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ON THE SPIRAL ARRANGEMENT  
OF THE BRANCHES IN SOME  
CALLITHAMNIEÆ

BY

L. KOLDERUP ROSENVINGE



KØBENHAVN

HOVEDKOMMISSIONÆR: ANDR. FRED. HØST & SØN, KGL. HOF-BOGHANDEL  
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## I. Introduction.

IT has long been known that the branches or the special lateral, hair-shaped organs of several Florideæ are arranged in a spiral. The spiral arrangement of the lateral members of the *Rhodomelaceæ*, more especially, has been the subject of several publications, partly induced by SCHWEN-DENER's theory (1880) of a mechanical explanation of the spiral arrangement in these plants, a theory which must be considered definitively confuted (cp. KOLDERUP ROSENVINGE 1902; here further literature quoted). In these plants, the spiral arrangement of the lateral organs is very regular, the angle of divergence is fairly constant, and the arrangement of certain other organs is likewise very regular. Thus, in *Polysiphonia*, the spiral normally always turns to the left, the first side-branch of the hair-shaped lateral organs ("leaves" or "trichoblasts" as I have named them, cp. KOLDERUP ROSENVINGE (1903)) is always placed on their right side, seen from the outside, the axillary branches are always more or less displaced to the left, and the trichoblasts are always placed in the upper left angle of the first-formed pericentral cell of the joint. This suggests the existence of a correlation between the spiral arrangement and the orientation of the other, above-named organs, but it has not been ascertained, whether such a correlation really exists. The examination of a shoot of *Polysiphonia violacea* having exception-

ally the trichoblasts arranged in a spiral turning to the right seemed, however, to prove that only the orientation of the trichoblasts to the first-formed pericentral cell of the bearing segment is in correlation with the direction of the spiral (KOLDERUP ROSENVINGE 1902, p. 357).

A spiral arrangement of the branches is also met with in several *Ceramiaceæ*. NÄGELI (1861) has demonstrated its frequent occurrence in the *Callithamniæ* and described it rather extensively in a number of species of this group. He found that the branches, when placed singly on the joints, either stand in two vertical ranks, alternating on the two sides, or on all sides and then arranged in a spiral with angles of divergence from  $\frac{3}{7}$  to  $\frac{1}{6}$ . He further found that the first branchlet of a side-branch in the spiral region is always placed on the right or left side of the branch and apparently rather constantly on the cathodic side; when the angle of divergence is  $\frac{1}{4}$ , the second branchlet stands on the outer side, the third on the side opposite to the first, and the fourth on the inner side of the mother branch.

More recently, KYLIN (1907) has described the spiral arrangement in a number of species of *Callithamnion* occurring at the western coast of Sweden. He found, in disagreement with NÄGELI, that the first, usually 2 to 4 or 5, rarely more, side-branches on the mother-branches stand on the right and left, alternating in a transversal plane, after which the spiral arrangement begins.

On examining the *Callithamniæ* of the Danish waters I found that the discrepancies between the two above-named authors are explained by the fact that the ramification varies more or less. Thinking that these plants might be particularly fitted for throwing light upon the agencies determining the spiral arrangement, owing just to the lesser and

varying degree of regularity of this arrangement, I have submitted five species of *Callithamnieæ* occurring at the coasts of Denmark to a more detailed examination as to the arrangement of the branches, viz. *Callithamnion tetragonum* (With.) Ag., *Call. corymbosum* (Engl. Bot.) Lyngb., *Call. roseum* Harv., *Call. Furcellariæ* J. Ag. and *Seirospora Griffithsiana* Harv.

The material serving for these studies was for the most part preserved in alcohol; in several cases, however, living plants were examined, and in one case only, dried plants were used. In preparing the plants for examination, care was taken that torsions of the filaments were avoided as much as possible. The branches of each shoot examined were marked on squared paper in diagrams like those represented below, where a point respectively indicates the point of insertion of a branch and the transverse wall between the cells in the mother axis, and the short lines issuing from the points indicate the directions of the branches. In main axes or in branches whose bases were not examined, a branch directed exactly towards the observer is marked by a line directed downwards; a branch standing on the opposite side is marked by a line directed upwards; a branch looking right or left is marked by a line directed to the right or to the left respectively, and the intermediate positions are marked in a corresponding manner. When a side-branch is represented with its branches from the base, the observer is imagined standing exactly before the branch, in the median plane containing the mother axis and the branch. A transversal line at the base indicates the insertion of the branch. A point without a line indicates (the upper end of) a joint which bears no branch. The position of the branches as well as each angle of divergence was de-

terminated by the eye and therefore not represented with full accuracy. A natural torsion of the branches might possibly take place, but I have not observed any sign of it. Only long shoots have been used for examination, the branches with limited growth having usually a different ramification.

In the diagrams it is further indicated on the left side whether the spiral turns to the left, or to the right; and on the right side, a number indicates for every side-branch whether the first branch of the II. order stands on the 1st, 2nd, 3rd etc. joint, while the following letter indicates whether it stands on the right (*d*) or the left (*s*) side of the branch of the first order. In the proportionally few cases where it stood exactly on the outer or on the inner side of the branch, in the median plane, it is marked with the letters *e* and *i* respectively. When the side-branch is unbranched, as is frequently the case with the first side-branches of a branch, it is marked with *o* only. When in some cases a ? is added to the letter, it is usually owing to the fact that with pseudodichotomous ("kamptopodial" NÄGELI) ramification it was impossible to decide which of the rays was the main axis and which the side branch.

The ramification in the genus *Callithamnion* is always monopodial in the common signification of this word. NÄGELI, however, (1861, p. 305—306) distinguishes between *Callithamnieæ* with monopodial, kamptopodial and sympodial ramification. In the first, the mother axis is vigorous and reaches higher than the side-branches. In the second group, the side-branch develops more quickly so that it soon reaches the same size as the mother axis, and the ramification then gets the appearance of dichotomy (*Call. corymbosum*). In the third ("sympodial") group, "entwickelt sich je der begrenzten



Tochterstrahl beträchtlicher als sein ebenfalls begrenzter Mutterstrahl, so dass er denselben bald an Länge übertrifft und ihm an Stärke gleichkommt; dadurch wird das unverzweigte Ende des Mutterstrahls seitlich geschoben, und der Tochterstrahl erscheint als die direkte Fortsetzung von dessen unterm Teil." For an example of this last group the reader is referred to Fig. 8 (l. c.) representing *Call. (Dorythamnion) tetragonum*. Cp. our Fig. 1. In these species, the main axis changes direction at each branching, the branch forming the continuation of the joint on which it is standing, but the axis bent in zigzag is the main-axis, and the ramification is totally different from that of the *Dasyeæ* where the zigzag axis is a true sympodium. It is therefore unfortunate and misleading (cp. KYLIN 1907, p. 156, 165) to designate this ramification as sympodial. The branch-bearing segments are always cut off from the apical cell by an inclined wall having its highest point where the branch will arise.

## II. Examination of the Species.

### 1. *Callithamnion tetragonum* (With.) Ag. var. *fruticulosum* (J. Ag).

This species is here taken in a wider sense than by most of the authors, as *Call. brachiatum* (Bonn.), *C. fruticulosum* J. Ag. and *C. spiniferum* Kylin are referred to it. NÄGELI has described the ramification under *Dorythamnion* (1861, p. 344), and KYLIN has described it in most of the above-named species, in most detail in *C. fruticulosum*. The specimens examined by me may all be referred to var. *fruticulosum*. They originate from the following localities: 1) No. 7448. Nordostrevet by Hirsholm, Northern Kattogat, July 11th 1904. 2) Off Hornbæk Plantage, June 16th 1919 (Henn. Petersen). 3) No. 8355. Near Ellekildhage May 23rd 1914.

4) No. 6416. Hellebæk, Sept. 25th 1898. 5) No. 3044. between Julebækshusene and Hellebæk Aug. 4th 1892. The four latter

localities in the Sound North of Elsinore.

The species is easily recognisable by the ramification on all sides, by the ultimate branchlets being pointed, never ending in a hair, and by the cells containing more than one nucleus continuing to the top or nearly so. The ramification is comparatively regular, the branches being always placed in a continuous spiral for the whole length of the shoot with the exception of the lowermost ones which, in the lateral shoots, are arranged in two lateral rows. The uppermost branches have a limited growth and produce only a few branchlets which

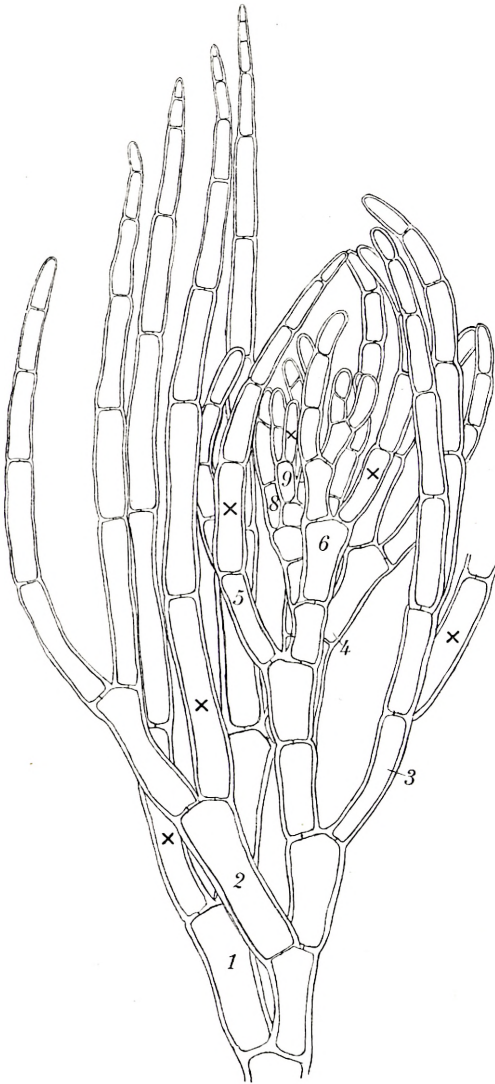


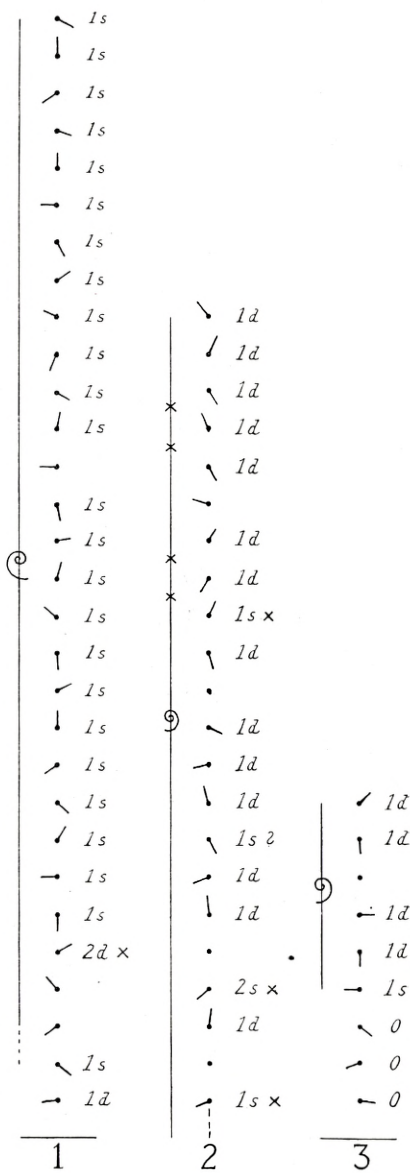
Fig. 1.

*Callithamnion tetragonum* var. *fruticulosa*.  
From Hellebæk (6416). The first branch of the second order is marked with X. 200 : 1.

are not arranged in a spiral, but these branches are connected with the long ones by intermediate stages.

As a rule each joint of the longer axes bears a branch from the very base of the axes, and it is very rare that a joint in the spiral region is without one. In one case where a joint bore no branch it could be seen that the branch had fallen off. But in the other cases, no trace of such a process was visible, and it must be assumed that the joint had never borne any branch, but notwithstanding this fact the spiral continued undisturbed, as if the branchless joint had borne a branch missing in the spiral. It was so at least in five cases (diagr. 2, 3); in a sixth case it was rather doubtful as the angles of divergence were very variable.

