullary cells normally are the first cells to stop their divisions, here the dilatation must give the first changes in form. G e o r g e s c u ascribes this elongated form to a supposed transversal pressure; it is however evident that such an unwarranted supposition may be spared.

b. *Radiate fasciation.* The explanation of the typical fasciation given above is fully applicable to the radiate fasciation, if only we assume that the external ring of differentiating organs in the
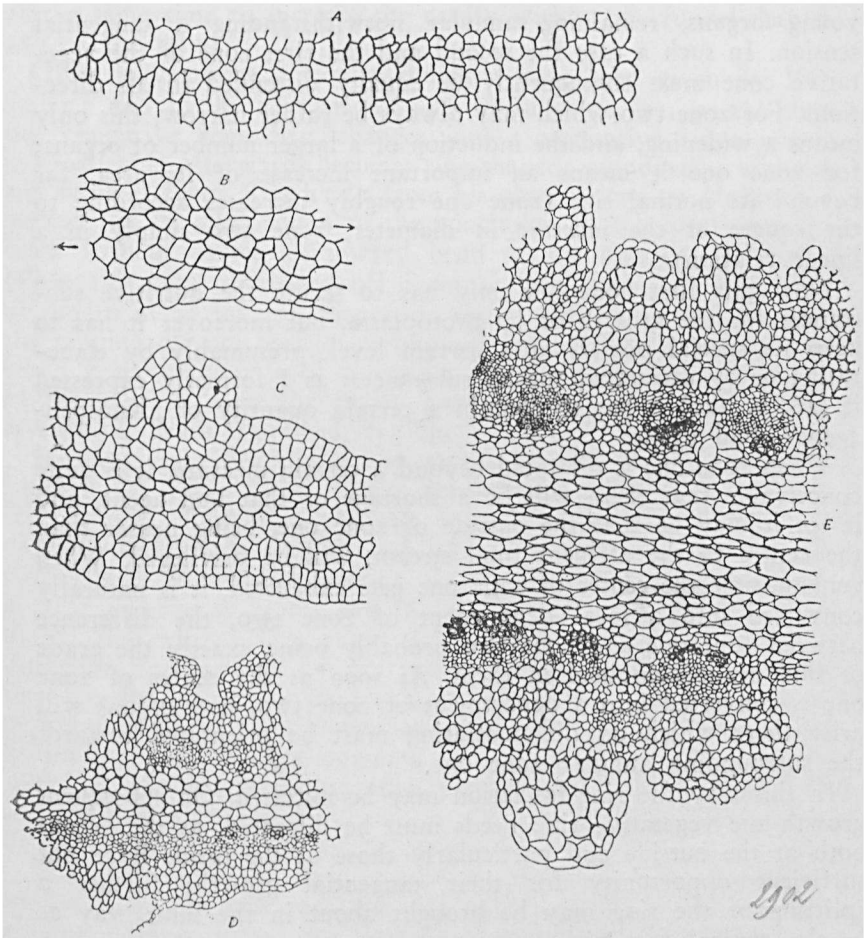
FIG. 1. *Celosia cristata,* series of transverse sections through vegetative ridge of fasciated stem. From Georgescu (9, p. 53, fig. 50).

beginning is not flattened but wrinkled. The rest then follows quite naturally, and it becomes obvious why in the same plants in which these extremely rare radiate fasciations have been observed, a much larger percentage of typical fasciations has been found (de Vries, 35, p. 548, Nestler, 20).

c. *Ring-fasciation.* I remarked above that this form of fasciation may be explained from the assumption of a ring zone of

young organs, remaining annular notwithstanding a tangential tension. In such a case the second and the first zone of the vegetative cone must consequently be equally distended in all directions. For zone two which may always be rather narrow, this only means a widening, and the induction of a larger number of organs; for zone one it means an important increase of its area, far beyond its normal size (zone one roughly increases according to the square of the increase in diameter, zone two simply in a linear relation).

