ON THE DEVELOPMENT OF THE CYSTOCARP IN THE GENUS GALAXAURA AND THE AUXILIARY CELLS IN THE ORDER OF NEMALIONALES

by

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The genus *Galaxaura* can in several respects be classed among the most remarkable *Florideae*. It is not only — with *Chantransia* — the genus richest in forms of all the genera belonging to the order of *Nemalionales*, which has more than 70 described species, it also offers, both in its interior and its exterior organization, such a high differentiation, and a tissue specialization going so far, that, as the monographer of the genus, the late Professor F. R. Kjellman (1900), said: "it may be difficult even in the great province of the *Florideae* to find forms with a higher or even as high a division of labour in the tissues of the shoot...".

Even if the number of species may actually diminish with further investigations, this is in a way connected with a peculiarity of organization, characteristic of the genus *Galaxaura*, namely that the sexual plant of a species has quite another anatomical structure of the cortical tissue than does the tetrasporic plant. This remarkable discovery was made by Howe (1917, 1918), who had had the opportunity of studying some species of *Galaxaura* in the West Indies, in their natural localities. This fact was not known of any *Floridea* at the time Kjellman wrote his monograph on this genus in 1900. Moreover, Kjellman had a quite different conception of the position of the tetraspores during the course of development of the *Florideae* than the one we have nowadays formed from the results of the cytological research. To Kjellman the tetraspores or, as he called them, the "tetragonidia", were a kind of propagation organ with the character of "Nebenfruktifikation", and thus not, as we must now regard them, the reproduction bodies of the diploid generation ending the diplophase in the alternation of generations. Thus, when Kjellman in his herbarial studies found forms of *Galaxaura* with otherwise similar organization but with quite a different cortical anatomy, it was quite natural that he described them as new species. One of the tasks of future taxonomical research will therefore be to combine such "species" of Kjellman as, in reality, are only the sexual and the tetrasporic generation of one and the same species. Naturally, this problem can only be solved by a botanist who has the opportunity of studying the development of the *Galaxaurae* in their native localities. Finally, only cultures will be really decisive. However, the number of species of *Galaxaura* will certainly be reduced.

As a matter of fact, Howe and other algologists, as Börgesen (1920) and Tanaka (1936), have already started to work out the species from this point of view. Tanaka, however, quite correctly points out that until such investigations are completed, it is hardly possible for those attempting to determine *Galaxaura* material to do anything else in the meanwhile but follow Kjellman's classification, even if it is quite obvious that it is untenable in important respects and must be re-made. ”But at present in treating this genus it is almost impossible to establish a new classification instead of Kjellman's one“. (Tanaka, 1936, p. 142).

As a preliminary introduction to such a revised system of the genus of *Galaxaura*, the development of some species must, however, be examined in detail. For, as Kjellman said: ”at present there is hardly one single species whose organization is, even in its outline, clearly made out.“ (Kjellman 1900, p. 27). This statement still holds good. In order to remedy this deficiency I have started an investigation of the development of such *Galaxaura* species whereof suitable established material has been available. I am especially indebted to Professor G. Papenfuss, University of Hawaii, for an excellent material from South Africa.

I have already published an investigation of the development of the spermatangia in *G. Diesingiana* (Svedelius, 1939, p. 591). One of the many peculiarities of this genus is that the spermatangia are immersed in deep cavities in the thallus, opening through the calcified cortex through a very small pore only — a most uncommon organization among the *Florideae*. The different structure in *Galaxaura* could, however, from the evolutionary point of view, be brought into harmony with that in other related, more normally developed generic types. I shall now give a preliminary account of the development of the cystocarp, which I have followed in detail in two species: *G. Diesingiana* Zanard., and *G. corymbifera* Kjellm. A more detailed account of the whole development, including also the cytology, will later be the subject of a special publication.

All closely investigated species of *Galaxaura* are unisexual and have their tetraspores on special plants, and for that reason male, female and tetrasporic plants are to be found in Nature of every species. As Börgesen (1927, p. 79) has already pointed out, a statement in the literature (Harvey-Gibson and Knight, 1913, p. 307) that *G. adriatica* have tetraspores and cystocarps together on one and the same plant and even on the same branch, is doubtful, and the more so as the tetrasporangia are there described and illustrated in a way unparallelled in any other described *Galaxaura*.