The angle of divergence as a rule varies between  $\frac{1}{4}$  and  $\frac{1}{3}$  of the circumference; it is usually greater



Diagrams of shoots of *Call. tetragonum* var. *fruticulosa*. 1 and 3 lateral shoots from the base.

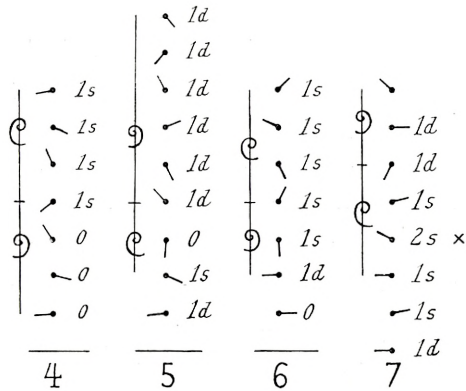
than  $\frac{1}{4}$  but may also be less, until  $\frac{1}{6}$ , and it may sometimes exceed  $\frac{1}{3}$ , but only rarely it approaches or attains to  $\frac{1}{2}$ , as in diagr. 2 $\times$ . The divergence 0 was only met with once in the spiral region and once below it; in the first case the continuation of the spiral beyond the superposed branch was unfortunately not observed. The average angle of divergence is always greater than  $\frac{1}{4}$ . On four shoots the average angle of divergence for a longer distance was determined to be  $104\frac{1}{2}^\circ$ ,  $105^\circ$ ,  $108^\circ$  ( $\frac{3}{10}$ ) and  $135^\circ$  ( $\frac{3}{8}$ ).

The spiral turns now to the left, now to the right, but a little more frequently to the left. Of 383 shoots 205 had a spiral turning to the left, 166 a spiral turning to the right, in 8 shoots the spiral changed direction and 4 had irregularly arranged branches. Thus, of the 371 shoots having a spiral with unchanged direction, 55.3 per cent had a spiral turning to the left, 44.7 per cent a spiral turning to the right. The difference between these figures is not very great; it seems, however, that a slight preponderance of the spiral turning to the left really exists. An observation concerning the relation between homodromy and antidromy, mentioned below, seems to favour this notion.

The direction of the spiral keeps unchanged on the same shoot. From this rule only very few exceptions were observed, in which cases the spiral following the biseriate arrangement at the base of a lateral shoot suddenly changed direction. In three cases the spiral made only 2 steps in the first direction (diagr. (4), 5, 6), in three other cases respectively 4, 6 and 9 steps (diagr. 7). The angles of divergence were not different from the usual at the place where the change took place; in one case, however, (diagr. 5) the first angle of divergence in the new direction of the spiral was

nearly 180°. In one shoot, the direction was twice changed, the spiral generally running to the left being interrupted by a short space of two steps where it turned to the right. Finally it must be mentioned that, in two shoots with an otherwise regular spiral running to the right, this was interrupted by a single step in the opposite direction, with an angle of divergence of 90° and 140° respectively (diagr. 22). In two shoots a short space with irregular arrangement occurred between the biseriate and the spiral arrangement.

No constant relation exists between the direction of the spiral on the branches and that on the mother axis, homodromy and antidromy occurring with almost equal frequency. There seems, however, to be a slight preponderance of the latter; on examining 30 shoots 134 cases of homodromy and 185 cases of antidromy were found, or in terms of per-



*Callithamnion tetragonum* var. *fruticulosum*.  
Four shoots with changing direction of the spiral.

centage: 42 per cent of homodromy, 58 per cent of antidromy. If the shoots are divided in two groups after the direction of the spiral, the figures shown in table 1 are obtained.

These figures show a decided preponderance of antidromy in the shoots with the spiral turning to the right, which suggests that a feeble tendency to antidromy combines with a feeble tendency to a spiral turning to the left, while these two tendencies oppose each other in the shoots with the spiral turning to the left.

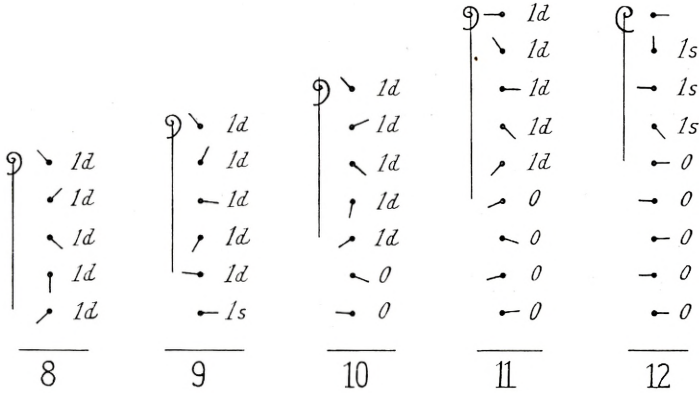
Table 1.

	Shoots with spiral turning to the left.		Shoots with spiral turning to the right.	
	Spiral of branches		Spiral of branches	
	homodromous	antidromous	homodromous	antidromous
number of cases	99	111	45	77
percentage . . . .	47,1	52,9	36,9	63,1

As mentioned above, the spiral arrangement does not begin at the very base of the primary axis. The first joints are usually branchless, and then follow a number of joints with branches before the spiral arrangement begins. In some young plants from Hirsholm (No. 7448), these branches were irregularly placed, but partly biseriate. By the same dredging some young sterile specimens were found which were remarkable by the primary axes bearing biseriate, alternate branches for a long piece above the branchless joints; in some plants the biseriate branches continued to the top of the shoot for a length of about 40 joints or more, in others the biseriate arrangement after finally, some 20—30 joints into, passed the spiral arrangement.

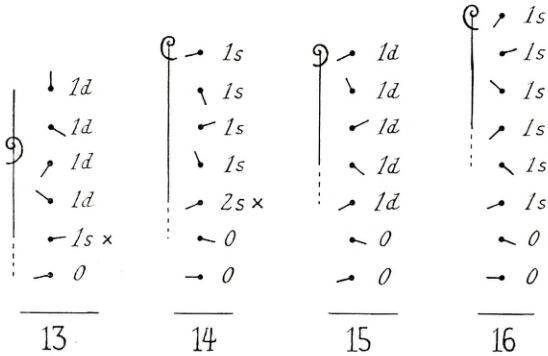
The side-branches are always branched from the very base. In six cases only, out of more than 800, the first joint was branchless. The first branch of the second order has always a transversal position, as stated by NÄGELI, but the following ones are, as a rule, also placed on the right and on the left and alternate, as shown by KYLIN. They are, however, usually not arranged exactly in two rows diverging  $90^\circ$  from the mother axis, but more or less approached to the outer side of the side branch, and this convergence usually increases with the distance from the base, though not regularly (comp. diagr. 1, 10, 11, 12, 3). The number

of such biseriate branches varies from 1 to 6 but is most frequently 3. The spiral arrangement begins, with very few



*Callithamnion tetragonum* var. *fruticulosa*. The spiral begins with the last alternate branch.

exceptions, immediately after the biseriate region, but from this it follows that, in several cases, the last step in the



*Callithamnion tetragonum* var. *fruticulosa*. The spiral begins with the penultimate of the biseriate branches.

biseriate region is at the same time the first step in the spiral region, and it is then before-hand impossible to ascertain with certainty where the spiral arrangement begins. Cp. the diagrams 1, 13—16, 19, 20. In the shoot diagr. 10,

which represents a very common case, the third branch is at the same time the last of the alternate (biseriate) branches and the first of the spirally arranged ones. On the other hand, in the shoot diagr. 15, which also represents a very frequent case, the fourth branch may be said to be the last biseriate branch and at the same time the first of those arranged spirally, but the spiral arrangement may with equal right be said to begin with the third branch. It is of importance to note this when trying to explain the efficient causes of the spiral arrangement. In the following table the number of biseriate branches is recorded for 100 shoots in which the spiral arrangement came immediately after the biseriate region, in the first column counting all the branches which could be regarded as biseriate, while in the second column the biseriate region is reckoned only to the first branch (inclusively) which could be included in the spiral.

Table 2.

	Number of biseriate branches.	
	All biseriate branches included	The biseriate region reckoned only to the first branch which could be included in the spiral region
1 transverse, biseriate branch	2	5
2 — — branches	17	21
3 — — —	42	55
4 — — —	29	14
5 — — —	7	4
6 — — —	3	1

In both columns we find a regular distribution of the figures with the maximum for 3 biseriate branches, but in the second column the maximum is more pronounced and the



distribution more symmetrical on both sides of the maximum.

In regard to the point of transition between the biseriate and the spiral arrangement the question arises whether the first step of the spiral arrangement might not be dependent on a tendency to produce branches by preference on the outer side of the mother branch (or possibly on the inner side). In order to investigate this I have, in table 3, dealt with all the 95 examined branches in which the spiral arrangement came immediately after the biseriate region<sup>1</sup>. In the table is indicated in how many cases the second branch in the spiral stood on the outer and the inner side of the mother branch respectively or exactly transversely (on the right or left). The branches are classed after the number of the joint on which they were standing. It must be noted that branches diverging more than 45° outwards from the transversal plane are usually not regarded as biseriate; only in very few cases have branches surpassing this limit been reckoned as biseriate, alternating, especially when one or more of the following branches deviated less from the transversal plane. On the other hand branches standing inside the transversal plane have in no cases been regarded as transversal, biseriate<sup>2</sup>.

The first section of the table (A), containing the shoots in which the spiral begins with the last of the biseriate branches, shows a very decided preponderance for the outer side of the mother branch (55 against 3) and the figures for the branches standing on the outer side show

<sup>1</sup> The material is the same as that dealt with in the foregoing table, only the branches in which the direction of the spiral was changed at a short distance from the beginning of the spiral were here omitted.

<sup>2</sup> In one case only, where the divergence inwards from the transversal plane was very slight, the branch was reckoned among the biseriate branches.

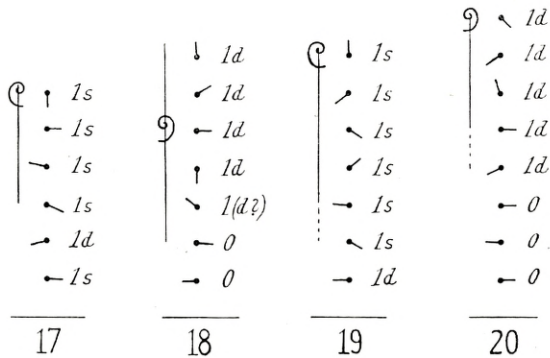
Table 3.

	A. The spiral begins with the <i>last</i> biseriate branch. The second branch in the spiral stands on the		B. The spiral begins with the penultimate biseriate branch.					C. The spiral in all cases reckoned from its first beginning. The 2nd branch in the spiral stands		
	outer side	inner side	outer side	inner side	on the outer side	on the inner side	transvers.	on the outer side	on the inner side	transvers.
1st joint										
2nd —	2	»	»	»	4	»	»	6	»	»
3rd —	8	1	»	4	4	»	2	12	1	2
4th —	<b>34</b>	1	»	6	<b>19</b>	»	1	<b>53</b>	1	1
5th —	8	1	»	<b>20</b>	4	»	1	12	1	1
6th —	2	»	»	5	2	»	»	4	»	»
7th —	1	»	1	1	»	»	»	1	»	»
	55	3	1	36	33	»	4	88	3	4

a very regular symmetrical distribution on the joints, with a very high maximum for the 4th joint. Two of the shoots in which the 2nd branch in the spiral stood on the inner side of the mother branch are represented in the diagrams 17—18. Shoot 17 would agree with the common rule, if the 4th branch were regarded as transversal although it is a little approached to the inner side; the spiral would then begin with the 5th branch, and the second branch in the spiral would then stand on the outer side. The same would be the case if the third branch in shoot 18 were reckoned among the biseriate ones.

