

A.

Study of the Genicula of Corallinæ.

By

K. Yendo, *Rigakushi.*

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*With one Plate.*

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INTRODUCTION.

The genicula of the *Corallinæ* are of special interest from both morphological and physiological point of view. The presence or the absence of a geniculum in Corallinaceous algae forms the essential character on which is based the division of the family into two subfamilies, viz., the *Corallinæ* and the *Melobesinæ*.

In certain other calcareous algæ, such as *Galaxaura*, *Actinotrichia*, *Halimeda*, *Cymopolia*, &c., we also find genicula of a similar appearance. Although these genera are systematically apart from one another, there can be no doubt that the physiological function of genicula is the same in all cases.

A comparative study of the genicula in all these members would surely afford us interesting results. In the present paper, however, the observation is confined to the *Corallinæ*.

As far as the present writer's observation extends, the literature relating to the subject in question is comparatively scarce. NELSON and DUNCAN<sup>1)</sup> jointly tried some investigations into the histology of

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1) On Some Points in the Histology of Certain Species of Corallinacæ.

the calcareous algæ, and left a valuable paper. SOLMS<sup>1)</sup> treated somewhat the same subject, and wrote a few lines about the formation of the genicula in the *Corallinæ*; and pointed out the difference between *Amphiroa* and *Corallina* in the structure of genicula. HEYDRICH<sup>2)</sup> noticed the critical points of the primary incrustation of *Corallina* and *Lithothamnion*. He took *Corallina officinalis*, L. as the representative of the *Corallinæ* and mentioned the genicular formation as an important diverging point of the two subfamilies.

The writer previously noticed several interesting facts about the genicula of the *Corallinæ*, while he was examining material from Japan and Canada. Some of the views arrived at a different conclusion from those of former investigators. They will be pointed out under the proper chapters.

The material worked over belongs mostly to the Japanese and the Canadian algæ. They were preserved in alcohol directly after they had been collected or after decalcifying the fresh plants in PERÉNY'S fluid. The specimens which were kindly sent to the writer by Dr. M. FOSLIE, Madame A. WEBER VAN BOSSE, Mr. F. S. COLLINS, Major THEO. REINHOLD were a great help to him in comparing results. The writer must not miss the chance to express his deepest thanks to these phycologists. Thanks are also due to Prof. J. MATSUMURA, Prof. M. MIYOSHI and others who have helped the writer in various ways.

The writer regrets to say that the study on *Amphiroa stelligera* and *Amphiroa aspergillum*, which play an important and interesting part in the present work, he has been obliged to undertake on dried material. He could not help omitting several important observations on these species, as, with dried fronds, he was unable to pursue the

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1) GRAF V. SOLMS-LAUBACH. *Corallina* p. 23.

2) *Lithothamnion* von Helgoland. p. 79.

course further. Moreover specimens of *Amphiroa australis* were not accessible to him. This is the only species which is reported to have the fronds constructed with globular cells. The writer does not doubt that minute study on the structure of this species might afford interesting facts to add to the present work.

Botanical Institute,  
Imperial University of Tokyo.

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### EXTERNAL APPEARANCE OF GENICULA.

The genicula of *Corallinae* appear with a brownish colour while the plant is yet living. In some of the members which have no significant genicula, the colour is, as a consequence, not remarkable. When the fronds are bleached and the articuli have turned into chalky white, the genicula are distinguishable as yellowish brown constrictions or rings around the calcareous fronds.

The genicula are entirely free from the deposit of calcium, and the substance is horny and flexible. This gives a special character to the fronds. Whether a frond is rebust or not depends essentially upon the relative size of the genicula and the accompanying articuli. Even in an individual the proportion differs in the basal and the upper parts of the frond.

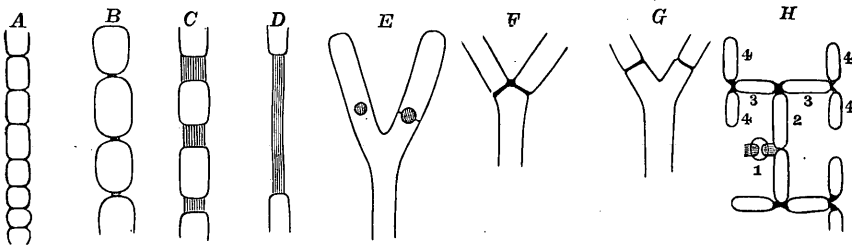
The majority of *Corallinae* have very short genicula at the basal part of the frond. The articuli at this region are mostly short and cylindrical. Hence the stem at this part becomes moniliform, the genicula taking the places of the constrictions. *Amphiroa dilatata*, *Amp. Bowerbankii*, *Amp. canaliculata*, *Amp. ephedraea*, etc., in short, those which would be grouped under the section *Eurytion*, Dcne., have the genicula with equal or nearly equal diameter with the articuli adjacent.

The genicula of *Amp. stelligera*, *Amp. Charoides* and their allied forms are the larger than those of the other species. Some of the matured genicula, indeed, are longer than the accompanying articuli. They are cylindrical, smaller in diameter than the articuli.

When the fronds of the *Corallinae* are observed with the naked eye, we can easily distinguish several forms of the genicula. These multitudinous shapes might be classified briefly into the following five types :

I. *Linear*: the majority of *Corallina*, *Jania* and some of *Amphiroa* belong to this type. As for the basal genicula, most of the members come under this category. The exceptions are the greater number of the *Eurytion*, *Amp. Charoides*, *Amp. stelligera* etc., and many species of *Cheilosporum* (Fig. A).

The gap between the articuli is very narrow, apparently seen only as a circumscribing slit around the geniculum. This sort of genicula has been called "lineæform" by the former systematists. In these the genicula are not so short as they appear from the external side. Both ends of the articuli which hold the geniculum between them are concave. Hence the greater part of the geniculum is covered by the overhanging margins of the relating articuli. I shall call this marginal portion, for sake of convenience, the circum-genicular cortex (Pl. fig. 1-2).



The genicula of *Amp. aspergillum*, when judged by the external appearance, come under this category. But the internal structure of the frond in this species is quite different from that of the other members of the *Corallinae*. As it will be treated further in the following pages, we can not clearly distinguish the genicular and the articular portions in its internal structure.

II. *Spotty*: many of the section *Arthrocardia*, Dcne. belong to this type, especially those which have the sagittate articuli ending in narrow base. (fig. B).

In these the diameter of the geniculum is much smaller than that of the adjacent articuli; and the greater part of the geniculum is exposed outside. Or, in other words, the part exposed to the outside is comparatively larger than the part hidden under the circumgenicular cortex. Hence the genicula of this type appear to the naked eye like brownish spots.

III. *Bandform*: the genicula at the lower portions of the members under the section *Eurytion*, Dene. belong to this type (fig. E).

This type of genicula has the diameter equal or nearly equal to that of the adjacent articuli. The length is comparatively great. The articuli are destitute of circumgenicular cortex. On the contrary, a portion of the distal end of an articulus is covered by the outgrowth of the successive geniculum. The details will be given in a later chapter.

IV. *Filiform*: the peculiar genicula of *Amp. stelligera*, *Amp. Charoides*, etc., belong to this type (fig. D).

They are very long genicula, often several times longer than the diameter. The diameter of the genicula is smaller than that of the articuli, hence the whole appearance is filiform. In the youngest stage of its development it is undistinguishable from "spotty" genicula as in the upper parts of *Amp. canaliculata*.

V. *Fenestraform*: the genicula at the upper portions of the fronds of *Amp. dilatata*, *Amp. ephedraea*, *Amp. Bowerbankii*, etc., belong to this type.

The genicula here mentioned are by no means the complete ones. They are always to be found at the upper and younger portions of the fronds which are without exception furnished with the "bandform" genicula at the basal parts. The "fenestraform" genicula, therefore, should be taken only as a young stage of the "bandform"

type. Yet the genicula of the present type characterise a species in a great degree. It would be better, therefore, to mention them on the same level with the other forms (fig. E).

The above mentioned five types are easily discernible with the naked eye. The divergency of the genicula into these types is due to the difference of the modes in the early stage of their development. Some minute account of the histological views will be given in the following chapters.