First of all I shall give an account of the earliest development, the fertilization and the development of gonimoblasts with regard also to the cytology — questions that have never before been studied in detail in any *Galaxaura*. All that is hitherto known of the earliest stages is confined to the scanty statements given by Askenasy (1888). He has observed that the carpogonial branch is established in a cavity at the boundary between the inner pith and the later, more or less calcified cortical zone, and this observation is, as I shall prove, quite correct. On the other hand, Askenasy's statement that the ensuing development occurs in such a way that the outer branchlets of the gonimoblast form a kind of involucre or pericarp, enclosing the whole cystocarp and keeping it from the surrounding tissue, is not correct but based on a faulty observation. It is evidently this statement from Askenasy that has been repeatedly quoted in literature and handbooks, as, for instance, in the treatise on the *Chaetangiaceae* by Schmitz and Hauptfleisch, where an apparently wrongly interpreted figure is also given of the cystocarp in *G. fragilis* Lam. (Engler and Prantl, Die natürl. Pflanzenfam. 1896, I: 2, p. 338).

Kjellman says in his monograph that he has not been able to get clear information as to the juvenile structure of the carpogonium, but he mentions that a great number of branchlets, entangled in each other and the greater part of which having a part in the formation of the cystocarpic involucre, develop very early from the carpogonium and from the carpogonial branch (Kjellman, 1900, p. 21). Thus, Askenasy's and Schmitz and Hauptfleisch's mistake is repeated, and it is probably on these authorities that Kylin bases his opinion in his "Anatomie der Rhodophyceen" (Linsbauers Handb. Abt. II, Bd. VI: 2, p. 202) when he gives a similar description of the cystocarp of *Galaxaura.*

In this connection, I must also mention a small paper "On the Anatomy of *Galaxaura corymbifera*" by de Valéra (1938, p. 938). In addition to some slight notes on the anatomy of *G. corymbifera,* some statements are here given on — according to the author — the carpogones and the cystocarp. What are here reproduced as a young "carpogonial branch in situ" (de Valéra, 1938, Fig. 1, E) and "an almost mature cystocarp" (l. c., Fig. 3) are, however, evidently a young spermatangial primordium and full-grown spermatangia in their deep conceptacles. This is easily seen by a comparison with, for instance, my reproductions in Figs. 1—3 and 6 (Svedelius, 1939, p. 596). De Valéra has thus quite simply confused the male and female organs in the *Galaxaura* she had examined, and described and reproduced young spermatangia as the carpogonial branch and the spermatangial cavity as a cystocarp.

The two species I am now going to describe, *G. Diesingiana* and *G. corymbifera,* belong to two different sections of the genus according to Kjellman's classification, and the organization of their thalli is very different. In *G. Diesingiana,* only the basal part of the thallus is roundish, whilst the upper part is flattened, strap-shaped. In *G. corymbifera,* on the other hand, the thallus is quite round and built up of numerous short prolifications, thus articulated all through as well as distinctly furcate. In spite of the obvious difference in the external vegetative organization of the two species, however, they show a practically complete conformity in the development of the cystocarp. The description is here founded on observations from both species.

I have best been able to observe the earliest stages of a carpogonial branch on *G. corymbifera* (*Fig. 1-a, b*). The carpogonial branch arises just beneath the apical growing zone lateral to one of the numerous longitudinal filaments making up the whole plant. Thus it originates in the same way as in *Scinaia* (Svedelius, 1915). The primordium is easily recognized by its breadth, which is greater than the vegetative cell-rows, and by its larger nucleus. From the very beginning, the increase of the carpogonial branch is checked in comparison with the neighbouring vegetative branchlets, which therefore soon grow up above and around the young carpogonial branch, situated at the boundary, where the later calcified cortical zone turns into the inner uncalcified tissue — thus, quite as Askenasy has stated (1888, p. 33).