In part B of the table, where the first step of the spiral is at the same time the last step in the biseriate arrangement, the distribution of the 2nd branch in the spiral is quite different according to whether the spiral is reckoned

from the last or from the penultimate of the biseriate branches. In both cases, the distribution is very regular and symmetrical on the joints with the maximum in the middle of the row, but in the first case, I, the 2nd branch of the spiral always, with one exception only, stands on the inner side of the mother branch, while in II in the great majority of cases it stood on the outer side of the mother branch and showed a distribution on the joints agreeing perfectly with that in A, with a high maximum on the 4th joint. In no cases did the second branch of the spiral stand on the inner



*Callithamnion tetragonum* var. *fruticulosum*. Lateral shoots.

side of the mother branch. In four cases it had a transversal position, but in all these cases the first step of the spiral was made on the outer side of the mother branch. If the spiral had turned in the opposite direction with the same angle of divergence, the branch in question would have been placed on the inner side (diagr. 19, 20). The agreement between B<sup>II</sup> and A in the the table, and the discrepancy between B<sup>I</sup> and A, speak much in favour of the assumption that the spiral must be reckoned from the first branch which can be included in it. In accordance with this assumption all the shoots have been recorded in section

C of the table which shows that in the great majority of the shoots the 2nd branch of the spiral stands on the outer side of the mother branch. The distribution on the joints shows an extraordinary regularity and symmetry on both sides of the 4th joint which represents a very high maximum. In all the shoots recorded in the first column of C the first step of the spiral took place on the outer side of the mother-branch, and the same holds good for the 4 shoots in which the second branch in the spiral had a transversal position (table C, last column), as stated above. Consequently, the number of shoots in which the first step of the spiral takes place on the outer side of the mother-branch amounts to 92. This is shown in table 4, where the shoots are arranged after the position of the first branch of the spiral; in four shoots only did the first step of the spiral turn towards

Table 4. Position of the first Branch of the Spiral.

	The first step of the spiral takes place on the	
	outer side	inner side
1st joint.....	5	
2nd — .....	14	2
3rd — .....	54	1
4th — .....	13	1
5th — .....	4	
6th — .....	1	
	91	4

the inner side. As mentioned above, two of these shoots might possibly be referable to the first column, in which case the number 91 would be increased to 93.

We may thus conclude that it is warranted to reckon the beginning of the spiral from the first branch which

can be included in it, also in those cases in which the first step of the spiral region coincides with the last step of the biseriate one. In accordance with this assumption we have found that the first step of the spiral in almost all cases takes place on the outer side of the mother branch. This may also be expressed in the following manner: when the first branch of the spiral stands on the left side of the mother-shoot, the spiral turns to the left; when the first branch of the spiral stands on the right side, the spiral turns to the right. This holds good for all the 88 shoots recorded in the first column of table 3 C.

The same was found on examining a slightly greater number of branches, some shoots with irregular arrangement of the lowermost branches being included. In 71 of 74 side-branches having a spiral turning to the left, the first branch in the spiral stood on the left side of the mother-branch, in 3 on the right side; and in 31 out of 34 shoots having a spiral turning to the right, the first branch in the spiral stood on the right side, in 3 on the left side.

It must be concluded from the foregoing that the side-branch, at the moment when the spiral arrangement commences, is influenced by a force issuing from the mother axis with the effect that the second branch in the spiral in the great majority of cases arises on the outer side of the mother-branch. It seems legitimate to conclude that it is the same factor which causes a tendency in the biseriate branches at the base of the mother branches to converge towards the outer side. It is evidently the same factor which in many Algæ makes the first lateral organs arise on the outer side of the branches, as shown by BERTHOLD (1882, p. 621) for several Floridææ. This effect reminds one of *exotrophy*, by which term WIESNER

(1892) designates the cases where the outer side of a lateral organ — or the outer leaves of a lateral shoot — is more strongly developed than the side turning towards the mother axis, (Ektauxese WEISSE 1895). As, in the cases here dealt with, it is a question not of a stronger development of the lateral organs standing on the outer side but of the formation of new organs on the outer side in preference to the inner side, it seems legitimate to give another name to this effect; it might be called *ectoblastesis*.

In the first branches of the II. order in *Call. tetragonum* the effect of this agent is however wanting or combined with the effect of one or two other agents, and this brings about a transversal, biseriate arrangement of the branches. The tendency to a biseriate ramification is more pronounced in other species of the genus (*C. Hookeri*, *polyspermum*), and it may also be so in the primary axis of *C. tetragonum*, as mentioned above; but in the lateral shoots it appears only in the first 1 to 6 branches, and the spiral arrangement usually begins in continuation of them. When ectoblastesis is active in the biseriate region, it will cause convergence of the branches towards the outer side. But at the moment when the biseriate arrangement ceases and the spiral arrangement begins, the effect of ectoblastesis will be that the second branch in the spiral will arise on the outer side of the mother branch and thus determine the direction of the spiral. When once the spiral arrangement is settled, the mother-axis has no longer any influence on the ramification of the branch.

There exists a very pronounced correlation between the direction of the spiral and the position of the first branch of the second order (1r<sup>II</sup>). When the spiral turns to the

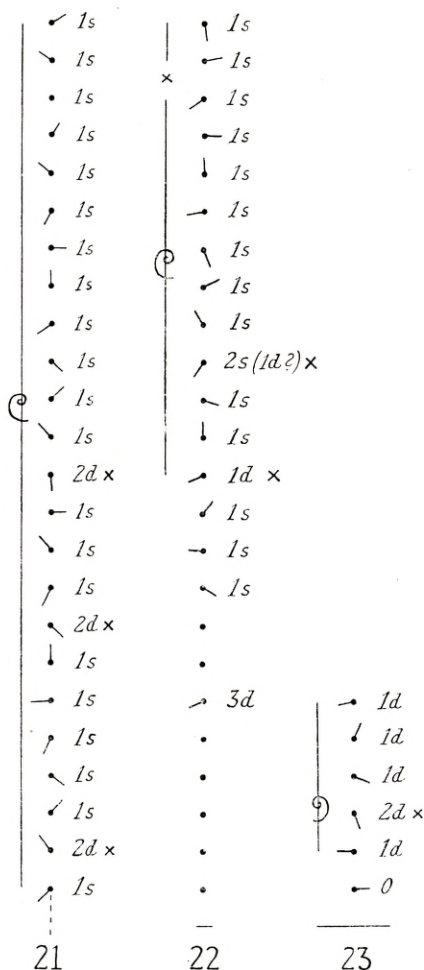
left, the  $1r^{II}$  stands on the right (seen from the outside) on the first joint of the branch; when the spiral turns to the right, it stands on the left side. Thus the  $1r^{II}$  always stands on the anodic side<sup>1</sup>. This rule is so fixed that only a small number of exceptions have been met with. In above 800 branches examined, only 19 exceptions were found within the regular spiral region, and 10 of these occurred at the beginning of the spiral, on the first or second branch in the spiral. In 6 of the 19 cases  $1r^{II}$  was placed on the cathodic side of the second joint, thus in the place where the second branch of the II. order would have been if  $1r^{II}$  had been placed on the anodic side of the first joint. These cases (diagr. 1, 21, three cases) may be interpreted to the effect that  $1r^{II}$  has not been developed, and that the branch on the second joint is really the  $2r^{II}$ . In four other cases (14, 7, 23), the  $1r^{II}$  was indeed standing on the anodic side of the branch, but on the second joint; the first joint seems in these cases to be virtually branchless. In 9 cases the  $1r^{II}$  stood on the cathodic side of the first joint; 3 of these cases occurred on the first branch in the spiral, 4 on the second branch, and 2 cases only at a greater distance from the beginning of the spiral (diagr. 13, 22), a very small number in proportion to the great number of shoots examined<sup>2</sup>.

As the exceptions have proved to be most frequent at the beginning of the spiral, I have, in the table 5, recorded the position of  $1r^{II}$  on the three first branches of the spiral

<sup>1</sup> It is remarkable that NÄGELI (1861, p. 344) states that the first branch of the second order in *Dorythamnion*, which also includes *Call. tetragonum*, is placed on the cathodic side of the branch.

<sup>2</sup> It must, however, be admitted that in a comparatively great number of shoots the position of the  $1r^{II}$  was only recorded to a short distance above the beginning of the spiral arrangement.

in all the branches examined where the spiral came directly after the biseriate region, and further the position



*Callithamnion tetragonum* var. *fruticulosa*. Three shoots, 22 the primary axis.

of 1r<sup>II</sup> on the last branch before the spiral, the designation being as if the branch had belonged to the spiral region. In the table, the shoots in which the spiral begins with the last of the biseriate branches, and those in which the spiral begins with the penultimate of the biseriate branches, are treated separately. The latter are treated in two different manners, in B as reckoning the spiral from the penultimate biseriate branch, in C as reckoning it from the last biseriate branch. The different numbers of 1r<sup>II</sup> on the different branches of the I. order are due to the fact that these branches were in several cases shed, or it was impossible to decide with certainty which of the rays in the pseudichotomous branch

was the main axis and which the branch; the latter cases are omitted.

The figures for the three first branches show a great



Table 5. Position of the 1r<sup>II</sup>.

Number of branch (r <sup>I</sup> ) in the spiral on which 1r <sup>II</sup> is recorded	A. The spiral begins with the last biseriata branch			The spiral begins with the penultimate of the biseriata branches					
				B. The spiral reckoned from the penultimate biseriata branch			C. The spiral reckoned from the last biseriata branch		
	anod.	kathod.	r <sup>I</sup> un-branched	anod.	kathod.	r <sup>I</sup> un-branched	anod.	kathod.	r <sup>I</sup> un-branched
on the 3rd branch I	43	1	1	19	0	1	18 <sup>2</sup>	0	0
- - 2nd —	35	2 <sup>1</sup>	2	12	2 <sup>1</sup>	5	19	0	0
- - 1st —	27	1	14	6	2	14	12	2 <sup>3</sup>	5
- - last branch before the spiral	3	11	31	2	2	13	6	1	14

*anod.* signifies that 1r<sup>II</sup> stands on the anodic side of the first joint.

<sup>1</sup> Further one case of 1r<sup>II</sup> standing on the anodic side of the 2nd joint.

<sup>2</sup> Including two cases of 1r<sup>II</sup> standing on the cathodic side of the first joint.

<sup>3</sup> Further one case of 1r<sup>II</sup> standing on the anodic side of the second joint.

preponderance for the anodic side in all the sections of the table, though diminishing towards the base; they show that the correlation exists from the first member of the spiral. The preponderance for the anodic side in the first branch of the spiral is very great in the shoots registered in A (27 : 1), still very remarkable in C (6 : 1), slightest in B (3 : 1) where the absolute figures are very small owing to the great number of unbranched branches. In the latter case the small numbers do not permit any certain conclusion as to the existence of the correlation: at all events they do not contradict it and are thus reconcilable with the assumption that the spiral may be reckoned from the first branch which can be included in it.

In table 6 all the shoots are treated collectively, in A so that the spiral is in all cases reckoned from the first branch which could be included in it, in B so that the spiral is reckoned from the last biseriata branch. The table shows that the correlation is present from the beginning

Table 6. Position of the  $1r^{II}$ .

Number of branch in the spiral	A. The spiral reckoned from the first branch which can be included in it				B. The spiral reckoned from the last biseriate branch			
	anod.	kathod.	anod. in %	$r^I$ un- branched	anod.	kathod.	anod. in %	$r^I$ un- branched
3rd branch . . . . .	62	1	98,4	2	61	1	98,4	1
2nd — . . . . .	47	4	92,2	7	54	2	96,4	2
1st — . . . . .	33	3	91,7	28	39	3	92,9	6
last branch before the spiral . . . . .	5	13	»	44	9	12	»	25

of the spiral, but that the constancy of the correlation is slightly diminished towards the base. For the 4th branch in the spiral the percentage for the anodic side would have been 100. The comparison of A and B in the table shows that there is no essential difference whether the spiral is reckoned from the first beginning or from the last biseriate branch.

The position of  $1r^{II}$  on the last branch before the spiral has been registered for the purpose of examining whether the tendency of  $1r^{II}$  to place itself on the anodic side of the branch in the spiral may possibly be present before the beginning of the spiral. As will be seen in the table, there is no trace of such a tendency. Owing to the small figures no importance can be attached to the slight preponderance for the cathodic side in the table.

In the cases where the spiral changed direction, this took place suddenly, as mentioned above, the last branch in the first spiral being at the same time the first branch in the spiral with the reverse direction. In all the seven cases where the position of  $1r^{II}$  was recorded, it was in correlation to the new direction of the spiral. In two cases the foregoing branch too had the same position (diagr. 6). In the

above-named shoot where a single step to the left occurred in a spiral which otherwise turned regularly to the right, the 1rII stood on the left in all branches, as if no disturbance of the spiral had taken place (diagr. 22).

2. *Callithamnion corymbosum* (Engl. Bot.) Lyngb.

