XVIII.—On some Relationships of Inflorescences. By G. Sigerson, M. D., Ch. M., F. L. S. [Abstract.]

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I.

The relationship which exists between the inflorescences of plants is a subject of not a little importance, for several reasons, and yet it is one which has not hitherto received much attention from scientific botanists. As helping to throw light upon obscure affinities of orders, and as symptomatic of the position and subordination of plants and divisions, it appears to merit more consideration than it yet has received, and on this account I have ventured to put together some suggestions on the subject. These remarks, however, must be regarded as merely an outline or an abstract, more or less imperfect, of that mode of dealing with the question which has appeared to give the surest clue to some of its intricacies.

Heretofore, observers appear to have taken the capitulum as their starting point in dealing with some relationships which are not obscurely apparent, as well as with a few other *quasi*-relationships, the correctness of which does not seem clear and evident. In the capitulum the florets are sessile. If we suppose them elevated upon footstalks, it has been said, an umbel will be the result. Again, if the receptacle of the capitulum be supposed sufficiently elongated, we shall have the spike produced as a consequence; and from the spike, by the development of the flower stalks, the raceme may be supposed to be formed. If, however, the inferior peduncles be prolonged to a greater extent than the upper ones, then we shall have the corymb; whilst, supposing the peduncles to branch, the panicle becomes evident as a result of the ramification of this form.

To this it has been added, that the cone is a modification of the spike, the rachis in this instance bearing persistent scales; and the spadix is said to result from the rachis of the spike becoming fleshy, and bearing the flowers more or less imbedded in it.

Whilst many of the above relationships appear to be natural enough, there are some, especially the latter suppositions, which cannot well be regarded as unexceptionable. There is no particular order of subordination marked out; whilst, in assuming the capitulum as a sort of starting point or centre, whence the several inflorescences are supposed to have radiated, we must ignore those forms which preceded it, and consequently neglect many relationships by which they are allied with higher forms.

After a careful analysis of the lower forms of inflorescence amongst Phanerogamia, from which many of the more complex forms may be deduced, it appeared to me necessary to revert to cryptogamic plants, in order to ascertain their antecedents. These two sub-kingdoms have been popularly regarded as so essentially separated and distinct, that an apology for so doing might be by some considered necessary. But with the advance of the science, and the greater knowledge possessed of the inferior section, so many close affinities have been traced, and so many ties of relationship made evident, that a reference to new points of likeness cannot well be regarded as intrinsically erroneous, or out of the line of progress. The object of the present paper being chiefly to endeavour to clear up some of the relationships of the inflorescences among phanerogamous plants, and settle their subordination, those of the Cryptogamia are but incidentally alluded to, and only in so far as they may contribute to make these relationships more evident, and tend to illustrate their natural sequence.

On referring, then, to the manner in which the reproductive organs are borne in the Fucaceæ, we find that here they are gathered together into cavities or conceptacles, which are collected into heads or receptacles at the extremity of fronds. The conceptacle communicates with the external medium by an opening or pore. The central portion or axis of the receptacle is frequently formed of mucus and long-jointed cells; but occasionally, however, as in *Pycnophycus tuberculatus*, the interior is more solid, and is occupied by a denser cellular tissue, which may be taken as representing the pith of higher plants. Some of the Fucaceæ are diœcious, others diclinous, and a like arrangement occurs not unfrequently among the lower Phanerogamia.

On examining one of these conceptacles, it is seen that the reproductive organs within it arise from the walls or parietes, and that it contains besides a number of filaments or paraphyses, which in the female conceptacles surround the spores. The filaments are not always sterile. Occasionally they form antheridia, and these may be in separate conceptacles, or in the same. Whilst the antheridia, therefore, are analogous to the stamens, the filaments may be regarded as analogous to the staminodes, or the filaments of stamens, when barren, and consequently to the floral envelopes, however great the apparent difference, because the stamens are admittedly capable of being transmuted into such appendages. In certain Phanerogamous plants, indeed, the limb of the floral organs is so much depauperated as to make the difference seem much less; thus occasionally the calyx is represented merely by a circle of hairs, which bear a close morphological resemblance to the filaments alluded to. The floral envelopes of Phanerogamia may therefore be regarded as represented in an extremely rudimentary state* in the conceptacles of Fucaceæ.

* As the floral envelopes may pass into bracts, and even into leaves, it may possibly happen that hereafter botanists, in pushing forward the theory of development, will come to regard the cryptomatic frond, bearing within it means of reproduction and rudimentary floral envelopes and leaves, as represented by the cotyledonous growth of higher plants, which enclose the possible plant, with its higher organs, floral envelopes, and

In mosses, the paraphyses, which generally accompany the antheridia, at once suggest the usual position of the floral envelopes with regard to the stamens, and represent them.