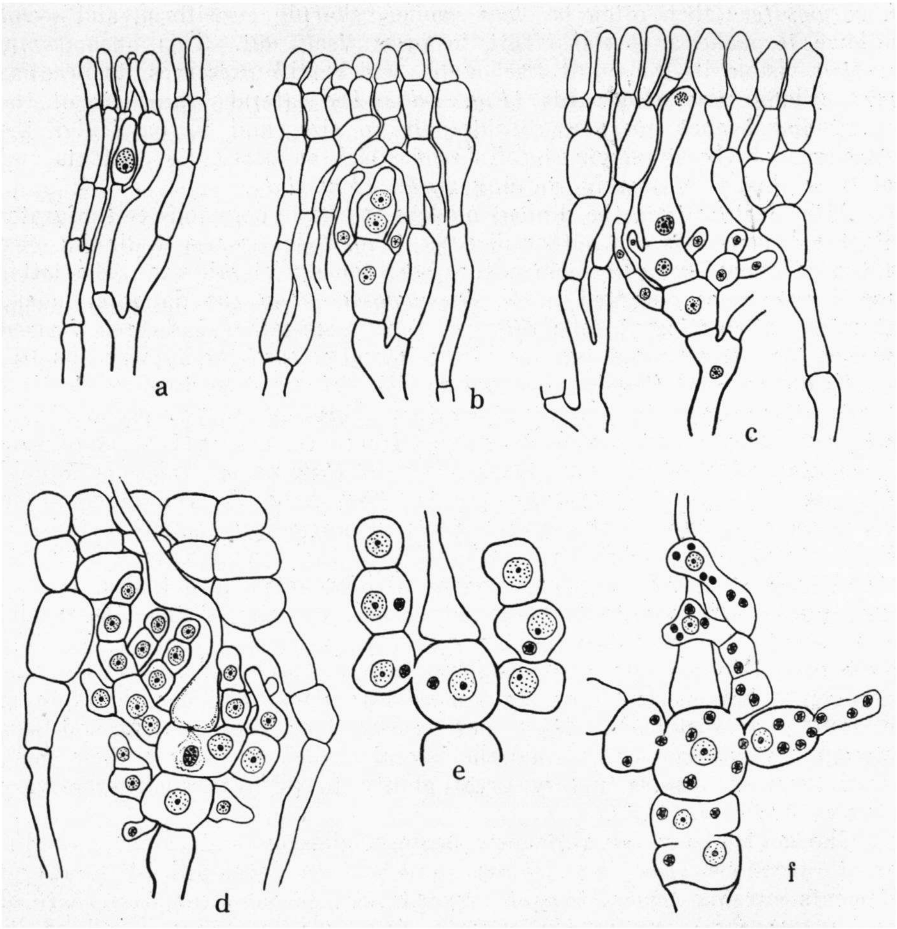

Fig. 1. *Galaxaura corymbifera* Kjellm.: *a, b,* very young carpogonial branches; *c,* mature carpogonial branch of *G. Diesingiana* Zanard.; *d,* the immigration of the fertilized diploid nucleus in the hypogynous cell in *G. corymbifera*; *e, f,* small diploid nuclei in the side cells of the carpogonial branch of *G. corymbifera.* The larger nuclei are the primary nuclei of the cells.

The carpogonial branch is 3-celled (*Fig. 1-c, d*), and all the lower cells have developed side-branchlets at a very early stage. In the carpogonium a trichogyne nucleus is detached, remnants of which I have now and then been able to observe (*Fig. 1-c*). In due course the trichogyne penetrates the cortical tissue, which is quite uncalcified at an early stage and which therefore offers no resistance to the advance. In *G. corymbifera*, under certain circumstances, the cortical tissue seems to be able to offer a somewhat greater resistance than in *G. Diesingiana*. The trichogyne of *G. corymbifera* then often becomes swollen, sharply cuneiform, and seems to have to make a special effort to press itself out. This phenomenon is often visible in the adult trichogyne, which still preserves its peculiar form a long time afterwards (*Fig. 1-d*). The lateral branchlets of the carpogonial branch increase considerably in size, and in particular the branchlets of the hypogynous cell become rich in plasmatic contents and get large, but very weakly staining nuclei (*Fig. 1-d*).

After fertilization, the diploid nucleus in the hypogynous cell migrates into the hypogynous cell, either directly (*Fig. 1-d*), or else it divides once in the carpogonium, after which the daughter nuclei migrate. The latter case I have once observed in *G. Diesingiana*, when the daughter nuclei migrated into different cells after a direct connection had been formed between the carpogonium and one of the lateral cells of the hypogynous cell.