The ramification of this well-known species has been briefly described by NÄGELI under the genus *Poecilothamnion* A. *Eupoecilothamnion* (1861, p. 359) and by KYLIN (1907, p. 165). The specimens examined by me were collected at Frederikshavn, in the harbour, and by Hatterbarn in the Samsø Waters at a depth of 15 meters.

The branches are usually, as shown by the above-named authors, arranged in a spiral beginning at a shorter or longer distance from the base, and continued without interruption to the top of the shoot. The spiral turns as frequently to the right as to the left. Out of 60 shoots 26 had a spiral turning to the left, 24 a spiral turning to the right, 3 had a spiral with changing direction and in 7 the branches were irregularly arranged. As to the frequency of antidromy in proportion to that of homodromy my observations are too few to draw any conclusion from; 20 cases of antidromy and 12 cases of homodromy were found.

The divergence varies about  $\frac{1}{4}$  of the circumference, usually between  $\frac{1}{3}$  and  $\frac{1}{5}$ , but sometimes exceeds these

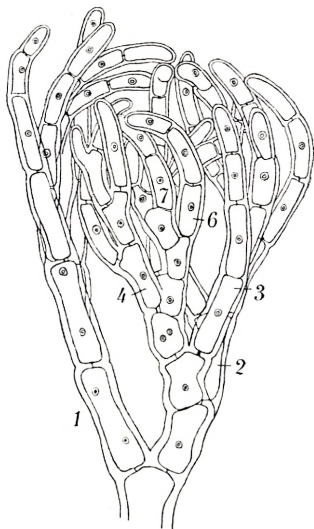


Fig. 2.  
*Callithamnion corymbosum*.  
Upper end of shoot of plant collected in December; the young branches are incurved over the top. 270 : 1.



limits, more especially the lower one. It varies in various shoots but also in the same shoot. If the average divergences of the single shoots are determined, values lying between the same limits are usually found. I have not found them greater than  $\frac{1}{3}$ ; on the other hand, average divergences of  $\frac{1}{6}$ ,  $\frac{1}{7}$  and  $\frac{1}{8}$  were found, each in one case, but only in shorter parts of shoots comprising only a single turn of the spiral. The divergences 0 and  $\frac{1}{2}$  do not, so to speak, occur within the spiral region. The divergence 0 was only observed once<sup>1</sup>, namely in the shoot 25, where the divergences before and after the divergence in question were proportionally small. A divergence of exactly  $180^\circ$  was not met with within the spiral region, but in one shoot (27) a divergence a little greater than  $180^\circ$  was met with in a spiral otherwise turning regularly to the left. The interpretation of this divergence as an unusually great step in the spiral turning to the left is supported by the fact that the 1r<sup>II</sup> had the same position on the branch coming after this angle of divergence as in the other branches (cp. below). A similar deviation was observed in another shoot where the spiral turning to the right was interrupted by a single step to the left or, in other words, by a divergence of about  $200^\circ$  to the right<sup>2</sup>.

As mentioned above, the spiral changed direction in 3 shoots. The number of shoots with changing direction of the spiral was, however, strictly speaking, somewhat greater, the spiral being preceded in a number of shoots by a short region with an irregular position of the branches, which could be interpreted as being composed of one, two or more short parts

<sup>1</sup> Besides shoot 30 mentioned below.

<sup>2</sup> The interpretation of this shoot is more uncertain, as the direction of the spiral had changed 4 joints under this angle of divergence and as the position of 1r<sup>II</sup> had not been recorded.



one shoot the interruption extended over no less than 14 joints all bearing the branch on the same side (diagr. 30).

Interruption of the spiral without subsequent change of direction of the spiral was observed, besides in the two shoots mentioned above, in a primary shoot where the interruption comprised three joints with two divergences of  $180^\circ$  and one in the reverse direction of the spiral (or  $200^\circ$  in the direction of the spiral (diagr. 31)).

Within the spiral region, each joint bears a branch; only three cases were recorded where a joint was branchless. In shoot 32, a branch is wanting on the 6th joint from the top, where a branch on the outer side of the shoot would fit into the spiral. In two other cases, 33 and 25, it was doubtful whether a member of the spiral was wanting or not. Below the spiral region branchless joints occur more frequently, in particular at the base of the primary shoots. On the branches, the ramification begins from the very base; only exceptionally is the first joint branchless. In very rare cases I have found two branches on the same joint, one more slender than the other and probably formed later (diagr. 24).

As shown by NÄGELI, the first branch of a lateral shoot has always a lateral position (on the right or on the left); I have however met with no less than four shoots in which its position was not transversal but median or nearly so, in the three cases on the outer side, in the fourth on the inner side of the shoot. The following two or even three branches have, as a rule, also a transversal position, being alternate, biseriate, as formerly shown by KYLIN (1907, p. 165). There is no general tendency to a deviation from the transversal position towards the outer side of the shoot as ascertained in *Call. tetragonum*.

The spiral arrangement in the lateral shoots may come immediately after the alternate, biseriate branches, but in several cases it is separated from these branches by a number of irregularly placed branches. When it was examined whether the second branch in the spiral region was standing on the outer or the inner side of the shoot, only the shoots with a regular spiral arrangement, without change in the direction of the spiral at the base, were taken into consideration. In all the (13) shoots where the spiral followed in immediate continuation of the biseriate region, the second branch in the spiral stood on the outer side of the shoot. In the shoots where the spiral came after a region with irregularly arranged branches, the second branch in the spiral in 8 cases stood on the outer side of the shoot, in 3 cases on the inner side, and in 4 cases it had a transversal position. The direction of the spiral is thus most frequently, at all events in the cases where the spiral comes immediately after the biseriate region, determined by the second branch in the spiral being placed on the outer side of the shoot. In agreement with this it was found that the first branch of the spiral stood on the right side of the shoot in all the 11 lateral shoots examined in which the spiral turned to the right. In the 9 shoots examined in which the spiral turned to the left, the first branch in the spiral stood on the left in 7 cases, on the right in 2 cases.

The first branch of the II. order ( $1r^{II}$ ) is almost always placed on the anodic side of the first joint, within the regular spiral region, as will be seen in the diagrams, and in table 7, which shows the position of  $1r^{II}$  in all the shoots examined with the exception of five with irregularly arranged branches and two which will be mentioned later. Only in 3 shoots out of 21 was the  $1r^{II}$  found on the



Table 7. Position of 1r<sup>II</sup> in the Branches of the Spiral and under the Spiral, the latter in Brackets.

	anodic side		kathodic side	
1st joint.....	<b>213</b>	(17)	<b>4</b>	(7)
2nd — .....	<b>0</b>	(2)	<b>10</b>	(2)

kathodic side of the first joint of the branch, altogether only in 4 cases, while, in 213 cases it stood on the anodic side of the first joint. In 10 cases only it was placed on the second joint and then always on the kathodic side. There is thus a very marked correlation between the direction of the spiral and the position of the 1r<sup>II</sup>, and moreover a remarkable alternation according as the 1r<sup>II</sup> stands on the first or on the second joint. In very few cases only did the 1r<sup>II</sup> occur on the 3rd joint, and no correlation to the direction of the spiral on the mother shoot could then be perceived. As to the 4 cases of 1r<sup>II</sup> occurring on the kathodic side of the first joint it could be observed that two of them occurred on a shoot with procarps, a circumstance which might probably influence the correlation in question, as the procarps are developed very early. The two other cases occurred in the first and the second branches of the spiral respectively.

In table 7 the 1r<sup>II</sup> occurring below the spiral region are further recorded in brackets in the columns where they would have been put down if the branches on which they were standing had belonged to the spiral region. The table shows that the 1r<sup>II</sup> was placed on the “anodic” side of the first joint in 17 cases, in 7 cases on the “kathodic” side. These figures are rather small, they suggest, however, that the tendency of 1r<sup>II</sup> to be placed on the anodic side of the

branches within the spiral may be present, though in slight degree, before the spiral is established. When only the last branch before the spiral is taken into account, the following figures are obtained:  $1r^{II}$  was placed on the anodic side of the first joint in 4 cases, on the cathodic in 1 case, further in 1 case on the anodic and in 1 case on the cathodic side of the second joint. Here, too, there is a preponderance for the anodic side, but the figures are too small to allow of any certain conclusion.

In this connection it is interesting to consider an aberrant shoot represented in diagr. 30. It is a branch beginning with a branchless joint followed by 7 joints bearing branches arranged in a spiral turning to the left. On these branches, the  $1r^{II}$  was placed on the cathodic side in 6 cases, thereof in 4 on the first joint, in disagreement with the prevailing correlation. After the spiral followed no less than 13 superposed branches, all with  $1r^{II}$  standing on the left, after which the branches were arranged in a spiral turning to the right, likewise with  $1r^{II}$  standing on the left side, which is here the anodic one. Apparently the position of  $1r^{II}$  was here fixed long before the spiral turning to the right, with which it must be supposed to be in correlation.

In the shoots having irregularly arranged branches the  $1r^{II}$  occurred with almost equal frequency on the left and on the right side of the branches (diagr. 28).

### 3. *Seirospora Griffithsiana* Harvey.

This species has been examined by NÄGELI (1861, p. 364) who found that the branches are arranged in a spiral with rather variable angles of divergence. The material serving for this investigation originates from the following localities, all situated in the Northern Kattegat: Frederikshavn (No.

6361  $\frac{27}{7}$  1896) and 8635  $\frac{11}{7}$  1919), Tønneberg Banke (No. 5359  $\frac{27}{9}$  1894) and Herthas Flak (No. 6370  $\frac{29}{7}$  1896, 26 meters depth).

In 59 of the 61 shoots examined the branches were arranged in a spiral, in one case with a change in the direction of the spiral (diagr. 42); only two shoots had irregularly arranged branches, but as these shoots, or the parts examined, were short, they would possibly have turned out to have spiral arrangement of the branches too. The spiral arrangement begins at a shorter or longer distance from the base and continues undisturbed to the top; in four of the shoots, however, it was interrupted by a shorter or longer piece with irregularly placed branches.

The divergences vary between  $\frac{1}{5}$  and  $\frac{1}{3}$ , most frequently between  $\frac{1}{4}$  and  $\frac{1}{3}$ . They rarely exceed these limits, thus approaching  $0^\circ$  and  $180^\circ$  respectively. These values are never reached in the spiral region, but a divergence of  $180^\circ$  frequently occurs out of it, at the base of the branches and in the above-named interruptions. Just as the angle of divergence varies on the same shoot, so the average divergence for the single shoots may be rather different. The following average divergences were determined for 11 shoots:  $\frac{1}{4}$  ( $90^\circ$ ),  $\frac{3}{11}$  (c.  $98^\circ$ ),  $\frac{5}{18}$  ( $100^\circ$ ),  $\frac{2}{7}$  (c.  $103^\circ$ ),  $\frac{3}{10}$  ( $108^\circ$ ),  $\frac{1}{3}$  ( $120^\circ$ ).

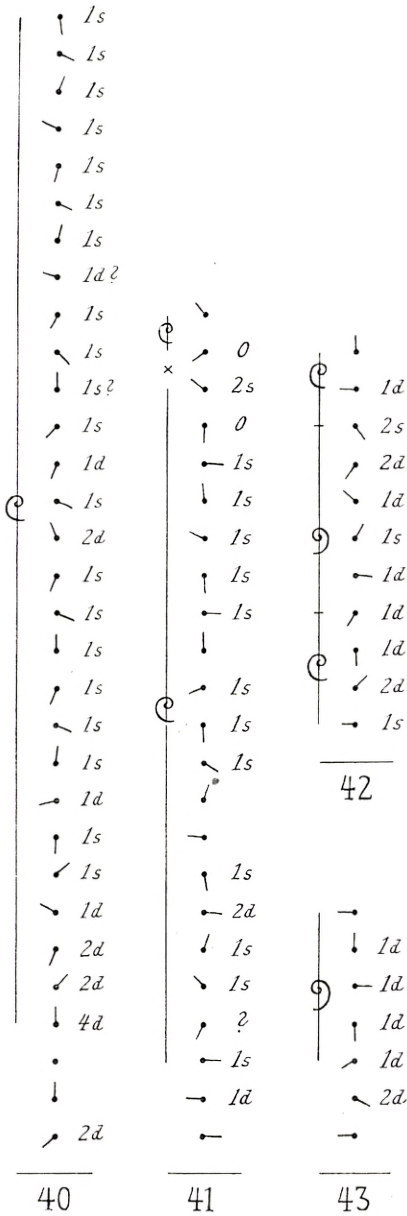
As a rule, each joint bears a branch within the spiral region. A small number of branchless joints were, however, met with. In most of the cases a member of the spiral was just missing on the joint in question (diagr. 35, 36). As regards shoot 36, it is so at any rate for the uppermost branchless joint. Nearer the base two consecutive joints (nos. 12 and 13 from the base) are branchless, and two branches also seem to be missing here, one on the right and



inwards on the 12th joint, and one on the left and inwards on the 13th joint. At a higher level two consecutive joints are likewise branchless, but only one branch is here missing which probably should have been placed on the lowermost (16th) joint inwards. The two following joints were short and the lowermost of them did not seem able to produce a branch; the two joints had the appearance of constituting a unity, one internode. Two branchless joints in another shoot which were both shorter than the others must be understood in the same manner as being virtually branchless. There are thus two kinds of branchless joints, 1) virtually branch-bearing and 2) virtually branchless, the latter being shorter than the usual ones.