In certain of the Rhizogenæ the seeds are imbedded in filaments or setæ, which may be likened to these paraphyses. Here, indeed, my views are fortified by the observation of Mr. Griffith, who remarked that the hairs in which the fruit were imbedded in the genus Phæocordylis present a striking analogy to the paraphyses of Drepanophyllum and certain Neckeræ, and also with the antheridia of ferns.

Bearing these things in mind, and recollecting that the tendency of development is generally to division, and advance from simple forms to complex, might not even the perichætial leaves of mosses be regarded as representative of the parietes of a conceptacle fissured and divided into parts?

II.

Suppose, now, that we take the receptacle of a Fucus, which consists of numerous conceptacles, and imagine that this tendency to division has caused the pores to be extended and united to each other by lines of suture (as in figure 2), the form which we then obtain will be found to be an antetype of the strobilus or cone. It is hardly necessary to indicate how strictly the analogy can be carried out, or do more than remark that the reproductive organs are situated in a similar way in both forms. They are enclosed in peculiar processes, and these in the young cone are in close approximation, so as to leave merely the sutural lines evident; but, as they develope, they divide, and, separating when they grow older, leave the resemblance naturally less evident.

The development of sutures isolates the processes of the axis; and observers who looked at them superficially, and out of this connexion, have been tempted to call their further removed forms "scales," and to regard them as modified leaves. It might be urged that analogous processes are present in Equisetaceæ, which show branches rather then leaves as appendages; and, perhaps, the generally unbranched condition of the fertile stems, as compared with the barren ones, might be partially accounted for by accepting these processes in the cone as a cluster of transformed branches.

It is of the essential character of these axial processes that in some way they shall bear the organs of reproduction, whether as in Fucaceæ

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leaves. In the lower section, that which represents the cotyledon, *i.e.* the frond, is the part most developed, whilst the other is rudimentary; in the superior section the frond is seen reduced to a minimum in the cotyledon, sufficient simply to assist the organism in its first stage, whilst the more highly organized portion here is more highly developed. Thus a possible mode of development or passage from the Cryptogamia into Phanerogamia might be obtained, which would account, without violent and unnatural changes of plan, for the geological revelations of plant growth, and which would likewise account for the apparent absence in Cryptogamia of cotyledons (the frond actually serving as such), and for their presence in Phanerogamia, where they still remain as relics of the frond, and as indications of an anterior stage of growth.

they be united so as to form cups or conceptacles, or separated by fissures so as to be more or less isolated. These organs may be borne all over the parietes, as in the Fucaceæ—within the rim of the isolated peltate process, as in Equisetaceæ—on the upper surface of the process near the axis in some Pinaceæ, or beneath, as in the peltate scale of Cycadaceæ, or on the sides, as in their leaf-like processes. Then the anthers are on the under surface of certain male cone scales; and beneath, likewise, in the peltate male scales of the Taxaceæ. Thus, whilst in Fucaceæ they are borne all over the parietes, their arrangement in higher plants shows that there is no part of the parietes of the isolated processes on which they may not likewise be found.

The so-called "scales" therefore are, in point of fact, essentially reproductive organ bearers, and hence should properly be regarded as peduncles. Peduncles, it is admitted, are not unfrequently various in form; they are not always stalk-like and round, but are occasionally flattened and fasciated.

In certain plants, such as *Ruscus aculeatus*, they even assume the appearance of leaves; and, when this is seen to be the case, there is no reason for feeling a difficulty, when in cones the processes become flattened and scale-like.

Taking these things into consideration, it is impossible to agree with Dr. Lindley, when he contends that cone scales are metamorphosed leaves. Whilst they differ from true leaves in function, in form, and in structure, they differ also in occasionally arising, as in *Pinus silvestris*, from the axils of degraded or rudimentary leaves. This is what occurs likewise in the case of *R. aculeatus;* and, whilst Dr. Lindley argues that leaves may arise in the axils of leaves, it cannot be denied that it is not what usually happens. Schleiden, indeed, in putting forward the view that these peduncle processes of the cone were axillary buds of carpellary scales, broadly stated that *folium in axillâ folii* would be without example in the vegetable world.

Accepting the cone as a form of inflorescence composed of a number of peduncles arranged in a peculiar manner, and remembering the tendency to separation of parts in development, certain forms will be seen to fall in easily as more highly modified forms of this. For instance, we may place here, in relationship to it, the superficially dissimilar, but really analogous, many-branched spadix of Palmaceæ; and, in fact, if we look at a compound fruit of one of the Pandanaceæ, where the flowers are borne on a spadix, we discover (as in *Freycinetia imbricata*) a superficially striking resemblance to the strobilus, arising from the manner in which the peduncles are arranged.