Galaxaura and *Chaetangium* agree with *Scinaia* according to Martin's investigations in virtue of the migration from the carpogonium of the fertilized nucleus, but the first-named differs in an important point. No immediate reduction division takes place in *Galaxaura*, which is diploid with special diploid tetrasporic plants. Nor have I ever observed in *Galaxaura* any stages that might indicate an immediate reduction division. When the diploid nuclei have entered into the hypogynous cell or its lateral cells (*Fig. 1-e*), a lively nuclear division sets in, so that numerous small nuclei are soon to be observed in all the cells of the carpogonial branch, with the exception of the empty carpogonium itself (*Fig. 1-f*). These diploid nuclei are much smaller than the nuclei of the cells of the carpogonial branch, but they stain more intensively and are therefore to be seen very distinctly. Open pore connections are now formed also between the hypogynous cell and the lateral branches. In fact, these small nuclei seem to possess a very great ability to push through even very narrow pore connections.

The gonimoblast filaments now begin to develop and elongate in different directions (*Fig. 2-a*). Thus, branches are developed by means of filaments curving either straight upwards, out through the basal part of the carpogonium; or, further, directly from the hypogynous cell or its lateral branches; or, thirdly, from the first, lowest cell of the carpogonial branch, *i. e.* the one situated beneath the hypogynous cell.

The gonimoblast filaments that later grow out from the lower cells of the carpogonial branch differ particularly from the other gonimoblast branches (*Fig. 2-b*), being very elongated, narrow and tubular, and they do not curve upwards at once but grow straight sidewards. By and by, however, they also curve upwards, and give rise to the specific carpospore-forming branches (*Fig. 3*). Already before this development has begun, the cells of the carpogonial branch have fused with adjacent lateral cells and formed together a large, irregular fusion cell (*Fig. 3*). The elongated, laterally stoloniferous cells, moreover, form several new centres for the formation of gonimoblast filaments, which give rise to carpospores (see