### THE POSITION OF GENICULA.

The embryonal stage of the *Corallinæ* is a mere thin calcareous incrustation upon a substratum. In this stage it is not easily distinguished from a sterile form of some *Melobesia*. The tiny epiphytic species, such as *Corallina pusilla* and *Cor. radiata* have their basal incrustation in the shape of a verruculose circular disc.

Every member of the *Corallinæ*, however, soon develops a mamillary process perpendicular to the surface of the incrustation. The process becomes provided with an uncalcified joint, the primary or the basal geniculum, slightly above the level of the surface of the incrustations. cf. HEYDRICH'S paper on "Lithothamnion von Helgoland."<sup>1)</sup> The mamillary process continues to grow upward acropetally, having the geniculum at fixed distances. The intergenicular portions are so-called articuli.

The intergenicular distance or the height of an articulus is always comparatively short at the basal part of a frond. As the plant grows larger, the successive upper articuli become larger and larger, sometimes compressed simultaneously, inclining to its proper shape in each species. This circumstance is nearly similar in every member except tiny and epiphytic forms.

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1). P. 79.

When the articuli at the basal portion grow in thickness, after they have been geniculated, the consequence is that they always assume a moniliform shape: and if the growth of the diameter of the genicula has corresponded to that of the articuli, we have a homogeneous cylinder with parallel rings at certain distances. In the former case the result is always "linear" in form, as in *Amp. aberrans*, *Cor. officinalis* and many others: in the latter case "bandform" genicula are formed, as in *Amp. dilatata*, *Amp. ephedraea*, &c.

At the upper portions of the fronds we find several differences in the position of the genicula. These various positions may be divided into two, the normal and the abnormal.

#### A. THE NORMAL POSITION.

The normal position of genicula is always at the ends of the articuli, situated in the direction of the rachis. This position is most common in the members of the *Corallinae*. And the genicula belonging to the axial stem or to the main branches are of this type.

There might be two equal or several unequal genicula at the distal end of an articulus. In the former case the two genicula are mostly separated in the meridional plane. This results in the branching mode which I have called the "direct" dichotomy<sup>1)</sup> (fig. F). In some dichotomous fronds, a single geniculum is on the top of each arm of Y-shaped articuli, instead of two genicula at the diverging point, forming the branching mode which I have called "indirect" dichotomy (fig. G). In *Cor. decussato-dichotoma* and its allied species, the two genicula are situated, side by side, at the top of an articulus. But the partition plane of both genicula is always

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1) YENDO: *Cor. veræ Japon.* p. 10. footnote.



at right angles to that of the next order. The consequence is that the dichotomy of one order comes in the plane at right angles to that of the adjacent one. This mode of dichotomy is what I called "decussato-dichotomy." (fig. H).

A peculiar mode of bifurcation is found in the main stems of *Amp. aspergillum*. In this species the articuli of the main stems are as broad as their length and strongly compressed except those at the basal portion. A few of the successive articuli below a bifurcating articulus are much more complanated and have a longitudinal groove along the meridional line, as if the tendency of the bifurcation at the upper articulus were already indicated in the lower articuli.

When several unequal genicula have been formed at the distal end of an articulus, the branching mode becomes much more complex. In the pinnated fronds, the two minor genicula are on both sides of the middle one; and when several minor ones are around the axial one, the mode is whorly. In either case the middle and large one is situated in the direction of the rachis and is always at the center of the distal area.

Strictly speaking, the size and the position of the genicula at the distal end of an articulus from which the trichotomy and the pinnation begin are different. In the trichotomy three genicula, equal in size and in value, start at the end of an articulus from the same level. In the pinnated branchlets, the two genicula on both sides of the axial geniculum are much smaller than the latter. The genicular cells of the axial one start from the zone lower by one than that of the genicular cells of the pinnules (fig. 3). This was actually observed in *Amp. aberrans*, *Cor. officinalis*, *Cheilosporum maximum*, etc. (cf. fig. 11, Plate 1. *Cor. veræ Japon.*).

The genicular cells have no power to develop into articular cells by division or elongation. They are always transformed from the

cells of a certain portion of an articulus. The difference of the level from which the genicula start illustrates the fact that they are of separate origin. Hence at least in the last mentioned species the genicula of the ramuli or the pinnules are not genetically related to those of the neighbouring axial articulus. It should be admitted that the pinniferous articulus might be taken conveniently as a sagittated one with the shoulders enormously prolonged and finally jointed.

*Amp. stelligera* and *Amp. Charoides*, as well as their allied forms, have a peculiar mode of ramification. This has been already remarked by KÜTZING in his *Tab. Phyc.* vol. VIII. p. 26. The branches never start like all other members of the *Corallinae* directly from an articulus. The primary geniculum of a ramus or ramulet always starts from a certain limited part of the axial geniculum, and not from an articulus. The whorly branchlets of these species, therefore, have quite a distinct morphological significance from those of *Cor. pilulifera*, *Cor. vancouveriensis*, etc. which are mentioned below. Hence in the former species the branchlets are practically developed at the expense of the axial geniculum. I was not able satisfactorily to trace the origin of the branchlets, as the material would not allow me to do so ; but it was clearly observed that the embryonal stage of the branchlets is readily recognizable around the immature axial geniculum. How the genicula could give out branchlets will be noticed hereafter.

The genicula of the pinnated and the whorly fronds are always at certain angles to one another. The angles between the genicula of the axis and the pinnules are geometrically adjacent angles to the angle formed by the axial articulus and the pinnules. Here the angle between the genicula means that which has been formed by the planes perpendicular to the periclinal axes of the axial articulus and the pinnules concerned.

The extreme case of pinnation is that of *Amp. aspergillum*. The more or less compressed articuli of the main stem are regularly jointed at certain distances. The genicula are linear, with subequal diameter to the articuli. The primary articulus of the branchlets arise decussately from the upper end of the periclinal edge of the compressed articulus. The insertion of the pinnae or the primary genicula is at right angles to the axial geniculum.

As the position of genicula is dependent upon the mode of branching, the plants with irregular branching have naturally the genicula at indefinite positions. The larger number of the section *Euamphiroa*, Dcne. are examples of this category.

In *Amp. valonioides* a branch often arises obliquely upwards from the distal end of an axial articulus with its primary geniculum at some distance further than the diverging point. This gives an appearance of sympodium until we examine the internal structure. cf. *Cor. veræ Japon.* Pl. I. fig. 3.

*Amp. cretacea* has an irregular mode of branching. It sometimes gives out branches at the distal end of an articulus showing apparant dichotomy. On the other side, several branches arise decussately from the periclinal side of a cylindrical articulus. The latter is by no means the abnormal but a special mode of ramification belonging to this species. cf. Pl. IV. fig. 2. l. c.

These decussate branches have the primary geniculum in two forms. The first is that of the geniculum directly situated upon the surface of the axial articulus ; that is, the geniculum starting without any process on the surface of the articulus. The second form has the genicula upon the process, perpendicular or obliquely, produced on the surface. These modes of geniculation might correspond to "direct" and "indirect" dichotomy. But the character is not

constant in equal degree as in the case of dichotomy ; and both types may be found in the same individual. cf. Pl. IV. fig. 2. l. c.

Some of the plants which belong to the section *Eucorallina*, and might be classified near *Cor. officinalis*, have often numerous genicula around the axial one. The writer has mentioned actual examples in *Cor. pilulifera* and *Cor. vancouveriensis*, *f. densa*.<sup>1)</sup> The subordinate genicula belong mostly to the stalks of the conceptacles. Although this arrangement of conceptacles characterises the plant in some measure, in considering the position of the genicula, the whorly genicula in this species would better be treated as of less importance. It should not be forgotten, however, that the origin of these whorly genicula is entirely different from those of *Amp. stelligera*, etc.

#### B. ABNORMAL POSITION.

As has been already remarked in the preceding chapter, every geniculum accompanies an articulus, whether it be of branch, pinnule or stem. Hence the abnormal position of a geniculum means a geniculum belonging to an abnormal branch or branchlet. The most common case of such abnormality is found on the flat surface or margin of an articulus. Illustrious examples have been given in *Amp. aberrans*<sup>2)</sup> and *Amp. canaliculata*.<sup>3)</sup> In these species the branchlets consisting of one or more articuli originate on the surface or the margins of the articuli. In most cases the form of branches and the shape of the articuli of these abnormal ramules are much modified. To give the minor points of these modifications is, at present, not necessary. These abnormal branches have the genicula directly on the surface of the articuli. Very often, in the case of *Amp. aberrans*,

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1). *Cor. veræ* of Port Renfrew. Pl. LVI. fig. 17: *Cor. veræ* Japon. Pl. III. fig. 16.