The ramification of the branches may begin from the very base, or the first joints may be branchless. The number of the branchless joints is most frequently 1, more rarely 2, still more rarely 3 or more. The specimens from the different localities were different in this respect. From the gathering No. 5359 two specimens were examined; in one, the first branch of the II. order was in the great majority of cases placed on the first joint within the spiral region, and this was also the case with the specimens from Herthas Flak; but in the other specimen from No. 5359, and in all the specimens from Frederikshavn, the  $1r^{II}$  were mostly placed on the second joint, much more rarely on the third or the first joint (cp. table 11). The position of the  $1r^{II}$  is generally the same below the spiral region, except that the first branches of the I. order are sometimes unbranched.

The spiral in all the (45) shoots examined in the specimens from Frederikshavn and Tønneberg Banke turned to the left; in three shoots from Frederikshavn and in one from Tønneberg Banke, the spiral was, however, interrupted



*Seirospora Griffithsiana*. From Herthas Flak.

over a shorter or longer distance by irregular arrangement of the branches. The specimen from Herthas Flak differed strangely in this respect. Only 4 of 16 examined shoots had a spiral turning to the left; in 9 it turned to the right, one had a spiral with changing direction<sup>1</sup> and 2 had irregularly arranged branches. The first-named shoots are, as a natural consequence, homodromous, whereby it may be observed that, in the specimens from Frederikshavn, the direction of the spiral was determined in 4 generations of shoots of the same plant. In the specimens from Herthas Flak 2 cases of homodromy and 3 of antidromy were observed. Where the spiral was interrupted by a stretch with irregular position of the branches, a divergence of 180° was usually very fre-

<sup>1</sup> In one shoot with otherwise regular spiral turning to the right (diagr. 41) one step in the reverse direction occurred.

quent and the branches therefore largely biseriate. One part of such a stretch could certainly be regarded as a part of the spiral if the divergences of  $180^\circ$  were included in the spiral, but some of the divergences could not be included in the spiral turning to the left (diagr. 37). It is remarkable that in all the shoots in question the spiral turned in the same direction after the interruption as before. In shoot 42, where the spiral twice changed direction, the change was in both cases sudden, the last branch of the first spiral being at the same time the first of the spiral turning in the opposite direction.

The first branch in the lateral shoots is always transversal, as stated by NÄGELI (1861, p. 364), either diverging exactly  $90^\circ$  from the median plane or a little approached to the outer side; it is usually followed by one or more transversal, alternate, and thus biseriate branches. These branches may be exactly transversal or more or less deviating from the transversal plane, frequently outwards but also not rarely inwards; at all events no marked tendency towards the outer side could be demonstrated. The number of biseriate branches varied from 1 to 6<sup>1</sup>. In most cases the spiral arrangement began in immediate continuation of the biseriate arrangement, so that the last biseriate branch was at the same time the first branch in the spiral (diagr. 34), or the spiral began with the penultimate biseriate branch (diagr. 35). In other cases the spiral arrangement was separated from the biseriate region by a short stretch with irregularly arranged branches (diagr. 37). The number of such irregularly placed branches was usually only 2 or 1.

<sup>1</sup> In one shoot (diagr. 38) 5 biseriate branches arranged in an oblique plane not diverging much from the median plane were present.

The first step in the spiral most frequently takes place towards the outer side of the mother branch. Reckoning the beginning of the spiral in all cases from the first branch which can be included in it, the following figures were obtained:

Table 8. Numbers of Lateral Shoots in which the Second Branch in the Spiral was placed on

the outer side	the inner side	transversally
22	7	4

The table shows a considerable preponderance for the outer side of the mother branch. In 3 of the 4 shoots, where the second branch of the spiral had a transversal position, the first step of the spiral was directed towards the outer side of the branch, in the fourth towards the inner side. But also in 2 of the 7 shoots recorded under the second head, the first step of the spiral was directed towards the outer side of the mother branch, the second branch in the spiral being in both cases nearly transversal, only slightly approached to the inner side. Thus, the first step of the spiral was directed towards the outer side in **27** shoots, towards the inner side in **6** shoots only. This is in accordance with the figures obtained when we register the direction of the spiral on the shoots according to the position of the first branch in the spiral on the left or the right side respectively. As shown in Table 9, the first branch in the spiral stood three times as often on the left as on the right side, and then the spiral in the great majority of cases turned to the left. In the eight cases where it stood on the right side, the spiral turned with equal frequency to the right and to the left.



Table 9.

First branch of the spiral on the left side of the mother branch. The spiral turns to the		First branch of the spiral on the right side of the mother branch. The spiral turns to the		First branch of the spiral on the inner side
left	right	right	left	
22 shoots	2 shoots	4 shoots	4 shoots	1 shoot

The second branch of the spiral occurred on the second to the eighth joint of the mother branch.

In all the specimens examined a very distinct correlation between the direction of the spiral and the position of the first branch of the second order was ascertained, but remark-

Table 10.

Locality	Position of 1 r II on the		
	kathodic side	anodic side	
No. 6361. Frederikshavn			
1st joint.....	0	2	
2nd — .....	25	206	
3rd — .....	59	12	
4th — .....	2	8	
No. 8635. Frederikshavn			
1st joint.....	3	3	
2nd — .....	3	16	
3rd — .....	1	1	
No. 5359. Tønneberg Banke			
a) 1st joint.....	63	2	} kathodic anodic side side
2nd — .....	2	8	
b) 1st joint.....	4	1	
2nd — .....	6	44	} 1st joint. 67 3
3rd — .....	13	2	} 2nd — 8 52
			} 3rd — 13 2
No 6370. Herthas Flak			
1st joint.....	5	98	
2nd — .....	4	1	

able differences appeared between some of the specimens, as shown in table 10 where the specimens from the different gatherings are treated separately. In one case there were differences even between two specimens from the same gathering.

In considering this table, to begin with, we disregard the specimen from Herthas Flak. The plants from the other localities show a very remarkable alternation manifesting itself in the fact that, when most of the 1r<sup>II</sup> stand on the first joint of the branch the great majority of them stand on the kathodic side (5359 a); when most of them occur on the second joint, the great majority are placed on the anodic side (6361), and when a considerable number occurs on the third joint, most of them are placed on the kathodic side, and finally, No. 6361 shows even a preponderance for the anodic side of the 4th joint. Only when the figures are very small there is no remarkable alternation, as in the 3rd joint in No. 8635 and in the first joint in Nos. 6163 and 8635. Further, it will be seen that Nos. 6361, 8635 and 5359b essentially agree with each other. In all these shoots the 1r<sup>II</sup> was for the most part placed on the second joint and then in the great majority of cases on the anodic side. When these shoots are combined we obtain the following figures:

Table 11.

	Position of 1r <sup>II</sup> on the	
	kathodic side	anodic side
1st joint . . . . .	7	6
2nd — . . . . .	34	<b>266</b>
3rd — . . . . .	<b>73</b>	15
4th — . . . . .	2	8

The table shows a very marked alternation for the 2nd to the fourth joint. No. 5359 a differs from the others by the 1rII being mostly placed on the first joint and almost all on the anodic side. On the 2nd joint, however, the majority of the 1rII stand on the anodic side, and the shoots thus agree with those just mentioned. When this plant is combined with the others, the following figures are obtained.

Table 12.

	Position of 1rII on the		Relation between the highest and lowest number
	kathodic side	anodic side	
1st joint . . . . .	<b>70</b>	8	8,8
2nd — . . . . .	36	<b>274</b>	7,6
3rd — . . . . .	<b>73</b>	15	4,9
4th — . . . . .	2	<b>8</b>	4,0

The alternation here is even more distinct than in the foregoing table and extends also to the first joint, and this confirms our right to treat these plants together. The table shows that the 1rII occurs most frequently on the second joint, with the least frequency on the 4th joint. And further it shows at once very clearly the above-mentioned alternation in the occurrence of the 1rII on the first four joints. The last column shows that the preponderance for either the kathodic or the anodic side decreases with the increasing distance from the base. Thus there evidently exists an interference between an influence from the mother shoot on the branch and a tendency in this to an alternate, biseriata ramification at the base. It may be assumed that the mother axis, through the spiral arrangement of its branches, influences the young bran-

ches with the effect that the first joint becomes disposed to produce a branch of the II. order on the kathodic side. When this branch is not developed it must be supposed that the young branch has been thus influenced that the position of the branch on the second joint in the great majority of cases will be the same as if the branch on the first joint had been developed, and as a consequence of the tendency to an alternate, biseriata ramification it will then

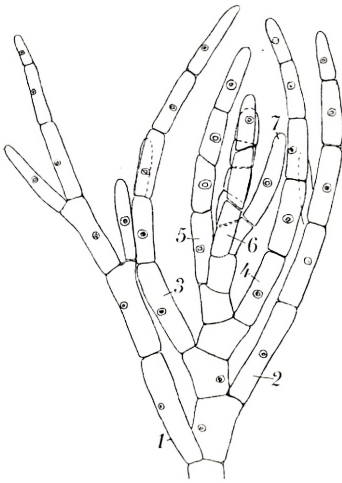


Fig. 3.  
*Seirospora Griffithsiana*. Upper  
end of shoot, from Frederiks-  
havn (6361). 300 : 1.

appear on the opposite, i.e. the anodic side. In a similar manner it may be explained that the 1rII occurs in most cases on the kathodic side of the 3rd joint and on the anodic side of the 4th joint when the two, resp. three first joints are branchless. This assumption is not a mere surmise but it is supported by the observation that the transversal walls in the young branches are oblique and alternate, not only between the branch-bearing segments, but also between the first usually branchless segments, and the first segment wall has then its highest point on the kathodic side (cp. fig. 3). This orientation of the first wall must be due to an influence from the mother shoot, but the effect of this influence upon the orientation of the first branch of the second order only appears later, and it is dependent on the number of the segment on which the first branch arises. The decreasing constancy of the correlation with increasing distance from the base is pro-

appear on the opposite, i.e. the anodic side. In a similar manner it may be explained that the 1rII occurs in most cases on the kathodic side of the 3rd joint and on the anodic side of the 4th joint when the two, resp. three first joints are branchless. This assumption is not a mere surmise but it is supported by the observation that the transversal walls in the young branches are oblique and alternate, not only between the branch-bearing segments, but also between the first usually branchless segments, and

bably due to a decreasing regularity of the alternation of the oblique walls.

The specimen from Herthas Flak differed from the plants hitherto mentioned by having the 1r<sup>II</sup> in the great majority of cases on the anodic side of the first joint; the comparatively few 1r<sup>II</sup> occurring on the second joint in most cases stood on the cathodic side. An alternation was thus perceivable here too, but the orientation was the reverse of that in the other specimens. As mentioned above, the specimen from Herthas Flak differed by the spiral turning now to the right, now to the left, but there was no difference as to the position of 1r<sup>II</sup> between the shoots with the spiral turning to the right and those turning to the left.