III.

For a better understanding of the author's views, reference is requested to the accompanying illustrations.

In Fig. 1, Plate I., the receptacle of a Fucus is represented in vertical section. The reproductive organs are contained in the conceptacles, which, communicating outwards by pores, give the margin an indented appearance. Looking at this receptacle from another point of view, we shall find it to be composed of a central axis, which divides out into short processes that bear the reproductive organs. This is their essential function in common with that portion of the axis included between their bases. These axial processes in the present instance are not isolated, but united together; so that, looked at from without, only an oval body, pierced with pores, is observed.

Development, however, is accompanied by the division and separation of parts. This we may suppose to happen here by the gradual isolation of the axial processes already mentioned. The united exterior of the receptacle is split up by fissures, running from pore to pore, as imagined in Fig. 2; and we have then the axial processes isolated from each other and distinct. What was essential with them—the bearing of the reproductive organs—remains constant; though these, instead of being spread over the whole interior surface, may be restricted to particular parts.

The division and isolation spoken of do not take place in the Fucaceæ. We must look for it in a higher order, and shall readily discover it in the strobilus of the Equisetaceæ. In Fig. 3 we have a vertical section of this cone. Considered in this light, its affinities with the receptacle of the Fucus become obvious, and scarcely require to be pointed out. Everything remains the same, except that the spores are not dispersed over the whole interior of a conceptacle, but restricted to the inner rim of the peltate head of the axial process. Of course, as these processes are isolated, a view of the exterior of the perfect cone does not show pores, but fissures. In point of fact, it is identical with the fissured receptacle as imagined in Fig. 2.

Having arrived at this stage, the next modifications are accomplished by simple changes in the axial processes, taken by themselves, or with regard to the axis. In the first instance, the receptacle is wholly cellular, as is the plant which bears it. Some difference has been observed between the laxer cell-tissue of the centre and the denser parenchyma which surrounds it. In more highly organized plants a similar relationship is preserved between the axial and the peripherical tissues.

Passing from the preceding examples to Figs. 4 and 5, we come to explicable developments of those forms in the higher order of the Pinaceæ. In the first-named figure we have a vertical section of a galbulus (of *Cupressus sempervirens*); in the second, a similar section of the strobilus or cone (of *Pinus sylvestris*). In the galbulus the axial processes are not so remote in form from what we have seen them in the cone of Equisetum as not to allow of the relationship being recognised without difficulty. Here also they are peltate; and the only remarkable difference is, that the ovules are not borne exactly in the same spot as the spores, but a little removed from it. This, however, was mentioned as to be expected.* In the Pine cone (Fig. 5) the axial

* These female cones are strictly analogous to the ovaries of Angiospermia, being in fact ovaries. Considering them as such, it is interesting to note that the diverse distri-

processes have become more elongated, but they still have something in their thickened extremities to remind us of the more primitive forms. This is lost or modified in other members of the same family.

Recollecting that these axial processes are peduncles, we may discover them in Angiospermia, under various modifications. For instance, in Fig. 6, we have a fruit which bears an external resemblance to a cone, in consequence of the axial processes coming off in a somewhat similar manner. This is the fruit of *Freycinetia imbricata,* one of the Pandanaceæ, or Screw Pines. Isolation and separation of parts proceeding still, we shall have the branched spadix of Palms as a resulting form, the spathe perhaps standing for the involucre present in the composite and umbelliferous plants.

In the lowest forms mentioned the extreme receptacles are occasionally outgrown; and where in the Pine we have the compound or male cone, the axis is sometimes prolonged into a tuft of leaves. Now, in some Arads we have this condition of things visible in a modified manner. In *Arum maculatum,* for instance, the axis or spadix bears the female and the male organs, next a few "nectaries," rudimentary leaves probably, and finally is prolonged into a cellular or fleshy club.

Fig. 7 represents a vertical section of the cænanthium of the Fig. The peduncle has been said to be "excavated," the flowers being inside. Might we not, however, rather regard a conceptacle of the Fucus as a distant antetype of this inflorescence? That also may properly be called a cænanthium; for the "flowers"—*i.e.,* the reproductive organs and their filaments—abide together in community. Both are cavities containing these, and opening to the air, each by a pore, be it large or small. Around this opening are filaments, sometimes protruding in one instance, and scales to represent them in the case of the Fig. These in further developed forms receive the name of involucres.