2). *Cor. veræ* Japon. Pl. II. fig. 1-2.

3). Martens: Preus. Exp. nach Ostas. Tange. Pl. VI.

a knotty protuberance is found at the point of insertion of the geniculum into the articulus. In *Amp. canaliculata*, Mart. the genicula are always directly attached to the margins of the articulus, that is to say, the genicula grow from the margins without any protuberance or prolongation of the calcified portion.

In most cases the abnormal genicula seem to have generated from the cortex. In *Amp. cretacea*, a number of the cortical cells increase layer upon layer at a certain portion of the surface of an articulus in such a degree as to produce a wart-like protuberance. One of the cellular layers elongates to an extraordinary degree, in like manner as a normal genicular formation, and thus the primary geniculum is built up.

Some of the branches of *Amp. cretacea*, *Amp. valonioides*, etc. originate from the cortex in the manner just described above. In *Amp. aspergillum* the primary genicula of the pinnules are always generated from the cortex. These ramules are by no means abnormal branches in these species, but a characteristic mode of ramification limited to them.

Thus the genicula at the distal end of an articulus which give rise to dichotomy, trichotomy, whorly or pinnation (not of *Amp. aspergillum*) are originated from the medulla; and those of the lateral branches or processes are mostly from the cortex. The abnormal genicula generally belong to the latter category.

#### RELATIVE POSITION OF THE GENICULAR AND THE ARTICULAR CELLS.

The structure of the articuli of the *Corallinæ* may be easily divided into two portions. The internal part is constructed with long filamentous cells bound together along the periclinal side of the cells. These cells occupy the greater part of the diameter. The cells at the

middle portion run in the direction of the axis of the articulus. Those at the peripheral portion more and more become inclined, diminishing, at the same time, in the length, until they result in globular or cubical cells running radially to form the cortex. The medullary cells are mostly arranged in zones. These zones are easily observable when the calcium carbonate in the frond has been dissolved. They appear as concentric parallel lines, convex toward the apex of the frond (figg. 3, 5, 6).

A geniculum is built up with one or more zones of the periclinal cells. The majority of the *Corallinae* belong to the former category. In the case when one zone of the periclinal cells shared the formation of geniculum, the middle portions of the cells serve as the geniculum proper. Both ends of the cells have the deposit of calcium carbonate and have no proper function as genicular cells. The calcified distal ends should for the sake of convenience be called the extra-genicular portion (figg. 9-10).

The bordering line between the articuli and both ends of a geniculum varies more or less according to the species. As has been mentioned above, a geniculum is not built up by the mass of the entire cell but by a mass of parts of the cells. In other words, the cells at the critical portion which divide a geniculum and an articulus are separated into two parts, the one serving to build the geniculum and the other the articulus (figg. 1, 2, 4). Hence the word "borders" does not apply to the continuation of the cell boundaries. It means the continuity of the transitional points of the genicular and the articular portions of the cells; or the critical points of the genicular and the extragenicular portions.

In the hair-like *Jania* the number of the genicular cells is much less than that of the robust forms, and they are arranged in a less regular manner. Generally speaking, the cells at the middle portion

of a geniculum are longer than those in the periphery. But there occurs much fluctuation in the length, and the longitudinal section of a geniculum always shows a zigzag appearance. cf. *Cor. veræ Japon.* Pl. III. fig. 3.

In *Amp. aberrans* the genicular area changes abruptly into the articular portion, and the boundaries between them are exceedingly sharp. The boundaries are more or less convex toward the articular parts at both ends of the geniculum. The majority of the *Corallinæ* are of this respect, although the sharpness of the boundaries may fluctuate in a slight degree (fig. 3).

*Amp. dilatata*, which shows special characters in various points, here also gives us an aberrant type in this respect. The upper boundary is a concave plane running into the geniculum and the lower is a convex one running toward the lower articular, with special outgrowth at the central portion of both planes (fig. 5). This character, however, is limited to the genicula of the upper and middle portions of the fronds. The genicular cells of this plant undergo further development and an old geniculum has an appearance quite foreign to that of the younger ones.

In *Cheilosporum anceps*, the zonal arrangement of the periclinal cells is entirely disturbed. The cells are not straight but undulating, and are connected with one another through the large lateral openings (fig. 4). In this respect it resembles the cellular arrangement of the *Jania*, especially *Cor. yenoshimensis*. cf. *Cor. veræ Japon.* Pl. III. fig. 3.

Although the zonal arrangement of the periclinal cells is thus irregular, the transition parts are regularly and sharply defined (fig. 4).

In *Cor. decussato-dichotoma* and *Cor. yenoshimensis* the periclinal cells are not undulated as in *Cheil. anceps* but the perforation on the

lateral walls and the non-zonal arrangement of the cells are similar to those of the latter species.

The above mentioned genicula are all those in the normal position. The characters are more or less constant to the species. In the abnormal genicula, as it were, these descriptions may not be often sharply applied.

The greater part of this chapter does not hold good in the fronds of *Amp. aspergillum*. In this species an articulus is built up of two and only two zones of the periclinal cells, covered with a few layers of cortical cells. The lower of the two zones practically fills up the entire portion of the medulla. The cells constructing it are much-elongated filaments of nearly equal length, running longitudinally in an exact sense. The upper zone is a layer of elliptical cells, each of which is situated at the top of the filamentous cell. These elliptical cells have their longer axis in the same direction as the filamentous cells below them, but those at the peripheral region bend horizontally by degrees and finally become confluent with the cells of the innermost cortical layer. Hence in the longitudinal sections of an articulus we have a  $\cap$ -shaped layer of minute cells holding the bundle of the filamentous cells wholly inside of it. The boundary of the neighbouring articuli lies at the points where the basal extremities of the filamentous cells of an articulus come into contact with the terminal extremities of the elliptical cells of the lower articulus. The slit between the articuli which suggests a linear geniculum in the external appearance of a frond, is around this region (fig. 7).

We have several reasons for believing that the lower half of the filamentous cells serves as the genicular portion proper of the other species. In the preparations the cortex around this portion seems to be entirely free from continuation with the filamentous cells like a circumgenicular cortex of other species. But it would be a little



dangerous to give further details on this point, as the material worked over has been from a dried specimen. It might be stated, however, that at least a small portion at the base of the filamentous cells is not calcified and flexible as in the genicular portions of the other *Corallinæ*.

These peculiarities of structure suggest the convenience of omitting the above mentioned species from the general discussions of genicula. The following chapters will be applicable to the other members of the *Corallinæ*, except *Amp. aspergillum* unless it is specially mentioned.

### STRUCTURE OF GENICULAR CELLS AND COMPARISON WITH ARTICULAR CELLS.

The genicula of *Amp. dilatata*, *Amp. echigoensis*, *Amp. Bowerbankii*, *Amp. epheræa*, etc.,—probably all members of the section *Eurytion*, Dcne.—are built up with several zones of periclinal cells. The genicula of this category have special characters and should be treated further.

In *Amp. rigida* the genicula seemed to have been built up with two zones of periclinal cells. They are, however, always formed of a single zone, the cells being often intertwined at the equatorial points and looking like two zones. cf. *Cor. veræ*. Jap. Pl. I. fig. 6.

The presence of the extragenicular portion is an important matter. Former investigators seem to have overlooked this. NELSON and DUNCAN<sup>1)</sup> remark that the long cells (of artículus) are often distinctly continuous with the filiform cellular processes of the articulations (genicula), especially with the deeply seated ones. They seem to have noticed nothing about the extragenicular portion. Among the multitudinous illustrations of "Tabulæ Phycologicæ"<sup>2)</sup> only two figures indicate this circumstance in any degree. And in

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1) l. c. p. 206

2) Vol. VIII Taf. 56. and 60.

the illustrations of "Etude Phycologique"<sup>1)</sup> and "Sur les Corallines"<sup>2)</sup> no precise point about it is given.

To begin with, we will treat of the unizonal geniculum; that is to say, a geniculum built up with a single zone of periclinal cells.