In order to ascertain the moment of the origin of the correlation and the degree of its constancy at the base of the spiral region, the position of the 1r<sup>II</sup> was determined in the first four branches in the spiral and in the last branch before the spiral in all the lateral shoots examined, and the number of cases in which the position of the 1r<sup>II</sup> was the same as or the reverse of that of the majority in the spiral region was determined. As shown in table 13, it must be taken for granted that the correlation is present

Table 13. Position of 1r<sup>II</sup>.

	as in the majority of cases in the spiral	the reverse
on the 4th branch of the spiral . . . . .	19	4
— 3rd — - — . . . . .	15	9
— 2nd — - — . . . . .	13	7
— 1st — - — . . . . .	17	5
— last branch before the spiral . . .	7	11

from the beginning of the spiral, but the degree of constancy is much diminished in the three first members of the spiral. In the 4th branch it approaches the average frequency in the spiral region (cp. table 11). The table further shows that, in the last branch before the spiral, there is no tendency to the same position of  $1r^{\text{II}}$  as in the spiral region.

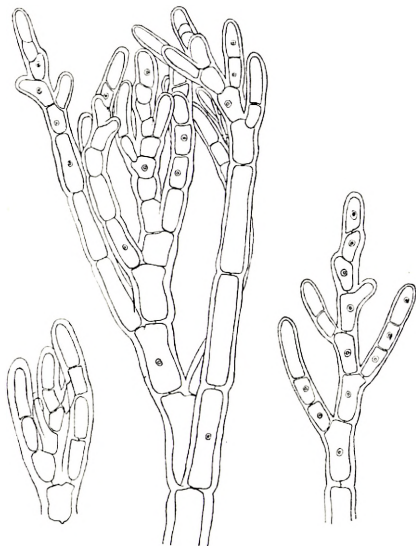


Fig. 4.

*Callithamnion roseum*. Upper ends of shoots; in that on the left the spiral turns to the right, in the middlemost to the left, in that on the right the branches are biseriata. 290 : 1.

#### 4. *Callithamnion roseum* Harvey.

The specimens examined were all collected in the harbour of Frederikshavn. It is doubtful whether our species is identical with that mentioned by NÄGELI under the same name (1861, pp. 329—335). My specimens quite agree with HARVEY'S description and figures (1849, Plate 230).

In all the long shoots examined a spiral arrangement of the branches was met with, at all events in the upper part of the shoots. The first joint of a branch is always branchless (one exception only was observed among about 770 branches examined), and the same is frequently the case with one or more of the following joints. The number of such branchless joints is greatest in the feebler shoots, and the lowermost branches of the second order, which have a limited growth, are usually entirely branchless though

composed of a considerable number of cells. The first joints of the primary axes too are branchless.

The spiral arrangement never begins from the very base of the shoot. The first branches on a lateral long shoot are usually irregularly arranged; however, they are not rarely partly alternate, biseriate in one plane, and this plane may be transversal, but it is by no means always so; in very few cases only the first branches were regularly biseriate and transversal (diagr. 48). The number of branches not arranged in a spiral below the spiral region varies from 1 to 16. As further branchless joints occur, not only at the base but also frequently between the not spirally arranged branches, the first member of the spiral is usually situated at a considerable distance from the base, namely on a joint the number of which, counted from the base, varies between 3 and 22 (average 13.5).

As the spiral arrangement begins at a rather great distance from the base on the lateral shoots, an influence of the mother shoot on the direction of the spiral in the branch was a priori little probable, and this was also confirmed by examination of the position of the second branch in the spiral in relation to the mother axis: in 8 cases it was placed on the outer side, in 12 cases on the inner side of the branch, and in 4 cases it had a transversal position.

Within the spiral region each joint usually bears a branch. Sometimes, however, a single branchless joint occurs or, more rarely, two consecutively. In some cases the absence of a branch does not cause any disturbance in the spiral arrangement, this continuing as if there had been one, not two joints between the two consecutive branches. In other cases a branch in the spiral is missing just in the branch-





less joint. This is for instance quite evident in shoot 48, ( $\times$  above), while other cases are doubtful in this respect (diagr. 48  $\times$  below).

In a few cases the spiral region was interrupted by short stretches with irregular arrangement of the branches, but continued after the interruption with the same regularity and with the same direction as before. Branchless joints may occur in such stretches, and superposed branches were observed too.

The spiral may turn to the left or to the right. Out of 33 shoots examined 17 had a spiral turning to the left, 11 to the right and 5 had changing direction of the spiral. Homodromy and antidromy occur with equal frequency. Of 23 branches, 12 were homodromous, 11 antidromous with the mother shoot.

The angle of divergence is rather variable, as a rule most constant on the upper part of the long shoots where it is often rather exactly  $\frac{1}{4}$  of the circumference, while it otherwise varies from  $\frac{1}{5}$  or less to  $\frac{1}{8}$ . The average divergence was determined in eight shoots as varying from  $67^{\circ}\frac{1}{2}$  to  $106^{\circ}$ , in most cases under  $90^{\circ}$ . Very small angles of divergence were found in several cases, even the divergence 0 was met with; more seldom occurred divergences approaching to  $180^{\circ}$ . On the whole the divergence is less variable than in the related *Call. Furcellariae*.

In all the five shoots presenting a change of the direction of the spiral this took place suddenly, the last branch in the first spiral being at the same time the first in the spiral with opposite direction. It was so at any rate in the four shoots (diagr. 45, 46), in the fifth (diagr. 47) the change in direction took place through an angle of divergence of  $180^{\circ}$  between the last branch of the first spiral and the first branch of the spiral in the opposite direction. In the other

shoots the divergences next to (before and after) the turning point were greater than the average divergences, namely  $120^\circ$ — $160^\circ$ ; only one of the adjacent angles of divergence measured only  $100^\circ$ .

In order to examine whether there might be any correlation between the position of the 1 r<sup>II</sup> and the direction of the spiral on the mother shoot, I have noted for all the 21 shoots examined whether the 1 r<sup>II</sup> was placed on the cathodic or on the anodic side of the branch, and classed them after the number of the joint on which it was placed. Only some examples are given here:

Table 14. Position of 1 r<sup>II</sup>.

	1. Nr. 6281		2. Nr. 8581		3. Nr. 8581		4. Nr. 8581		All the shoots	
	kath.	anod.	kath.	anod.	kath.	anod.	kath.	anod.	kath.	anod.
1st joint. .	0	1	0	0	0	0	0	0	0	1
2nd — ..	0	2	3	0	1	7	4	7	36	52
3rd — ..	7	11	8	3	5	7	4	5	84	79
4th — ..	6	2	7	4	5	10	4	1	67	57
5th — ..	8	9	»	»	2	1	0	1	17	25
6th — ..	5	5	»	»	2	1	0	1	12	12
7th — ..	4	2	»	»	»	»	»	»	4	2
	30	32	18	7	15	26	12	15	220	228

The last column, which gives the aggregate amounts for all the shoots examined, shows that the total amounts for the cathodic and the anodic side are alike, and the figures for the single shoots are either almost alike or slightly different. The greatest differences occur in the 2nd and the 5th joint where there is a preponderance for the anodic side of scarcely 50 per cent. The total amounts for the single shoots show almost equal figures in more than half of the cases, in other cases predominance for the anodic or the cathodic

side (cp. table 14, 2, 3). The figures for the single shoots give no evidence of any regularity. There is no trace of an alternation like that demonstrated in the foregoing species. It must thus be concluded that there is no obvious correlation between the direction of the spiral and the position of the first branch of the II. order. The preponderance for the anodic side in the second joint only may perhaps be regarded as the outcome of a correlation analogous to that in *Seirospora Griffithsiana*.

##### 5. *Callithamnion Furcellariæ* J. Agardh.

The ramification of this species, which is related to *Call. byssoides* (Arnott), has been described by KYLIN (1907, p. 167) who found that the branches of the main axes are arranged in a spiral with divergences of  $90^\circ$ . The lowermost branches of the lateral shoots, usually 3—5, sometimes up to 7, are biseriate, placed on the right and the left, while the following branches are arranged in a spiral. In the upper parts of the long shoots the divergences may vary from  $\frac{1}{3}$  to  $\frac{1}{2}$ . The shoots with limited growth ("Kurztriebe") have biseriate branches placed on the right and left. On examining several plants from various localities in the Danish waters I have found that the ramification is more variable than stated by KYLIN in specimens from the western coast of Sweden, not only in specimens from different localities, but also in different specimens from the same locality and in different shoots in the same specimen. The specimens examined originated from the following localities: 1) Harbour of Frederikshavn July 1899. 2) No. 7516, near Fladens lightship, eastern Kattegat 22.5 meters depth, July 1904. 3) No. 4974, near Ostindiefarer Grund, southern Kattegat, 15 meters depth, July 1894. 4) No. 7380, near Hatterbarn, east of

Samsø, June 1904, 15 meters. 5) Fænø Sund, Lille Belt, June 1891. 6) No. 6939, near Salthammer reef, east of Bornholm, 24.5 meters, July 1901.

In the 42 shoots examined the arrangement of the branches was the following:

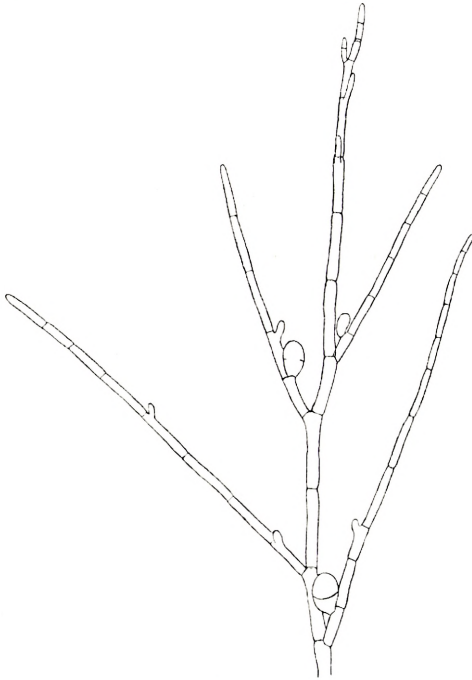


Fig. 5.

*Callithamnion Furcellariae*. Upper end of plant from Fænø Sund, with irregularly arranged branches and dispores. 70 : 1.

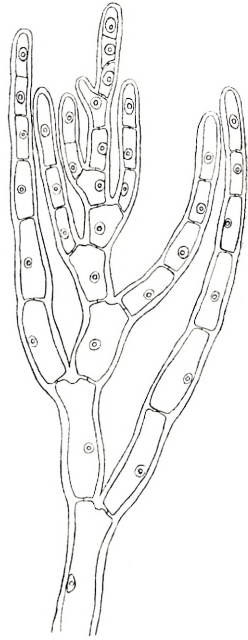


Fig. 6.

*Callithamnion Furcellariae*. Upper end of plant from Bornholm, with biserially arranged branches. 270 : 1.

In 11 shoots the branches were arranged in a spiral turning to the left,

in 11 in a spiral turning to the right (besides two shoots mentioned below which had the branches arranged in a spiral over a short stretch but otherwise the branches irregularly arranged or biserially),

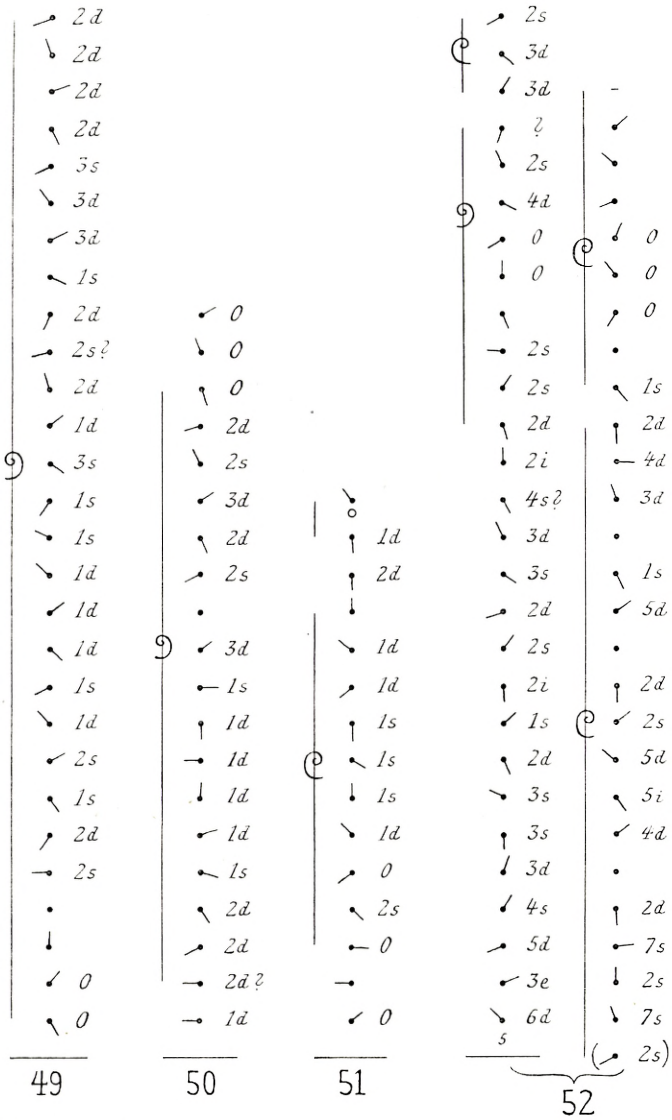
in 8 the direction of the spiral was changing,

in 10 the arrangement was irregular, in one, however, the branches were arranged in a spiral turning to the right over a short stretch,

in 2 the arrangement of the branches was chiefly biseriate, in one shoot, however, over a short stretch in a spiral turning to the right.