The direction of growth being coincident with the direction of the axis, the tendency here is to push up the bottom of the cavity, and, in fact, to turn the cænanthium inside out. In *Dorstenia contrayerva* (Fig. 8) it will be noticed that this process has gone so far as to level up the cavity, disparting its edges. In Fig. 9, the female capitulum of *Artocarpus incisa,* the process has been fully completed. These three are instances from plants closely allied. The capitulum of a Composite shows the tendency described, changing the form of the peduncle extremity as it flowers and ripens. In Fig. 10, for instance, the common Dandelion flower and peduncle extremity are shown. The peduncle is "excavated" occasionally more deeply than what is seen in this hasty sketch; as it flowers and ripens, however, the centre rises into a conical form, and the globular shape of the head of the perfectly ripened seed is well known. On following this process attentively, it will be seen that the scales around the mouth of the cænanthium have been displaced so as to become the involucre of the capitulum.

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bution of what represent the ovules in the loculi is explicable by what we see there. Taken in this connexion, Schleiden's opposition to the theory of marginal placentation receives support.

Isolation and separation continuing, we have the simple umbel (Fig. 11) arising from the capitulum by the development of foot stalks to the flowers. This natural advance suggested itself to my mind before I was aware that it had been previously noticed. Compound umbels, from ramification of the peduncles of their simple umbels, seem to follow as a matter of course, and have been so set down. However, I am not convinced that the peduncles ramify into pedicels, and produce involucels occasionally. The true course of development is otherwise. If an umbel come from a capitulum, and that from a concave cænanthium, whose antetype is a conceptacle, we must return back for a clue and an illustration. Take an inflorescence, such as Fig. 4, and say that here there are five conceptacles. Each of these five cavities, being turned inside out, so as to form conical heads (as shown with regard to the Fig), we shall have five capitula. Let them have a peduncle developed to each, and we shall have an inflorescence, such as that seen in Fig. 12, *Matricaria camomilla*—a loose corymb, bearing composite flowers. If those peduncles should arise at one point, and the sessile flowers of the capitula get stalked, we should have a compound umbel of five principal radiating peduncles. The involucres of the composite capitula become the involucels of the umbellules, and the leaves in whose axils these peduncles arise cluster together to form the general involucre.

Supposing the axis of the composite flower to be prolonged, the spike (Fig. 13) might be the result, as has been stated. It might even have been added that the scales found often between the florets become bracts. But what of the involucre? Until the absence of anything to represent it be explained, I shall believe it more natural to deduce the spike as well as the spadix from the simpler forms; as, for instance, through the cone the abortive leaves, in whose axils (Fig. 5) the peduncles arise, becoming bracts in the spike; then, as the axis was mentioned as prolonged into a tuft of leaves beyond the male cone of *Pinus sylvestris*, so in Fig. 14 we have the axis prolonged beyond the flower head, leaving it as a glomerulus. This is a cymose circle of definite inflorescence.

What form anterior to, and yet foreshadowing the cyme of definite infloresence, is to be observed? At the extremity of the axis here the reproductive organs are produced, and the plant becomes forked, continuing to develope by axillary growth. Now, this is precisely what we have in *Ceramium* (Fig. 16), one of the Florideæ, or red sea weeds. Their favellæ terminate axial growth there, and are subtended by axillary ramuli in the same way. Any one who compares Figs. 15 (*Cerastium*) and 16, will at once observe their essential identity. This is additional proof from morphology that the favellæ are reproductive organs, whilst the tetraspores, immersed in the ramuli, should be regarded as analogous to bulbels.

IV.

This arrangement of affinities appears corroborated by the acknowledged relationships of certain families to certain others; and likewise by the position and priority of vegetable groups as revealed by geological research. Thus it brings into some sort of progressive connexion Fucoids, Equisetaceæ, Coniferæ, and Palmaceæ. Even in members of the same family corroboration is received from previously recognised peculiarities. Thus in the Ash order we have the Ash having apetalous flowers, and the Privet having flowers with petals. The inflorescence in the first case is a raceme, in the second it is the more developed panicle. This, however, is a portion of the subject to which I have not had time to give sufficient attention; and the developments of parts may not always be coequal.

Considered from a geological point of view this arrangement of affinities fairly coincides with scientific discoveries. For, in the Lower and Middle Palæozoic epochs, Fucoids, Equisetaceæ, and Gymnosperms are first found; whilst in the Upper Palæozoic some doubtful Monocotyledons begin to present themselves. When, afterwards, the Dicotyledons make their appearance, the Amentaceæ are amongst the earliest to show themselves. In conclusion, I wish to remark that, where the word "type" or "antetype" has been used, I have not meant to indicate a fixed form, but merely a remarkable stage, which may be a resting point in transitional development.