The genicular cells are long filamentous cells, varying in the proportion of their length and their diameter according to whether they take the middle or the peripheral position in the geniculum. The diameter of the cells is constant or nearly constant in a species. The part at both ends which I have called "extra-genicular portion" has mostly a different diameter from the genicular portion proper. The diminishing or the increasing of the diameter occurs abruptly at the critical points between the two portions.

In regard to the length of the filaments, we find that it varies according to the species; but it is always several times, often more than twenty times, as great as the breadth. We can not tell the proportional length by the mere external appearance of a geniculum. This is owing to the relative size of the circumgenicular cortex.

In the cross sections of the genicula we find the cells more or less polygonal from mutual compression. The cell rooms are comparatively narrow and mostly roundish polygonal.

Staining with colouring materials, we can easily perceive the lamellar structure of the cellwall in the genicular cells. The comparison of the properties of the wall with those of the articular cells is highly interesting. In the present paper it is not the aim to give the details of the microchemical properties of the cellwall, but some remarkable features we shall not fail to point out hereafter.

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1) BORNET et THURET; Pl. L-II.

2) DECAISNE: Pl. 17. fig. 5

When stained with BOEMER'S hæmatoxylin and fuchsin after the method I mentioned in my former papers,<sup>1)</sup> we find at least three lamellæ stained in different degrees. The innermost lamella is pretty thick, sharply distinguishable from the other parts of the wall (fig. 13). This part stains deepest in dark violet. It is the thickest of the lamellæ and is peculiar to the genicular portion proper. The genicula of the *Corallinæ* stain in a much deeper degree than the articular part. This circumstance depends upon the property of this lamella. The second lamella envelops the innermost lamella and varies in its thickness, as it seems, according to the age of the genicula. It stains in pale violet or grayish blue. At the external part of the latter lamella we have another thin lamella. This thin lamella practically answers the middle lamella of the higher plants and is clearest at the peripheral portion of the genicula; and in some species it is entirely invisible at the interior part of the genicula (fig. 14). In *Cor. yonoshimensis* the three lamellæ are very clearly defined (fig. 13). As the cells are more or less polygonal and compressed by each other, the outermost lamella is comparatively thick at the points where more than two cells meet together. In some species this lamella is to be detected only at these points (fig. 14). In the genicular cells of *Amp. stelligera* only the outermost lamella gives a deep violet colour, while the other portions remain a light bluish colour.

A peculiar modification of the wall was observed in the peripheral portion of a geniculum which had been attacked by a parasitic alga. The middle lamella stained exceedingly deep, while the second lamella was quite indifferent to the colouring material (fig. 15). At first the writer was induced to consider it the extra-genicular portion cut lengthwise. But the staining mode is just contrary to the ordinary case, and a further examination of the longitudinal section

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1) *Cor. veræ* Japon. P. 3: *Cor. veræ* of Port Renfrew P. 711.

showed that this modification was due to the parasitic *Diatom*. The exact determination of the parasite is beyond the present purpose.

When the section had been treated in anilin blue for 24 hours, we gained a beautiful preparation stained metachromatically. The outermost layer which fills up the intercellular space and apparently takes the place of the middle lamella stains in deep purple. The next layer stains in light blue. The innermost layer which stained in deep violet in hæmatoxylin is now separable into two parts. The innermost is very thin, but stains in deep purple; the outer layer in purple also but more faint. These two layers stained in the same degree when treated with hæmatoxylin.

Hence we might divide the cellwalls of the genicular cells into four parts, with the exception of those of *Amp. stelligera*.

I. *The middle lamella*: filling up the intercellular spaces and often hardly distinguishable at the axial portion of geniculum by virtue of the strong mutual compression of the cells: staining deep in hæmatoxylin and anilin blue.

This lamella corresponds in its position, especially when it is very thin, to the intercellular substance of DIPPEL.<sup>1)</sup>

II. *The primary cellwall*: staining in less degree with the colouring matters. With hæmatoxylin it stains in pale violet and with anilin blue in light blue.

III. *The secondary lamella*: staining in deep violet with hæmatoxylin, and in pale purple with anilin blue. It is this lamella which characterises the genicular cells when stained with the colouring materials. It stains much deeper than other parts in almost all colouring reagents.

IV. *The tertiary lamella*: staining in hæmatoxylin and anilin

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1) DIPPEL: Die Neuere Theorie über die feinere Structur der Pflanzenhülle.

blue very deep. When stained with the former it can not be distinguished from the second lamella: very thin: taking the innermost position of cellwall. Often this lamella can hardly be detected.

The extragenicular portion has several different characters in comparison with the genicular portion proper. The wall of the former part is not as thick as that of the latter, and there is always, after preparation, a longitudinal space left between each cell. When stained by an ordinary colouring reagent, this space remains unstained, apparently suggesting the intercellular space. When, however, the sections were treated in ruthenium red by the proper method, this space assumed an intense red colour. It is beyond doubt that the space is filled with a substance which has a peculiar character.

The cellwall of the extragenicular portion consists essentially of the continuation of the primary cellwall of the genicular portion proper. Its colouring reactions are always the same. And at the same time we do not doubt that this primary cellwall is that from which is constructed the whole framework of the articular cells. At the inner part of the wall we have a thin layer, which it is difficult to detect in some case, and which continues to the secondary lamella of the genicular cells. The thickness of the secondary lamella increases abruptly at the critical points between both the extragenicular and the genicular portions.

The extragenicular portions of the genicular cells, as has been formerly mentioned, contain deposits of calcium carbonate, while the genicular portions proper are destitute thereof. We often meet with preparations which have the genicular portions much shrunken and the extragenicular portions remaining in the original state. In those preparations we find the primary cellwalls of the genicular portions much fimbriated near the transitional points. This is probably due to the difference in the properties of the primary cellwall and the

secondary lamella : the walls of the genicular cells, the greater part of which is built up with the secondary lamella, contracting much more than the articular cells during the process of the preparation.

The middle lamella at the genicular portion proper stains intensely with ruthenium red, in the same degree as the apparent space just mentioned above. There is no doubt that both parts are continuous, although they are in some species entirely interrupted at the critical points. The space between the extragenicular portion of the cells is continuous to the intercellular spaces at the articular portion.

When a section of *Amp. tuberculosa* is stained in hæmatoxylin for a long time, say 24 hours in BOEMER'S, and treated with acetic acid thoroughly, we have a preparation stained in a contrary manner. The easily stained portions are easily washed away by the acid, and the articular cells which are hard to stain in the usual method now appear in a rather deep colour. The primary cellwall at the transitional point remains almost unstained and the distal ends of the extragenicular portion stain in the same degree with the articular cells. This fact shows something different in the properties of the primary cellwall in the transitional part and in the distal end of the extragenicular portion.

In this sort of preparation, the part of the primary cellwall in contact with the space mentioned stains intensely. cf. fig. 4. When treated with safranin the part now stained deep gains a yellowish colour.

It would not be useless to give some brief account of the middle lamella of the articular cells. The middle lamella of the extragenicular portion is practically continuous with that of the articular cells. When stained with ruthenium red, the part in connection with the genicular cells stains in the highest degree. The middle lamella of the articular

cells also stains clearly. Its thickness, however, is far less than that of the extragenicular portion. *Cheil. anceps*, *Amp. tuberculosa* and several species of *Corallina* have the periclinal cells running longitudinally but undulating; and their zonal arrangement is much disturbed (fig. 4). In these plants there are spacious rooms between the cells whenever the latter become parted. The middle lamella does not fill up these rooms and intercellular spaces in an exact sense are met with.

The cellwall of the periclinal cells at the medulla stains in some degree with ruthenium red, but those of the cortical cells in most cases remain unstained. In *Amp. tuberculosa* the genicular portion proper stained in only a very slight degree. But in most others the portion stains as deep as the cellwall of the medullary cells of the articulus. The cells at the circumgenicular cortex with its epidermal cells also have their cellwall stained in the deepest degree.

The genicula of *Amp. dilatata*, *Amp. ephedraea*, *Amp. Bowerbankii*, *Amp. echigoensis*, etc., probably all of the *Eurytion*, are built up with several zones of periclinal cells. I would call them multizonal genicula to distinguish them from the unizonal ones. They are widely different, in construction and formation, from the unizonal genicula.