The spiral arrangement may, though very rarely, begin at the very base of the lateral shoots (diagr. 49), but as a rule it is preceded by a number, sometimes by a considerable number, of branches having no spiral but a more or less irregular arrangement, sometimes partly alternate and biseriate in a transversal or oblique plane, and superposed branches occur too. In one case only, all the three branches before the spiral were alternate in the transversal plane (diagr. 51). The cases described by KYLIN are thus exceptions in the Danish specimens. The number of joints below the first member in the spiral varies from 1 to 15. The position of the first branch of the II. order in relation to the mother shoot is not fixed; it may be transversal but it has often another position (on the outer or inner side or oblique, cp. diagr. 49—52). In rare cases the spiral region was succeeded in the upper part of the shoot by irregularly arranged or biseriate branches.

As a rule each joint bears a branch, and the ramification in most cases begins from the first joint of the branch; now and then, however, it happens that the first joint in a branch is branchless, and in the specimens from Bornholm several joints were branchless at the base of the branches and at higher levels. When a joint is passed over within the spiral region, it may occur that the following branch has the same position as it would have taken up



*Callithamnion Furcellariae*. 52 from Frederikshavn, 49 and 51 from Fladen, 50 from a place near Ostindiefarer Grund.

if it had been separated from the foregoing branch by one instead of two joints (diagr. 49?). In several other cases a

branch of the spiral is missing just on the branchless joint (diagr. 50 joint 12; diagr. 52 joints 37, 43, 46, while joint 51 comes under the first category).

It not rarely occurs that a joint bears two branches standing at the same level at the upper end of the cell and diverging from one another at an angle of a little over or a little under  $90^\circ$ . One of these branches is usually greater than the other and undoubtedly the oldest, and it enters into the spiral (diagr. 54, 56).

As mentioned above, the spiral arrangement occurred only in about three-fourths of the examined shoots. The plants from the different localities presented differences in this respect. Thus, all the 7 shoots from Fladen had the branches arranged in a spiral, and likewise the 5 branches from Frederikshavn and the 3 from Hatterbarn. Of the 20 shoots from Ostindiefarer Grund, 12 had spirally arranged and 8 irregularly arranged branches. Of 4 shoots from Fænø Sund, 3 had spiral arrangement of the branches, in the two, however, continued by irregularly arranged branches, and one had irregularly arranged branches in its whole length and several branchless joints. Finally, of 3 long shoots from Bornholm, 2 had spiral arrangement only over one or two short stretches, for the rest irregular or biseriata arrangement, and the third had almost regular biseriata arrangement.

The angle of divergence is very changeable within the spiral region, it varies between  $0^\circ$  and  $180^\circ$  in the various shoots and even in the same shoot. The average divergence was determined in 7 shoots and found to be varying from  $67^\circ$  to  $131^\circ$ . The divergence 0 was met with 6 times within a spiral otherwise undisturbed (diagr. 53 joints 20—21). Still more frequently one or even two or







irregular arrangement of the branches, including also divergences of  $180^\circ$  and  $0^\circ$  (diagr. 54). In one shoot the spiral changed twice. No general statement can thus be made on the change of direction of the spiral; the divergences next to the turning point were, however, in several cases great, approaching to  $180^\circ$ .

As to the relation between the mother shoots and their branches it was ascertained that homodromy and antidromy both occur, and that shoots with branches arranged in a spiral may bear branches with irregular arrangement of the branches and vice-versa.

As shown in table 15, the first branch of the second order in most cases stood on the first joint in the specimens from three localities, most constantly in the specimens from Ostindiefarer Grund. In the specimens from Frederikshavn it stood on the second joint in one half of the branches; in the specimens from Fænø Sund the maximum came on the third joint, and in the specimens from Bornholm, where the distance from the base was very variable, the greatest number came on the sixth joint.

Table 15. Position of the 1rII.

	Specimens from					
	Ostindiefarer Grund. 4974	Hatterbarn 7380	Fladen 7516	Frederikshavn	Fænø Sund	Bornholm 6939
On the 1st joint	<b>263</b>	<b>44</b>	<b>56</b>	9	3	0
— 2nd —	76	26	50	<b>70</b>	8	5
— 3rd —	21	12	16	32	<b>12</b>	5
— 4th —	»	»	»	18	5	3
— 5th —	»	»	»	11	»	7
— 6th —	»	»	»	»	»	<b>12</b>
— 7th —	»	»	»	»	»	7
— 8th —	»	»	»	»	»	9
— 9th —	»	»	»	»	»	4

In order to examine whether there exists any correlation between the direction of the spiral and the position of the 1r<sup>II</sup>, the diagrams of all the shoots with spiral arrangement of the branches, of which only some examples are given here, were registered, but as the plants examined were different as to the frequency with which the 1r<sup>II</sup> occurred on the first joints of the branches, it was necessary to treat the plants from the various localities separately. The plants from the three first-named localities in table 15, where the 1r<sup>II</sup> in most cases stood on the first joint, are first treated. Table 16 shows a conspicuous preponde-

Table 16. Position of the 1r<sup>II</sup>.

	A. 12 shoots from Ostindiefarer Grund			B. 3 shoots from Hatterbarn			C. 7 shoots from Fladen		
	kathodic	anodic	Preponderance for anod. in %	kathodic	anodic	Preponderance for anod. in %	kathodic	anodic	Preponderance for anod. in %
1st joint	52	<b>75</b>	45	6	<b>10</b>	67	16	<b>31</b>	94
2nd —	17	18	6	0	<b>11</b>	∞	16	<b>26</b>	63
3rd —	2	»	»	1	<b>5</b>	400	4	<b>6</b>	50
Total...	71	<b>93</b>	30	7	<b>26</b>	271	36	<b>63</b>	75

rance for the anodic side in all the examined plants, greatest for those from Hatterbarn where it is very distinct for all the three joints, most remarkable for the 2nd joint. In the plants from Fladen the preponderance for the anodic side is also considerable, conspicuous for all the joints but greatest for the first joint. The plants from Ostindiefarer Grund show the slightest preponderance for the anodic side, obvious, however, for the first joint.

It is remarkable that in all cases there is a preponderance for the anodic side independently of the number of

Table 17. Position of 1r<sup>II</sup> in all the Plants from 4974, 7380 and 7516.

	kathod.	anod.	Prepond. for anod. side in %
1st joint.....	74	<b>116</b>	57
2nd — .....	33	<b>55</b>	67
3rd — .....	7	<b>11</b>	57
total...	114	182	60

the joint on which the 1r<sup>II</sup> was placed, except the 2nd and the 3rd joint in table 16 A, where the figures were respectively equal and very small. There is thus no trace of an alternation like that found in the three first-mentioned species. This is also evident in table 17 which comprises all the plants treated in the table 16. The table shows an evident but moderate preponderance for the anodic side of each of the three first joints.

The specimens from Frederikshavn showed no preponderance for the anodic side; on the contrary, there appeared a slight preponderance for the cathodic side of the 2nd joint (27 against 18 i. e. a preponderance of 50%) and a total of 37 cases for the cathodic side, 29 cases for the anodic side. As the figures are small and the differences rather inconsiderable, it is uncertain whether there exists any correlation in these plants; there was no indication of an alternation.

### III. Summary and Conclusions.

In all the species examined a spiral arrangement of the branches occurred, though with varying frequency. In *Callithamnion tetragonum*, *C. roseum* and *Seirospora Griffith-*

*siana* it was found in all the shoots examined or with an exception of two or three per cent of the shoots having irregularly arranged branches. In *C. corymbosum* the number of such shoots without spiral arrangement was 12 per cent, and in *C. Furcellariæ* 24 per cent.

In *C. corymbosum*, *C. roseum* and *C. Furcellariæ* the spiral apparently turns with equal frequency to the right and to the left. In the specimens of *Seirospora Griffithsiana* from two localities the spiral turned to the left in all the 45 shoots examined, while it turned to the right or to the left in a specimen from a third locality. In *C. tetragonum* there seems to be a slight preponderance of the spiral turning to the left (205 cases against 166 cases of spirals turning to the right, or 55·3 per cent of spirals turning to the left). The observation that the branches of shoots with a spiral turning to the right were more disposed to antidromy than those of the shoots with a spiral turning to the left (63·1 p.c. against 52·9 p.c.) favours the notion that a slight preponderance of the spiral turning to the left really exists.

The number of observations in regard to the relative frequency of homodromy and antidromy of the branches in proportion to the mother shoots is for most of the species too small to permit any certain conclusion. In some of the species the frequency seems to be equal (f. inst. *C. roseum*). Homodromy occurred exclusively in the specimens of *Seirospora Griffithsiana* which had all the branches arranged in a spiral turning to the left, while antidromy was slightly predominant in *Call. tetragonum*, most in the branches of the shoots with a spiral turning to the right.

The angle of divergence is less constant than in the higher plants; it is more or less variable, not only in different shoots, but also in the same shoot, even in the

species with the most regular spiral arrangement. Orthostichies do not therefore occur or only over short stretches. The divergences usually vary between  $\frac{1}{5}$  and  $\frac{1}{3}$  of the circumference, in *C. tetragonum* most frequently between  $\frac{1}{4}$  and  $\frac{1}{3}$ , but it may exceed these limits and approach to  $0^\circ$  and  $180^\circ$  respectively. In *C. roseum* it is often rather regularly  $\frac{1}{4}$  in the upper part of the shoots, and the average divergence varies in this species about the same numeric quantity in most cases it was however smaller than  $90^\circ$ , while in *C. tetragonum* and *Seirospora Griffithsiana* the average divergence is always greater than  $\frac{1}{4}$ ; in *C. tetragonum* it was found in four shoots to vary between  $104\frac{1}{2}^\circ$  and  $135^\circ$ . The divergence was most variable in *C. Furcellariæ* where it varied from  $0^\circ$  to  $180^\circ$ : the average divergence in 7 shoots varied between  $67^\circ$  and  $131^\circ$ . The divergences  $0^\circ$  and  $180^\circ$  did not occur or only in extremely rare cases within the spiral region in *C. tetragonum*, *C. corymbosum* and *Seirospora Griffithsiana*. In *C. roseum* the divergence  $0^\circ$  occurred in several cases within the spiral region, while divergences approaching to  $180^\circ$  were rare. In *C. Furcellariæ* the divergences  $0^\circ$  and  $180^\circ$  were both met with repeatedly within the spiral region. The superposed branches appeared in 3 or 4 cases as a repetition (in *C. corymbosum*, *C. roseum* and *C. Furcellariæ*); the spiral would have been regular if the repetition had not taken place. In other cases the superposed branches occurred in parts of the shoots where the angles of divergence were very small. In the three just-named species superposed branches also occurred frequently outside the spiral region, particularly in *C. Furcellariæ*. In *C. roseum* the superposed branches occurred in 4 out of 5 cases immediately before the spiral, and this was the case also in some cases in *C. Furcellariæ*. In an aberrant

shoot of *C. corymbosum* a row of 13 superposed branches occurred between a spiral turning to the left at the base of the shoot and a spiral turning to the right at the top.

As the two divergences  $0^\circ$  and  $180^\circ$  occur, though rarely, within spirals otherwise undisturbed, it seems legitimate to consider them, in these cases, as belonging to the spiral region, the more so as these do not ( $0^\circ$ ) or very rarely ( $180^\circ$ ) occur at the point where the direction of the spiral changes. A few cases where, in *C. corymbosum* and *C. Furcellariæ*, the spiral was interrupted by a single step in the reverse direction may perhaps be interpreted not as an interruption of the spiral but as angles of divergence of unusual magnitude, a little surpassing  $180^\circ$ . At all events, such cases are very rare.