Now this first zone not only has to secure the nutritive substances for the growth of its protoplasm, but moreover it has to keep its special powers at a certain level, presumably by elaborating or by attracting special substances: as I formerly expressed it (26, p. 320) it has to contain a certain quantity of „Knospenagens", bud agent.

When zone one is dilatated beyond a certain measure, it is quite conceivable that there will be a shortage of that bud agent, and if so, it may be that the outside of zone one, being nearer than the centre to the affluent food stream, will be privileged. When consequently the centre of zone one gets exhausted, it is naturally converted into a local department of zone two, the difference between zone one and zone two probably being exactly the grade of bud agent contained in them. As soon as the centre of zone one is converted into a department of zone two, new organs will arise there which on differentiating must be orientated towards the surrounding annular zone one.

In this way the ring-fasciation may be initiated. On subsequent growth the vegetative ring needs must be dilatated, as the organs both at the outside and particularly those at the inside have not sufficient opportunity for their tangential growth; further a splitting of the ring may be brought about in the same way as in the typical fasciation.

In literature some explanations of ring-fasciation have been given, on which some remarks may be made.

According to Worsdell (37, p. 91) the morphological explanation of ring-fasciation is the apical invagination of the organ, comparable to the turning inside of a glove-finger. In my opinion this at the outside is a rough description, not an explanation.

A much better description has been given by Compton who writes (5, p. 253) that ring-fasciation „may be considered to arise by the sterilisation of the apical spot of the normal paraboloid meristematic region, leaving the peripheral cells still active. Further growth tends to widen the diameter of this ring of meristem and

at the same time to increase the cavity within: the funnel-shaped axis is the result".

Other descriptions of lower standard have been given by V i-s c h e r and by R i c h t e r. V i s c h e r supposes (31, p. 24) that the vegetative cone first changes into a vegetative ridge which in broadening afterwards becomes ring-shaped; suppositions without any basis of facts; R i c h t e r from his observations on *Helianthus annuus* (24, p. 232) comes to the conclusion that a local pressure from without causes an inward bend of the marginal elements. When this bend is nipped off from the periphery an inner ring of organs in an inverse orientation ensues. The local pressure and the nipping off are both quite hypothetical, and no doubt R i c h-t e r's generalization is of no value for the explanation of ring-fasciation. Yet I might make some remarks on the cases of *Helianthus* heads described by him.

In these large heads we may safely suppose that the relation between the three zones during development undergoes consider-able changes. Probably zone one is growing fast for a time, to diminish afterwards rapidly and finally to disappear entirely. In such a way an unusual amount of zone two is formed in which a great number of bracts and flowers is induced at a rash pace, up to the centre. This rapid induction in some cases may be disturbed, for instance by the presence of local damage, so that the invasion of organ parastichies is locally either retarded or perhaps inhibited. Malformations such as those described by R i c h t e r may be the outcome.

d. *Connation.* From the facts related above in our second § the occurrence of fusion of two or more stem apices, or of two or more root apices, is not to be denied.

When we compare these connation products with fasciations, we see that the two categories of anomalies differ in their be-ginning (ribbon-shaped for connation, cylindrical for fasciation), in their course (constant for connation, exaggerating for fasciation) and in their end (solution into normal parts for connation, into normal and fasciated parts for fasciation). Our explanation of the causes of fasciation moreover makes clear that the two pro-cesses must be essentially different. N e s t l e r's exclusion of con-nation from the concept of fasciation therefore is well founded.

The first of the questions now remaining to be discussed is our understanding of the process of fusion of two or more vegetative cones. In literature the conceptions of this process are not always clearly expressed.

Although pressure is often made responsible for fusion, this is

surely a wrong assumption; we have to take for granted that the fusion is due to an extension of the areas of two newly induced vegetative cones, an extension which will usually take place before the cones are visible as primordia on the parent organ.

In any case the fusion has to occur at such a stage that the future cones only consist of first zones, no second zone having been formed as yet. For if this should have happened, organs would have been induced between the two apices, forming an insurmountable barrier. S t r e i t w o l f writes (29, p. 27) that he has great objections to the conception of fusion, as the young apices are always surrounded by young leaf primordia. This is a mistake; it is not difficult to prove the contrary.