The number of zones which share the formation of a geniculum in this category, varies according to the species and the individual. In *Amp. dilatata* the writer counted 15 zones (fig. 5) and in *Amp. ephedraea* only 4 (fig. 6). In every case there is more than one zone. SOLMS-LAUBACH<sup>1)</sup> remarked that the genicula of *Corallina* are built up with single layer of periclinal cells but those of *Amphiroa* always two layers. The present writer met with a number of instances which disprove the latter part of his remark.

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1). *Corallina* p. 29.

These zones as a whole does not form the geniculum ; but some of the zones, at both ends, share only partly. The zones of the periclinal cells, as has been already remarked, are concentric arcs, convex toward the apex of the frond. The boundaries of the geniculum, on the contrary, are very often convex toward the base. The consequence is that some of the zones partly share the geniculum (figg. 5-6). This fact has been formerly noticed by the writer in his paper "Cor. veræ Japon." (Pl. 1. fig. 21).

The genicula of *Amp. stelligera* and its allies are also constructed with a number of zones. Differing from the other multizonal genicula, the critical part between the articular and the genicular portion is much like the case of the unizonal genicula ; that is the ultimate ends of the distal genicular cells are differentiated into peculiar parts, corresponding, though not sharply, to the extragenicular portions of the unizonal genicula.

The staining material act upon the genicular cells in a similar manner as in the case of the unizonal geniculum. Hence we may easily point out the genicular portions with the naked eye when we stain the frond *in toto* after decalcification. In the apical portion of the fronds where the genicula have not yet been completely built up, we can tell exactly the future genicula by this method. cf. Cor. veræ Japon. Explanation of Pl. 1. fig. 21.

The cellwall of the genicular portion proper consists of the four lamellæ as in the case of unizonal genicular cells. The tertiary lamella, however, is sometimes very hard to detect. Almost all the members which belong to this category have the bordered pits in the lateral sides of the cells, besides the connecting pits at the distal ends of the periclinal cells. These bordered pits are not perforations between the cells but are septed by thin membranes of the middle lamella. They are, as a rule, in rows parallel to the zones and are



situated at the distance of about one-third of the length of the cells from the upper ends of the cells (fig. 11). In *Amp. dilatata* the tertiary lamella is remarkable in the part below the pits. This circumstance causes the upper one-third of the cells to stain in a less degree. Hence the longitudinal section of the geniculum, after staining, shows alternate parallel curves of faint and deep coloured zones (fig. 5).

In some cases we find transverse dissepiments in the periclinal cells (fig. 6). This character has never been hitherto found in the unizonal genicular cells, as far as the writer could observe. We shall give some account of these dissepiments in a later chapter.

The difference of the property of the cellwall at the genicular and the extragenicular portions is also remarkable in this case. As a rule, the cellwall at the genicular part is thinner than the extragenicular portion. The difference of the thickness occurs abruptly at the point of transition from one to the other. The decrease of thickness is essentially due to the primary cellwall. The middle lamella stains deep with hæmatoxylin at the genicular part; the primary cellwall in a less degree and the secondary (sometimes together with the tertiary) lamella stains in intense violet. In the extragenicular portion the middle lamella stains much weaker, and the secondary lamella is almost wanting here (fig. 11).

I have called it extragenicular portion here. But the area mentioned under the name is somewhat different from the case of the unizonal geniculum. As might be well understood from the structure of the genicula under treatment, there is no special portion which corresponds to the extragenicular portion of the unizonal genicula. The parts in contact with the articular portion, from the morphological point of view, have no special differentiation. A part, however, of each cell just related to the genicular portion is destitute of starch grains. The nourishment is probably consumed during the formation

of the geniculum. This phenomenon, of course, undergoes much fluctuation according to the condition of the genicula.

In *Amp. aspergillum* we find the lower half of the filamentous cells stained much deeper with hæmatoxylin than the surrounding regions. The upper zones, that is, the layer of the elliptical cells at the upper end of an articulus, stain in the same degree as the upper half of the filamentous cells. The elliptical cells have cellular connections at the distal ends and at the periclinal sides; and the transverse communication between the filamentous cells is confined to the uppermost part of the periclinal side.

### Formation and development of the Geniculum.

The formation of the geniculum takes place at an early period of the development of the frond. The first geniculum is already perceivable when the process of the frond has reached 1 mm. above the incrustation.<sup>1)</sup> As the frond grows higher, a geniculum is formed just below the apex of the frond.

The apical growth of the *Corallinæ* depends upon the division of the cell layer which covers the apex of the frond.<sup>2)</sup>

As far as the writer could observe, the genicular cells are not directly formed from the layer of the growth. The search for the youngest geniculum directly under that layer ended without success; but it was found always at a distance from the apical point. Several zones of the periclinal cells are generally found lying between the new geniculum and the apex. In the case of multizonal genicula this is especially the case, and in hair-like *Jania* the genicula are close to the apex.

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1). HEYDRICH: l. c. p. 79. Taf. II. fig. 26.  
YENDO: *Cor. veræ Japon.* Pl. II. fig. 5.

2). SOLMS: l. c. p. 29.  
KNY: Ueber echte u. falschedichotomie im Pflanzenreich.

By careful study of the shape, position and the length of the cells of the genicula, the writer arrived at the conclusion that the genicula are transformed from the zone or zones of the matured periclinal cell.

In normal cases the cells sharing the formation of a geniculum are limited to the medullary cells. An exception is the genicula of *Amp. stelligera* and its allied species. In these species the long filamentous genicula are formed of several zones of the medullary cells, generally much disturbed in the cellular arrangement. These genicula are coated with cortical layers from the beginning of their formation. In these species the cortical layers around the zonal cells play an important part in giving rise to the primary genicula of the whorly ramules.

Another example of a geniculum with cortical layers is found in certain species of the *Eurytion*. In this, the greater part of the overlying cortical layer is dropped off in the process of the genicular formation, which is described below; but those cortical cells closely adhering to the genicular cells remain as such. These cortical cells have similar characters with the genicular cells in every way and last as long as the genicula exist.

The primary geniculum of a ramule in *Amp. aspergillum*, *Amp. valonioides*, etc. is apparently transformed out of the cortical layers. These are, as a matter of fact, built up by a similar process as that by which the primary geniculum of the main stem started from the incrustation. The primitive stage of the ramules is a mamillary process on the surface of an articulus. It is built up with a number of layers of globular or rectangular cells not distinguishable from other cortical cells. As the process elongates upwards by the intercalary growth of the cells of one or more layers, the geniculum is transformed from one of the elongated cell layers. The cortical layers, at least the

innermost one, remain in the original state. cf. pl. 1. fig. 3. *Cor. veræ Japon.*

The unizonal and the multizonal genicula differ genetically. In the following paragraphs we shall try to give some details of the development of both.

One of the youngest geniculum formed from the single zone of the periclinal cell is illustrated by the writer in "*Cor. veræ Japon. Pl. 1. fig. 2.*" The figure shows a longitudinal section of a branched frond of *Amp. valonioides*. The geniculum of the branch is much younger than that of the axial stem. The genicular cells are hardly longer than the ordinary vegetative cells, with the circumgenicular cortex still remaining as such. The differentiation of the cellwall has already taken place in the genicular cells, staining the genicular portion proper in deep violet by BOEMER'S hæmatoxylin. The geniculum is already free from the deposit of calcium, while the extragenicular portion is calcified as in the remaining part.

As a general rule, the sum of the extragenicular portions at both ends of the genicular cells is nearly equal to the average length of the periclinal cells of the articulus. In some species (*Cheil. anceps* and *Jania* species) the zonal arrangement of the periclinal cells is much disturbed. As a consequence, the extragenicular portions of the cells are very variable in their length. Those cells which have a comparatively short extragenicular portion at one end have in almost all cases a much longer portion at the other :—the sum of both portions being nearly equal in each cell.

This circumstance teaches us that a certain zone of the periclinal cells is divided into two parts along a plane perpendicular to the long axis of the cells. At the division plane the intercalary growth of the cells takes place, stretching the zone lengthwise. The cells elongate, without deposition of the calcareous substance, and with a new

addition of the secondary lamella. The middle lamella follows the growth, though it is much thinner than in the articular cells.

The growth of the cells seems to be of such great rapidity that the cortical cells around the geniculum can no longer bear the strain. The result is the cracking of the cortex.