As a rule, each joint bears a branch within the spiral region. However, single branchless joints were met with in all the five species examined, most rarely in *C. corymbosum*. These branchless joints are of two sorts. One sort are virtually branchless, the spiral continuing undisturbed with the only difference that the internodium consists of two joints instead of one; they were met with in *C. roseum*, *C. Furcellariæ* and *Seirospora Griffithsiana*. In the last species these joints were shorter than the others. The other sort of branchless joints stood in such relation to the spiral arrangement that a branch in the spiral was missing on the branchless joint. This sort of branchless joints were more frequent than the other sort and were met with in all the species examined. It may happen that a joint has become branchless by the branch being shed early, but in the cases here mentioned there was no trace of this having occurred; it must be taken for granted that the joint has really produced no branch, but never-

theless the position of the next branch is the same as it would have been if the joint in question had produced a branch diverging equally from the foregoing and the following branch. In order to understand this it must be remembered that the branch-bearing segments are cut off from the apical cell by inclined walls, the highest point of which is situated where the branch will arise. It is then an obvious conclusion that these branchless joints have been cut off by oblique walls like the ordinary joints, but that the branch has not been developed for some unknown reason. Hence it follows that it is not the presence of the branch but the position of the upper transverse wall of the young joint which determines the position of the following lateral member. But then the question arises how the walls cutting off the segments from the apical cell can determine the direction of the spiral. It might be expected that the want of a branch in the spiral might occasion a change in the direction of the spiral. But this is by no means so; change of direction of the spiral never takes place through a branchless joint. If the orientation of the dividing walls of the apical cell were to have any causal importance for the maintenance of the direction of the spiral, one might imagine that the walls were not only oblique, having their highest point where the branch will arise later but that they were also asymmetrical, f. inst. more inclined on one side than on the other. This question deserves a thorough examination. The last-named branchless joints must thus be regarded as virtually branch-bearing. In the virtually branchless joints the segment walls by which they have been cut off have probably been horizontal.

In *C. roseum* and *Seirospora Griffithsiana*, the spiral was sometimes interrupted by a shorter or longer stretch with



irregularly arranged branches after which the spiral continued in the same direction as before the interruption. In such stretches branchless joints, superposed branches and divergences of  $180^\circ$  were met with. In *C. corymbosum* such an interruption also occurred, presenting two divergences of  $180^\circ$  and a divergence in the opposite direction. And finally it must be mentioned that in *C. Furcellariæ* the spiral was not seldom interrupted by a single step in the opposite direction (cp. above).

Change in the direction of the spiral was met with in all the species examined, most frequently in *C. Furcellariæ* and *C. roseum*. The change usually takes place suddenly, the last branch in the first spiral being the first branch of the spiral with reverse direction. In most cases the divergences at the turning point of the spiral did not differ from the usual ones, in very rare cases, however, the change took place through an angle of divergence of  $180^\circ$  or nearly so, (one case in each of the species *C. roseum*, *C. Furcellariæ* and *C. tetragonum*), and in *C. roseum* the angles next to the turning point of the spiral were usually comparatively great. The change in direction of the spiral took place in some cases in *C. corymbosum* and *C. Furcellariæ* through a shorter or longer stretch with irregularly placed branches, including, too, divergences of  $180^\circ$  and  $0^\circ$ . A curious case was found in a shoot of *C. corymbosum* where the intermediate region was composed of 14 joints bearing the same number of superposed branches.

The spiral arrangement of the branches never begins at the very base of the primary shoots. As a rule the first joints are branchless and then follow a varying number of joints with irregularly disposed or biseriate branches, before the beginning of the spiral. This region was parti-

cularly large in some, apparently aberrant, young plants of *C. tetragonum*, where it comprised 20—30 joints with biseriate branches.

The branching of the lateral shoots always or with rare exceptions begins at the very base in *C. tetragonum* and *C. corymbosum*, and in most cases in some specimens of *C. Furcellariæ* and *Seirospora Griffithsiana*. In other cases the first joint or joints are branchless (*C. roseum* and certain specimens of *Seirospora Griffithsiana* and *C. Furcellariæ*). The spiral arrangement of the branches does not begin at the very base of the lateral shoots: it occurred only in extremely few shoots of all the species except *C. roseum*. The first branch of the second order has always or almost always a transversal position, standing on the right or left, particularly in *C. tetragonum*, *Seirospora Griffithsiana* and *C. corymbosum*. Some exceptions were however found in the last species, and in *C. roseum* and *C. Furcellariæ* it is frequently not transversal. In the three first-named species the following branches are usually also transversal, the lateral shoot thus beginning with 1—6, in *C. corymbosum* with 1—3 or 4 biseriate branches. In the two other species the first branches are more or less irregularly placed, not rarely, however, biseriate, but the plane of ramification is then frequently not transversal but oblique; the number of such branches may be rather considerable. The biseriate branches in *C. tetragonum* are not all exactly transversal, some of them approaching more or less to the outer side of the mother branch; this convergence towards the outer side generally increases with the increasing distance from the base, though not regularly. A similar tendency to a convergence towards the outer side could not be substantiated with certainty in the other species. The spiral region follows almost always

immediately after the biseriate branches in *C. tetragonum* and usually in *Seirospora Griffithsiana*, frequently also in *C. corymbosum*. Otherwise it is separated from the biseriate region by a number of joints with irregular arrangement of the branches.

On examining the point of transition between the biseriate and the spiral region in lateral shoots of *C. tetragonum* and *C. corymbosum* it was ascertained that the first step in the spiral takes place, with very few exceptions, on the outer side of the shoot, the second member of the spiral standing on the outer side of the shoot, when the spiral is reckoned from the first branch which can be included in it, even in the cases where the first step of the spiral is identical with the last step in the biseriate region. In *Seirospora Griffithsiana* there was also a considerable preponderance for the outer side of the shoot (27 against 6); but in *C. roseum* and *C. Furcellariæ* no influence of the mother shoot on the first step of the spiral could be shown, perhaps owing to the fact that the spiral arrangement in the two latter species begins at a greatly varying and comparatively great distance from the base.

The fact that the first step in the spiral on the lateral shoots in the three first-named species always or in the great majority of cases is directed towards the outer side of the shoot must be explained as the effect of a factor seated in or emanating from the mother axis. Similar effects of the same factor are well known in several other Algæ where, as shown by BERTHOLD (1882), the first lateral organs arise on the outer side of the branches. I have named this effect "ectoblastesis" (cp. p. 20). The convergence of the biseriate branches in *C. tetragonum* is probably an effect of the same factor; but the position of these branches

is otherwise determined by another factor, a tendency to biseriate arrangement in a transversal plane. At the moment when the biseriate arrangement ceases and the spiral one is beginning, the ectoblastesis causes the second member in the spiral to arise on the outer side of the shoot and it thus determines the direction of the spiral. When the first member of the future spiral stands on the left, a spiral turning to the left results, when the first member stands on the right, the spiral will turn to the right. When the spiral arrangement is established, the mother axis has no longer any influence on the ramification of the branch, the position of the following branches of the second order being determined by the foregoing members of the spiral.

In four of the examined species a more or less marked correlation between the direction of the spiral and the position of the first branch of the second order ( $1r^{II}$ ) on the members of the spiral was met with, but this correlation manifests itself in a somewhat different manner in the different species. In *C. tetragonum* it is very constant and shows itself in the fact that the  $1r^{II}$  stands on the anodic side of the first joint of the branch of the I. order. Only very few exceptions from this rule were met with (19 out of more than 800). In 6 cases the  $1r^{II}$  stood on the cathodic side of the 2nd joint, which may be explained by the 1st joint having been virtually (potentially) branch-bearing but really branchless. In 4 cases the  $1r^{II}$  was placed on the anodic side of the 2nd joint in which cases the 1st joint may be supposed to be virtually branchless. 9 cases only were decided exceptions, the  $1r^{II}$  being placed on the cathodic side of the 1st joint; most of these exceptions occurred in the two first members of the spiral, 2 only at a higher level. — In *C. corymbosum* the correlation appears with a similar constancy as in the just

named species. The  $1r^{II}$  almost always stands on the 1st joint and then with very few exceptions on the anodic side (213 cases against 4 on the cathodic side). In 10 cases it stood on the 2nd joint and then always on the cathodic side, thus where the  $2r^{II}$  would have been placed if the  $1r^{II}$  had been developed on the 1st joint. — In *Seirospora Griffithsiana* too a marked correlation of a similar kind is present, but it is here combined with a very remarkable alternation according as the  $1r^{II}$  stands on the 1st, 2nd, 3rd or 4th joint of the shoot. However, a remarkable difference was found between the specimens from Herthas Flak and those from the other localities. The first were in this respect much like *C. corymbosum*, the great majority of the  $1r^{II}$  standing on the anodic side of the 1st joint, while there was a preponderance for the cathodic side for the few  $1r^{II}$  standing on the 2nd joint. In the specimens from the other localities the first joint was in most cases branchless, but in a specimen in which the great majority of the  $1r^{II}$  stood on the 1st joint, they were almost all placed on the cathodic side. Most of the  $1r^{II}$  occurred on the 2nd joint and then in the great majority of cases on the anodic side. When a great number of  $1r^{II}$  were placed on the 3rd joint, the great majority occurred on the cathodic side, and finally a preponderance for the anodic side was ascertained on the 4th joint (cp. table 12). This alternation must be due to an interference of an influence from the mother shoot and a tendency in the branch to an alternate, biseriate ramification in a transversal plane at the base. This is supported by the observation that the first transversal walls in the young branches are inclined, whether the joints are branch-bearing or branchless, and that the first segment wall has its highest point at the cathodic side. The orien-

tation of the first wall, (which determines the succeeding walls in the branch), must be due to an influence from the mother shoot, but the effect of this influence upon the orientation of the first branch of the second order only appears later in most cases, and it is dependent on the number of the segment on which the first branch arises. The decreasing constancy of the correlation with increasing distance from the base shown in table 12 is probably due to a decreasing regularity of the alternation of the oblique walls. As stated above, a similar alternation was evident in *C. corymbosum*; and the 6 cases of 1r<sup>II</sup> standing on the cathodic side of the 2nd joint in *C. tetragonum* bear witness to the same. — In *C. Furcellariæ* a rather slight preponderance for the anodic side (57—67 per cent, average 60 per cent) was met with, but it was present whether the 1r<sup>II</sup> was placed on the 1st, 2nd or the 3rd joint and almost of equal magnitude. The absence of alternation, as found in the species just mentioned, is certainly due to the absence of alternate, biseriate branches below the spiral region. — In *C. roseum* there is no correlation at all between the position of the 1r<sup>II</sup> and the direction of the spiral on the mother shoot or perhaps a slight preponderance for the anodic side of the second joint. This is perhaps due to the fact that the first joint of the branches is virtually branchless, and that the following 1—4 joints are usually also (actually) branchless.

In all the species where the correlation has been met with, it was present from the beginning of the spiral, though with somewhat diminished constancy. An examination of the position of the 1r<sup>II</sup> on the last branch before the beginning of the spiral arrangement, in order to learn if it might show a tendency to take a position corresponding

to that in the spiral region, gave no affirmative answer except for *C. corymbosum*, where a such tendency seemed to be present. It deserves to be noticed in this connection that in shoots of *C. corymbosum* and *Seirospora Griffithsiana*, where the spiral region was interrupted by a stretch with irregularly arranged branches, the 1r<sup>II</sup> in this region in all or in the great majority of cases had the same position as in the spiral region. The position of the 1r<sup>II</sup> thus appeared more fixed in these cases than the spiral arrangement of the branches, r<sup>I</sup>. When the direction of the spiral suddenly changed in *C. tetragonum*, the position of the 1r<sup>II</sup> on the branch occurring at the turning point, which was at the same time the last member of the first spiral and the first member of the spiral turning in the reverse direction, always corresponded to the new direction of the spiral.

As mentioned above, it may be supposed that the young segments of the axes, which bear spirally arranged branches, are asymmetrical. If that is so, it is highly probable that the correlation here treated is a consequence of the same asymmetry. A detailed study of the division of the apical cell and the shape and division of the young segments in these plants will certainly throw light upon the factors determining the spiral arrangement of the branches and the position of the first branches of the second order.

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