To this end I need only recall the dichasium of *Lonicera*, where the main flower usually aborts and the two lateral flowers approach each other at the peduncle apex. In some species the inferior ovaries of the two flowers are connate and in *Lonicera Alberti* (V e l e n o v s k y, 30, p. 823) this process may sometimes go so far that the two flowers have a common pleiomerous calyx, corolla, androecium and gynoecium. Evidently in such cases the two lateral flowers are fused, in spite of their position in the bracteole axils, over the peduncle apex, and this fusion must have taken place before the induction of any of their leaf whorls.

Another question to be dealt with is how to distinguish anatomically between connation and fasciation. Several authors, through lack of sufficient morphological criteria, have tried to find an anatomical distinction between connation and fasciation, and believed that the presence of a single stele in the ribbon-shaped organ was characteristic for fasciation, that of two or more steles for connation.

As F r a n k however wrote as early as 1880 (7, p. 234) connation may be so complete that the tissues are developed as in a single shoot; on the other hand a typical fasciation will form two steles as soon as a splitting of the vegetative ridge occurs; a section through the cohering organ part just under the splitting will already contain two steles. Thus an anatomical distinction is not possible: the presence even of medullary cells with an elongation in the sagittal plane being possible in both.

A last question, the answer to which unfortunately has to remain open, is whether a connation may lead to a true fasciation. Of course the arrangement of the organs along the vegetative ridge of a connation might initiate a dilatation and so give rise to a fasciation. As however the number of organs around the elliptical

apex is not abnormally high in proportion to its area, growth may go on normally as well.

If such an initiation of fasciation in connations occurs in some cases, the sharp distinction between fasciation and connation as made above, though theoretically not impaired and though nearly always easy in practice, might be rendered practically difficult in some rare exceptions.

CHAPTER II.

·Dichotomy as compared with fasciation.

When comparing dichotomy with fasciation, we cannot deny that there is a certain resemblance: in dichotomy the central part of the vegetative cone splits into two equal or unequal parts, and the same is usually, though not always, the case in fasciation.

The differences on the other hand are no less striking. In dichotomy we never meet with an unlimited increase in the number of leaf parastichies, with disturbances of the regularity of the phyllotaxis or with any other phenomena of disturbed harmony between the differentiating organ zone (our zone three) and the inner parts, the induction zone (our zone two) and the central neutral part (our first zone). Thus we never meet with ribbon-shaped organs: under every dichotomy the podium is only so much flattened as to provide a good base for the two shanks, no more, and the shanks are cylindrical.

The difference obviously is that while fasciation is a passive dilatation of zone two and zone one, by the tangential growth of zone three, dichotomy is an active process, staged in zone one. The tendency of so many authors to regard dichotomy as a basic principle of fasciation therefore seems to be ill-founded. Essentially there is no relation between the two processes, and the cases of unquestionable fasciation in *Psilotum* and in *Lycopodium* (K r o n-f e l d, 13) give a striking confirmation of this view.

The same conclusion is forced upon us when we realize the difference in distribution of the two phenomena in the plant kingdom. Whereas fasciation seems to occur in the greater part of, possibly in all, vascular plants, but nearly always as a very rare anomaly, the occurrence of dichotomy is restricted to limited plant groups, in which it is however quite normal.

So the question naturally arises as to what causes dichotomy may be due. For the solution of this problem a detailed statement of facts is of course the very first requirement. Having given a

review of these facts as far as available elsewhere (27, p. 9), it may suffice here to remind the reader of the existence of two forms of dichotomy in stems, the dichotomy without relation to the leaves and the dichotomy with an angular leaf. The first form is only to be found amongst vascular plants in the microphyllous Pteridophytes, the second in megaphyllous plants, namely in the *Filicinae* and in the rare instances of dichotomous Seed-plants *(Hyphaene)*. Both forms of stem dichotomy and the only form of root dichotomy show all gradual transitions from equal dichotomy through unequal dichotomy to lateral branching.