Regeneration seems to take place at the overhanging margin of the circumgenicular cortex after the splitting has occurred. On the freed ends of the cortex we actually observe the remnants of the decayed cells which have broken during the formation of the fissure; and generally we find the cells in the circumgenicular cortex dividing in the anticlinal and periclinal direction (fig. 4, 6 and 10). This circumstance, no doubt, effects the "linear" genicula, exposing a comparatively smaller portion outside, the larger part of the length being hidden under the circumgenicular cortex.

The best developed example of the circumgenicular cortex is found in *Amp. stelligera*. In this species we find a highly thickened portion at each distal end of an artichulus. This thickening is due to the unusual increase in the number of the cells of the circumgenicular cortex. (fig. 8).

While the geniculum is yet very young or the development is not comparatively rapid, the cortical layers remain around the geniculum (fig. 5).<sup>1)</sup> These layers in most of the species are destined to drop off sooner or later. HARVEY<sup>2)</sup> describes a plant with calcareous granules upon the genicula. His plant had probably the circumgenicular cortex split into several pieces, remaining attached upon the surface of the genicula. Very often we find similar cases in several other species. Fig. 9, shows one case in *Cheil. frondescens*,

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1). See also Pl. I. fig. 3. *Cor. verae* Japon.

2). *Nereis Australis*; *Amp. Bowerbankii*, Harv. p. 97. t. XXXVII.

having a few cortical cells, of course calcified, yet remaining undetached.

In the unizonal genicula the cells undergo further development in only the slightest degree. The cells of the basal genicula of *Amp. aberrans*, for instance, have their length nearly equal to the upper ones and the thickness of their walls seems to have received no addition. SOLMS-LAUBACH<sup>1)</sup> observed the formation of transverse septa in the genicular cells of *Corallina*. These transverse septa were quite common in the genicular cells of the *Eurytion*; but, as far as the present writer could examine, there was no septum formation in the cells of unizonal genicula, to which category all of *Corallina* belong.

The formation of the multizonal genicula is fundamentally different from that of the unizonal. The first step is the decalcification of a certain part of the frond, bounding several zones of the periclinal cells. This process seems to be carried on in a comparatively short time. The boundary of the decalcified area is very sharp, and can be easily traced by a staining reaction after the frond has been artificially decalcified. The area seems not to extend further than the limit formed at the first step of the formation.

While decalcification is taking place, the cortex around it remains unaltered for some period. But afterwards a part of the cortex, mostly on the flat surface of the frond, comes off in shape more or less corresponding to the decalcified area. The result is the "fenestraform" geniculum.

As the geniculum develops further, the cortex around it continues to break off, until a complete "bandform" geniculum is visible to the naked eye.

As soon as the fenestraform has appeared, the genicular cells begin to undergo further modifications. It is the formation of the

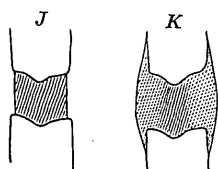
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1). *Corallina*: p. 29.

transverse septa in the periclinal cells. These septa begin to appear first in the cells at the peripheral region (fig. 6).

In the beginning each genicular cell has two or three septa at nearly equal distances. As the process is carried on further, more septa are continuously formed between the old ones. At last the long fibrous cells are divided into a number of collenchymatous cells, with a much thickened membrane and scanty room. The zonal arrangement of the cells is much disturbed.

The peripheral cells which are now globular from the septation begin to form a secondary cortex. The cells continue to divide tangentially and the thickening of the wall increases further. The consequence is a thick layer of cortex, overlapping the distal ends of the articuli at both sides. The length of the geniculum at the axial portion does not very much exceed that of a young geniculum. We always find the large bandform genicula at the basal portions of the fronds in those species such as *Amp. dilatata*, *Amp. ephedraea*, *Amp. Bowerbankii*, etc. The width of the genicula is often larger than the length of the neighbouring articuli. This modification is due to the peripheral part of the genicula extending to cover the distal ends of the articuli. The accompanying figures J and K show the longitudinal sections of the fronds of *Amp. dilatata* through the genicula. Fig. J is a completed geniculum but without the secondary growth of the



peripheral cells; fig. K. is a rather old geniculum with the peripheral part of the genicula overlapping the articuli at both ends.

In these old genicula, the medially and the cortical portions are more or less distinguishable. The former has the cells some what elongated and an obscure zonal arrangement of the cells is to be seen. The latter has cells with narrow rooms, thickened wall, and arranged in radial rows. The

thickening of the wall is accompanied by the formation of canals therein. The canals radiate from the center of the cells, some continuous to the canals of the neighbouring cells and some ending at the middle lamella. cf. *Cor. verae* Japon. Pl. 1. fig. 20, which illustrate the cross and the longitudinal sections of the medullary portion of an old geniculum.

The bordered pits are also modified by the thickening of the wall. At an early stage, only the canals which are modification of the pits are to be seen. But in the further advanced stage, a new formation of canals takes place by the thickening of the walls; so that we can not distinguish the canals of genetically separate origin.

These remarks do not apply to the genicula of *Amp. stelligera*, although they are built up with a number of zones. The cortical cells in these genicula remain persistent from the beginning and the zonal cells grow rapidly and increase in their number by transverse division. The cortical cells also accompany the growth and the multiplying of the cells. It is not certain how the primitive genicular are transformed from the calcified articulari. The presence of the extragenicular portions suggests the similarity of the mode of the genicular formation with that of the unizonal genicula. But already in a pretty young genicula, several zones of the periclinal cells have been clearly observed (fig. 8). I was not able to trace the origin of the genicula in the species, as the apical portions of the dried material are always due to the destruction of the cellular arrangement while imbedding in the paraffin. This must be kept for future study, until we have preserved material from fresh plants.

One thing which we must not omit mentioning here is that the primary genicula of the ramuli of *Amp. stelligera* are not directly connected with the articular cells but with the cells of the axial geniculum. Some of the zonal cells of the axial geniculum travel



obliquely upward and outward and protrude into the medulla of the primary genicula in the mode of emergence through cortical layers (fig. 8).

### The Difference in the Properties of the Cell-walls of Articular and Genicular Cells.

It was not the aim of the present paper to give a discussion in detail concerning the chemical properties of the genicular cells. In the course of study, however, some points which might interest the reader in some measure have been noticed about the differences in the properties of the cellwall of the articular and the genicular cells.

The calcareous matter is in the cellwalls of the articular cells. This has already been remarkable by former observers.<sup>1)</sup> The middle lamella seems especially rich in such matter. Although positive proof is lacking, this view is held from a microchemical examination of the cellwall, as will be described below. The mineral is in the form of fine ingredients mixed with other substances.

The cellwall of the genicular portion proper and the epidermal cells are entirely free from calcareous matter. The reproductive cells are, of course, similiary free.

The extragenicular portions of the genicular cells, and the articular cells, except the epidermis, have a calcified cellwall.

Briefly speaking, the cellwalls of the cells of the *Corallinæ* consist essentially of a compound of cellulose, gelose and lime. The proportion of the components varies according to the parts of the fronds. The energetic cells, such as epidermal cells of the grow-

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1). NELSON and DUNCAN. l. c. p. 199. and p. 205.

ing portions, the periphery, or the circumgenicular cortex, have a larger percentage of the pectin compound than of the cellulose. In this respect the growing points of the land plants furnish us an illustrious parallel. The middle lamella, especially at the extragenicular portion, and the connecting plates between the cells, are richer in the pectin compound. In phanerogamic cells we have calcium pectate in the middle lamella. In the present study the writer was not able to determine whether the middle lamella contained the mineral in the form of calcium pectate or calcium carbonate. Any how, the middle lamellæ of the articular cells, as in the case of the phanerogamic cells, are very rich in pectin compound.

The cellwall of the genicular portion proper has several diverse characters. By iodine it gains a deep bright yellow colour, almost brownish. So far as the ordinary cellulose reagents are concerned, the cellwall of this portion gives no reaction of cellulose. It is not a chitinous substance. Probably the cellulose reaction might have been retarded by some compound other than the pectin. The middle lamella of this portion gives also a distinct reaction of a pectin compound. This leaves us in doubt whether a trace of calcium compound occurs there or not, although we can by no means detect it.

The pectin compound in the cellwall is in the form of gelose as in the other algal members.

The cellulose reaction is not discernible before the gelose has been dissolved. But the gelose reaction is clearly visible without any treatment beforehand.

When the preparations<sup>1)</sup> are treated with 50% hydrochloric acid for 12-24 hours, both the cellulose and the gelose reactions begin to appear. In these ruthenium red stains the primary cellwall of all

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1). The study has been made upon preparations cut by microtome in the thickness of 3-4 $\mu$ . The object is imbedded, after decalcifying in PERENY'S fluid, in 52° paraffin.

parts in a greater or less degree; but the reaction is most vivid in the epidermal layer and in the cellwall of the subepidermal cells. The genicular portion proper retains a bright red colour. Treated with chloriodide of zinc, the epidermal layer assumes a deep yellow colour and the subepidermal cells have their cellwall stained in faint violet. The primary cellwall in every part becomes stained in violet. The middle lamella remains unchanged. The starch grains in the medullary cells assume a chestnut brown colour, while the cellcontents in the subepidermal cells change only to yellow. The genicular portion proper stains in deep brownish yellow. The gelose reaction by ruthenium red is seen without treating with hydrochloric acid, but chloriodide of zinc can never act upon the cellwall of the articular cells before the treatment with the acid.

Before treatment with hydrochloric acid the cellwall gives no reaction either by strong caustic potash or by potassium iodide iodine and sulphuric acid.

After boiling the sections in 2% hydrochloric acid for a few minutes, washing thoroughly in water, and again boiling in 2% caustic potash, a few drops of chloriodide of zinc were poured in under the coverglass; epidermal layer stained in bright yellow and the cellwall of the subepidermal cells in a slight degree. The cellwall of the articular cells gains a yellow tint, but the middle lamella of these, which was much swollen during the process, stains in pale violet. The connecting plates between the cells become exceedingly clear: the central portion of them staining in deep brown and the border in bright yellow. A preparation boiled in like manner was treated in ruthenium red. The middle lamella, if not swollen too much, is stained in some degree, the swollen portion remaining unstained: the connecting plates assume a red colour and their central portions in a greater degree.

When treated in 50% hydrochloric acid for 48 hours, the gelose reaction becomes fainter. The epidermal layer stains no more with ruthenium red; the middle lamella at the articular portion in some measure; and the cellwall of the genicular portion pretty strongly. On the other hand the genicular cells are stained deep brown by chloriodide of zinc and the middle lamellæ of the articular cells and of the extragenicular portions assume the deepest brown colour. The cellwalls of the articular portions, inclusive of the extragenicular portion, assume a deep violet. The epidermal layer gives no reaction with chloriodide of zinc.

Keeping 5 days in 50% hydrochloric acid, I observed the reactions. None of the parts was stained by ruthenium red. By chloriodide of zinc the middle lamella stained in deep violet, especially at the extragenicular portion. The cellwall of the genicular portion proper stains in deep brown, but nothing of a violet tone. The preparation thus kept was treated with copper ammonium oxide for 48 hours. The result was the entire dissolution of the sections except some of the genicular portion proper. This remnant when treated with chloriodide of zinc gives a brownish colour. Some of the preparations had been kept in copper ammonium oxide for 20 hours previous to the treatment with hydrochloric acid, the cellwalls of the articular portion were almost all dissolved, leaving the epidermal cells behind. The middle lamella of the genicular cells remained unchanged, but the cellwalls were almost gone.

I would point out some minor details which were met with during the treatments above mentioned, by the staining reactions of anilin blue, haematoxylin, safranin, etc.

The intercellular space in the articular cells is some times filled by the middle lamella, the so called intercellular substance of DIPPEL;<sup>1)</sup>

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1). Die Neuere Theorie über d. feinere Struct. d. Pflanzenhülle.

sometimes it is free from any packing. These differences depend upon the species. In some species which have no true spaces between the cells, the middle lamella has a considerable thickness; in those which have the rooms, the middle lamella is found adherent to the primary cellwall around the room. In either case the middle lamella runs into the genicular portion proper, often much compressed at the critical point and hard to detect. The middle lamella at the genicular portion proper is almost always much thinner than in the articular portion. The middle lamella is rich in pectin compound and stains very well with hæmatoxylin, safranin, anilin blue and ruthenium red.

The primary cellwall supplies the greater part of the framework. When the pectin compound had been dissolved by proper treatment, the cellulose reaction was seen in this part. An exception is the cellwall of the subepidermal layers: it makes no response to the cellulose reagents, but gives us a vivid gelose reaction.

The primary cellwall of the articular portion is continued to that of the genicular portion proper. It becomes much thinner when it enters the latter portion and seems to assume a chemical character different from the articular portion. This conclusion is reached from its giving no cellulose reaction even after long treatment with the gelose solvent. It is stained a pale blue by anilin blue and faint violet by hæmatoxylin. Ruthenium red stains it light red.

The secondary lamella lines the inside of all the cells and has a character similar to the middle lamella against the chemical and the staining reagents. It runs into the genicular portion proper and a secondary thickening takes place to form the tertiary lamella. These two layers are essentially equal in their character and hardly distinguishable in ordinary reagents. But when stained with anilin blue, the inner layer gains the deepest purple colour and is easily

distinguishable from the other. The tertiary lamella is characteristic of the genicular portion proper.

The lamellar arrangement of the cellwall in *Amp. dilatata* and its allied species comes under a somewhat different category. The tertiary lamella is only visible in the lower two thirds of the cells of the genicular portion ; in other words the parts below the row of the pits (figg. 11-12). It is hard in these species to recognize the layer which corresponds to the secondary lamella of the other members. On the other hand, a characteristic lamella is found at the meeting point of the cells, which are always eight in number. The lamella develops at the corner of the cell toward the center of the intercellular space to fill it up. This lamella has some space between it and the mother cellwall where some substance easily stained with hæmatoxylin is always found (fig. 12).

The majority of the *Corallinæ* have connecting plates at the distal ends of the cells both at the medulla and at the cortex. These plates show the characteristic reaction of the pectin compound, while the cellulose reaction is hard to detect. The connecting plates at the articular ends of the extragenicular cells are especially rich in the pectin compound.

Those species which have conspicuous canals or rather perforations between the cells have their plates in the form of thin septa. But when the canals are narrow passages, the colouring materials fill up the passages and prevent us from determining precise form of the septa.

In many species we often find large openings to allow the communication between the cells. cf. *Cor. veræ* Japon. Pl. II. figg. 21 and 23. These large openings seem to lack any kind of connecting plates. SCHMITZ<sup>1)</sup> observed the protoplasma of the neighbouring cells

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1). Untersuch. ueber d. Zellkern d. Thall. p. 122.

communicating with one another through the pores in *Jania rubens*. WILLE<sup>1)</sup> also mentions this character and seems to believe that probably all species of *Amphiroa* and *Corallina* have the same sort of pores. As will be understood from the present study, the pores in the cell-walls are limited to a certain group of the *Corallinae*. Some of *Amphiroa* have the pits and most of the *Eurytion* have the bordered pits. This will be described more in detail.

*Amp. dilatata*, *Amp. Bowerbankii*, etc., are those which have the bordered pits. These pits are found at the distal ends of the periclinal cells in like manner as the connecting plates in the other species, and also at the periclinal sides of the cells. They are exactly similar in the structure to those found in the *Conifers* (fig. 12). The large openings just mentioned above are not met in these species.

The bordered pits in the periclinal sides are almost always at points nearly one third of the length of the cells from the upper ends, as has been formerly remarked. Hence the pits, in a meridional section of a frond, are seen disposed in rows parallel to the zones of the cell connection. About the fate of the pits a brief account has already been given (p. 32).

There is an interesting parallelism in the pits of the land plants and the *Corallinae*. In the land plants the pits are normally found in such groups as *Coniferae*, *Drimys*, *Trochodendron*, etc., which are provided with poor vessels or none at all.<sup>2)</sup> It has not been hitherto described, as far as the present writer's knowledge extends, in the lower-cryptogamic cells. The principal part of the translocation of the nourishment is played through the thin membrane of the pits. *Algae* as a whole have no kind of the vessels and all communication must be furnished by the openings between the cells. And these

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1). Bidrag till Alg. Phys. nat. p. 40.

2). STRASBURGER: Ueber d. Bau u. d. Verrichtungen d. Leitungsbahnen. p. 161.

openings septated or non-septated, are always met in the cells of the *Dictyotale*, the *Florideæ* and many of the *Phæophyceæ* and some of the *Chlorophyceæ*.