Any theoretical conception framed with the intention of explaining the mechanism of dichotomous branching should take account of these facts; for the stem the phyllotactical phenomena accompanying dichotomy having also to be considered.

In equal dichotomy without an angular leaf phyllotaxis proves that the branching goes on inside zone one. For we always find that the phyllotactical pattern of the podium extends on three sides of the shanks, while in connection with it in the saddle new parastichies are added. So we may be sure that in the earliest stages the two shanks at least partly are surrounded by first zone areas. Here is probably a certain difference from the splitting in fasciation; in fasciation under the influence of unequal tension thicker and thinner parts are formed in zone one; when splitting follows, the separate parts of zone one from the beginning have been surrounded by zone two.

In the case of unequal dichotomy without an angular leaf the same holds true; yet the weaker shank evidently is formed somewhat more excentrically though still inside zone one. When the unequal dichotomy merges into lateral ramification, the lateral branch is either produced excentrically but still inside zone one, or it may be formed more to the outside, even inside zone two. This follows from the spatial relations between leaves and lateral branches, particularly in *Lycopodium* and in *Sigillaria* (S c h o u t e, 27, p. 18—22). Another highly remarkable fact is that these lateral branches may show a regular cladotaxis, so that we have to assume that the place of a lateral branch is determined by the places of lower buds.

Equal dichotomy with an angular leaf is also brought about by the induction of the two shanks inside zone one, as is borne out by the parastichies continuing from the podium on the shanks; but here we have to assume moreover a certain relation, of unknown nature, to the position of the angular leaf, a relation probably established at the stage when the angular leaf was the

lastly induced leaf of zone two.

In unequal dichotomy with an angular leaf the same relation exists, the angular leaf keeping the same position, even when the inequality is so pronounced that the dichotomy merges into lateral branching. The spatial relation of angular leaf and lateral branch in the ferns may vary to a considerable extent, and to one leaf even more than one lateral branch may be related; one of these various relations having become fixed in the Angiosperms, no doubt the relation between subtending leaf and axillary bud is of the same kind as that between angular leaf and dichotomy.

All these different facts should be considered for a satisfactory theory of dichotomy and related modes of branching. As far as I see however at the present state of our knowledge the time for such a theory has not yet come.

SUMMARY.

1. The distinction made by F r a n k between fasciations, arising by gradual expansion of the vegetative cone in one diameter, and other malformations arising by connation of two or more separate stems or separate roots, is a natural one; N e s t l e r's proposal to restrict the use of the term fasciation to the former category has to be accepted.

2. Fasciation is due to a disharmonic growth, the central zones of the vegetative cone being dilatated by tangential growth of the surrounding zone of differentiating organs.

The cause of this disharmony is to be sought for in an excessive strength of the neutral central zone of the cone, which in its turn is the cause of an abnormally wide zone of organ induction, and consequently of a disproportionate number of organs (leaves and leaf-traces in the stem, vascular strands in the root).

The gradual departure from the normal form of the organ, the often occurring splitting, the increased number of leaves and the irregular phyllotaxis are all secondary consequences of the dilatation.

3. The tangential tension in the zone of differentiating organs usually gives rise to a transverse flattening of the vegetative cone; as soon as this occurs the dilatation henceforth acts in such a way that the elongation of the central zone is limited to the sagittal plane, giving rise to a typical fasciation.

4. In some cases the tangential growth of the differentiating organs causes a wrinkling of this zone; instead of a typical fas-

ciation a radiate form ensues with otherwise the same characteristics.

5. In other cases the differentiating zone, being neither flattened nor wrinkled, dilatates the neutral part of the vegetative cone in an evenly distributed way; this leads to ring-fasciation by an exhaustion of the innermost part of the neutral zone in which consequently organs may be induced.

6. Connation of stems or of roots is due to confluence of the neutral zones of neighbouring vegetative cones during very young stages, in which no induction zones have been formed as yet by these cones. It is not accompanied by disharmonic growth phenomena.

7. Dichotomy is a spontaneous development of two centres in the neutral zone of a vegetative cone; the way in which this takes place is wholly unknown.

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