I have already mentioned in connection with *Amp. dilatata* (p. 25) that the cell contents in the surrounding cells of the geniculum are consumed. This may possibly always be the case in the other members. The cell contents are in greater part *Florideæ* starch. There is little doubt that the starch is transformed into a soluble hydrocarbon and carried on through the thin membrane of the bordered pits to be consumed during the formation of the geniculum.

### The Value of the Geniculum as a Systematic Character.

The presence of the genicula has been counted as the crucial point in distinguishing the *Corallinæ* from the *Melobesiacæ*. But little heed has been given to the systematic value of the geniculum in the study of the *Corallinæ*. The external shape of the articuli, which is undoubtedly highly variable, has been the important specific character; and the position of the propagating organs played a weighty rôle in the generic determination. The mere external appearance of the genicula has sometimes been mentioned by writers in describing the species.

The internal structure of the genicula, however, has some coincidence with the external morphological characters. SOLMS remarked the difference between the genicula of *Corallina* and *Amphiroa* as noted before (p. 23). But we found many examples which disprove his observation: some of the species reckoned under the genus *Amphiroa* have unizonal genicula, and some multizonal, as has been



related in the preceding chapters. KÜTZING<sup>1)</sup> insisted upon the view that the difference of the internal structure might serve to determine the genera of the *Corallinæ*. This is not absolutely true. But some of the members, probably almost all, of a section established by DECAISNE<sup>2)</sup> have common characters in respect of the internal structure. For instance, as would be already understood, most of the *Eurytion* have the bordered pits in the cellwall, and multizonal genicula which undergo further development. Most of *Jania* have the zonal arrangement of the periclinal cells irregular, and the unizonal genicula. And *Cheilosporum*, especially the *Eucheilosporum*, has a similar character to *Jania* in this respect. But we can not agree with the opinion that *Amp. stelligera* which has the peculiarities in the structure, as well as in the function, of genicula should be classified under the genus *Amphiloa*. So also *Amp. aspergillum*.

It should be admitted that the morphological characters, both of inner and outer, of genicula may play some important part in systematic survey. It may not be a generic character; but at least a group may be more sharply defined by the peculiarity, of any, of genicula, rather than by mere external forms of articuli. The position of the genicula in a frond has sometimes a unique character and may well play a part of specific importance.

These views, together with those of the former writers, are reserved for future discussion.

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1). Ueber die Polyp. Calcif.

2). Classif. des Alg. et des Polyp.

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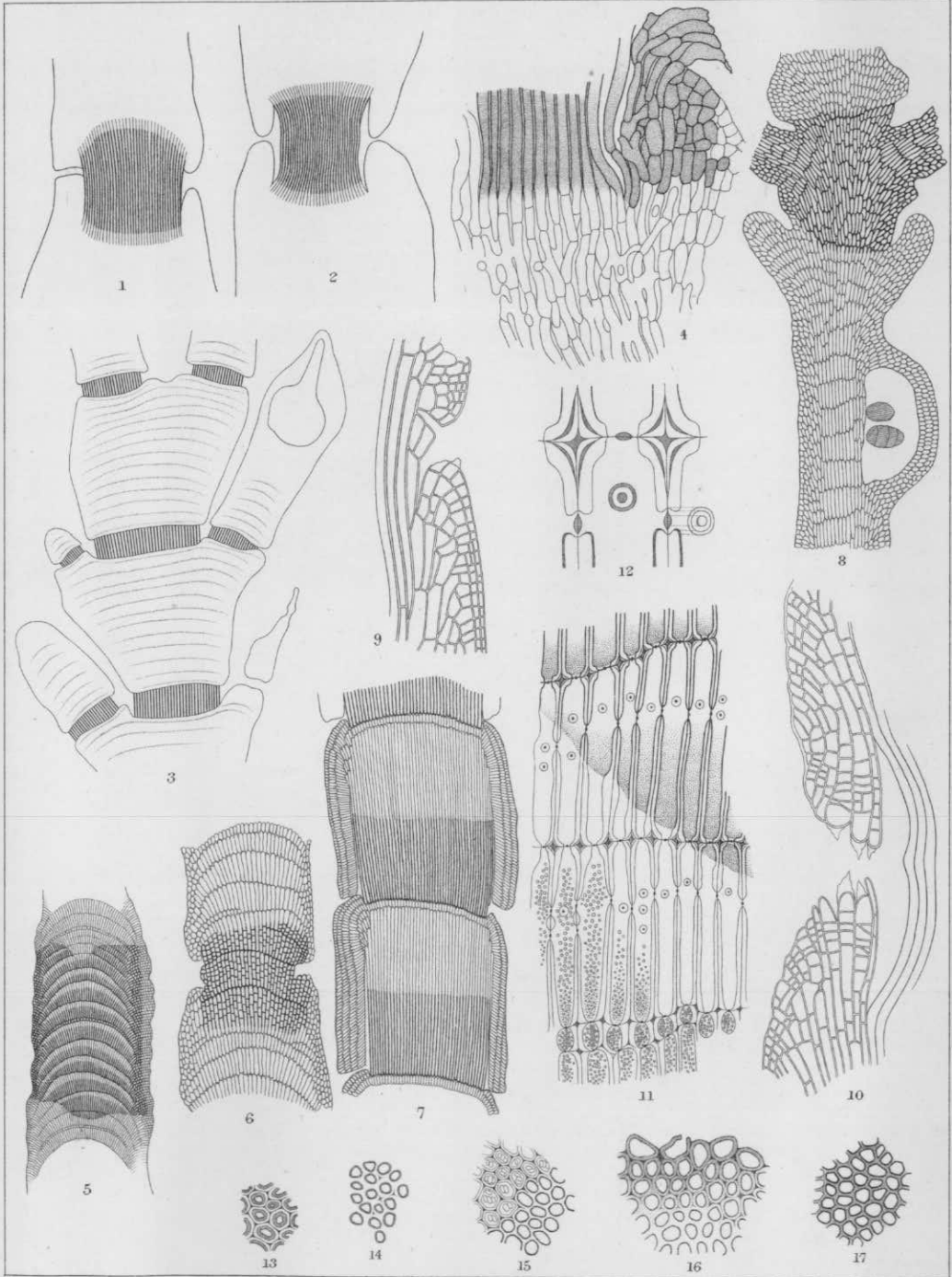
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PLATE.

## EXPLANATION OF PLATE.

All figures are Camera drawings, with the exception of fig. 12.

1. Longitudinal section of a frond through a geniculum ; *Corallina chilensis*. The extragenicular portions of the genicular cells are shown by the fine lines.  $\times 60$ .
  2. do. *Cheilosporum frondescens*.  $\times 60$ .
  3. Longitudinal section of a frond of *Amphiroa aberrans*. Observe that the genicula of the axial articulus and of pinnæ originated from different zones.  $\times 40$ .
  4. Longitudinal section of a frond through geniculum ; *Cheilosporum anceps*. The shaded portions gain a deeper stain from the colouring reagents.  $\times 285$ .
  5. A meridional section of a frond through the young geniculum ; *Amphiroa dilatata*.  $\times 40$ .
  6. do. *Amphiroa epheræa*.  $\times 40$ .
  7. Longitudinal section of a frond of *Amphiroa aspergillum*.  $\times 40$ .
  8. do. *Amphiroa stelligera*.  $\times 60$ .
  9. Longitudinal section of the circumgenicular cortex of *Corallina chilensis*.  $\times 165$ .
  10. do. *Cheilosporum frondescens*.  $\times 165$ .
  11. A portion of fig. 5.  $\times 650$ .
  12. The meeting points of the genicular cells of above : highly magnified.
  13. Cross section of the genicular cells of *Corallina yeuoshimensis*.  $\times 285$ .
  14. do. of *Amphiroa aberrans*.  $\times 285$ .
  15. External portion of a geniculum attacked by parasitic *Diatom* ; cut lengthwise : *Amphiroa aberrans*.  $\times 285$ .
  16. External portion of a geniculum of *Corallina chilensis* ; cut lengthwise.  $\times 285$ .
  17. Cross section of a geniculum of *Amphiroa aberrans* ; about the middle portion.  $\times 285$ .
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K. Yendo del.

K. Yendo : Genicula of Corallinae.