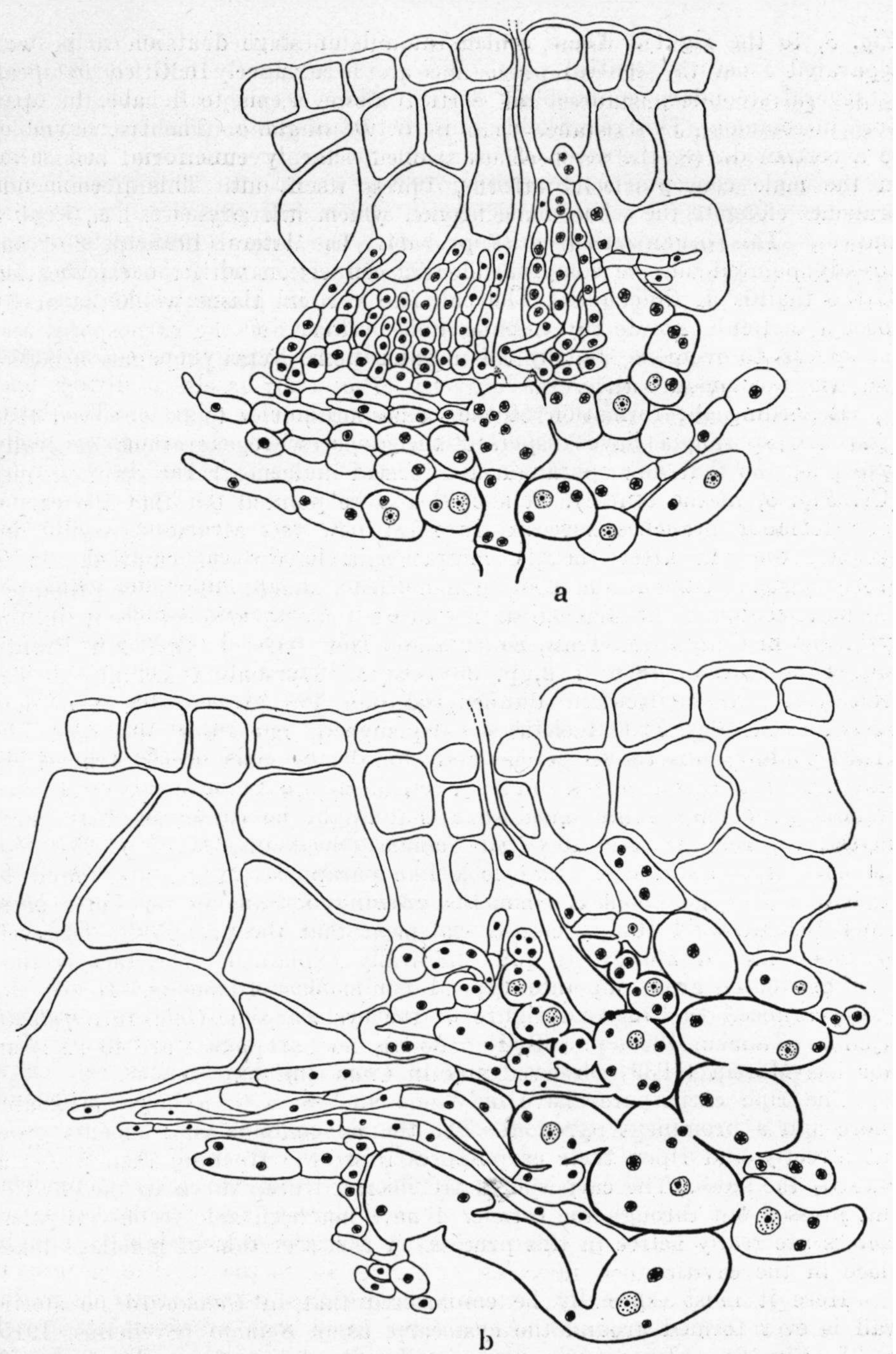

Fig. 2. *Galaxaura Diesingiana* Zanard.: *a,* the young primary gonimoblast filaments growing directly upwards from the carpogonium and the hypogynous cell; *b,* the primary gonimoblast and the horizontally extending gonimoblast filaments which later on form secondary gonimoblast centra.

Fig. 3, to the right). These centres at a later stage are seen to be well separated from the central part. We are here rightly entitled to speak of several secondary gonimoblast centra. However, they all have the open pore in common. This remarkable construction of the gonimoblast resembles to a certain degree the mode of branching of the spermatangial branchlets in the male conceptacle (Svedelius, 1939), where also stoloniferous side branches elongate the whole male branch system laterally (Cf. l. c., Figs. 5 and 6.) This organization must probably, as Wilke (1925, p. 25) has already pointed out, be comprehended in connection with the calcification of the thallus in *Galaxaura*. The calcified cortical tissue would naturally form a difficult, not to say impenetrable obstacle for the carpospores and the sperms to overcome, but by this organization several propagation bodies can use a common ostiole.

Regarding the formation of the carpospores, it is to be observed that after the sporangia have dispersed their spores, regenerations generally take place, so that new sporangia are formed underneath the emptied ones (Cf. *Fig. 3*, in the centre). It should also be pointed out that the carpospore-forming branches successively form new lateral ones growing up between the old after their carposporangia have been emptied. It is probably such young regenerating gonimoblast filaments that have prompted the statements in the algological literature that paraphyses occur in the cystocarp in *Galaxaura*. Thus, Schmitz and Hauptfleisch (Engler u. Prantl. Nat. Pflanzenfam. 1896, 1:2, p. 338) say: "Hymenium anfangs durchsetzt von sehr zahlreichen dünnen, sterilen Paraphysen, die von dem Fasergeflecht des Fruchtgehäuses entspringend, nach der Mündung der Fruchthöhlung hin convergieren, späterhin (mehr oder wenig frühzeitig) sind die Paraphysen verschwunden". Certainly, in the two species I have examined, no such formations occur that might be caracterised as paraphyses, as, for instance, those in *Scinaia* (Svedelius, 1915, p. 36). On the contrary, in all cases that look like paraphyses, these are found to be tender new gonimoblast filaments growing out among the older ones. Thus, Schmitz and Hauptfleisch's statement that the paraphyses observed by them later disappear, is quite naturally explained. The fact is that they gradually grow out into typical gonimoblast filaments. Hence the disappearance. In Tanaka's figure of the cystocarp in *Galaxaura falcata* Kjellm. (Tanaka, 1936, p. 160, Fig. 23 E), no paraphyses are to be seen. Nor has Martin (1939) observed any in *Chaetangium*.

The ripe carpospores have only one nucleus with a large chromatophore and a prominent pyrenoid. The central gonimoblast filaments grow out directly and ripen their carpospores first; the ripening then proceeds towards the sides. The carpospores are liberated deep down in the cavities and pressed out through the ostiole. I have not been able to observe what factors are really active in this process. A rich secretion of mucilage takes place in the cavities.

Here it must especially be emphasized that in *Galaxaura* no sterile wall is ever formed around the cystocarp, as in *Scinaia* (Svedelius, 1915, p. 35, Fig. 28). In *Scinaia*, these wall cells derive from the first cell of the carpogonial branch, i. e. the one situated below the hypogynous cell in the 3-celled carpogonial branch.

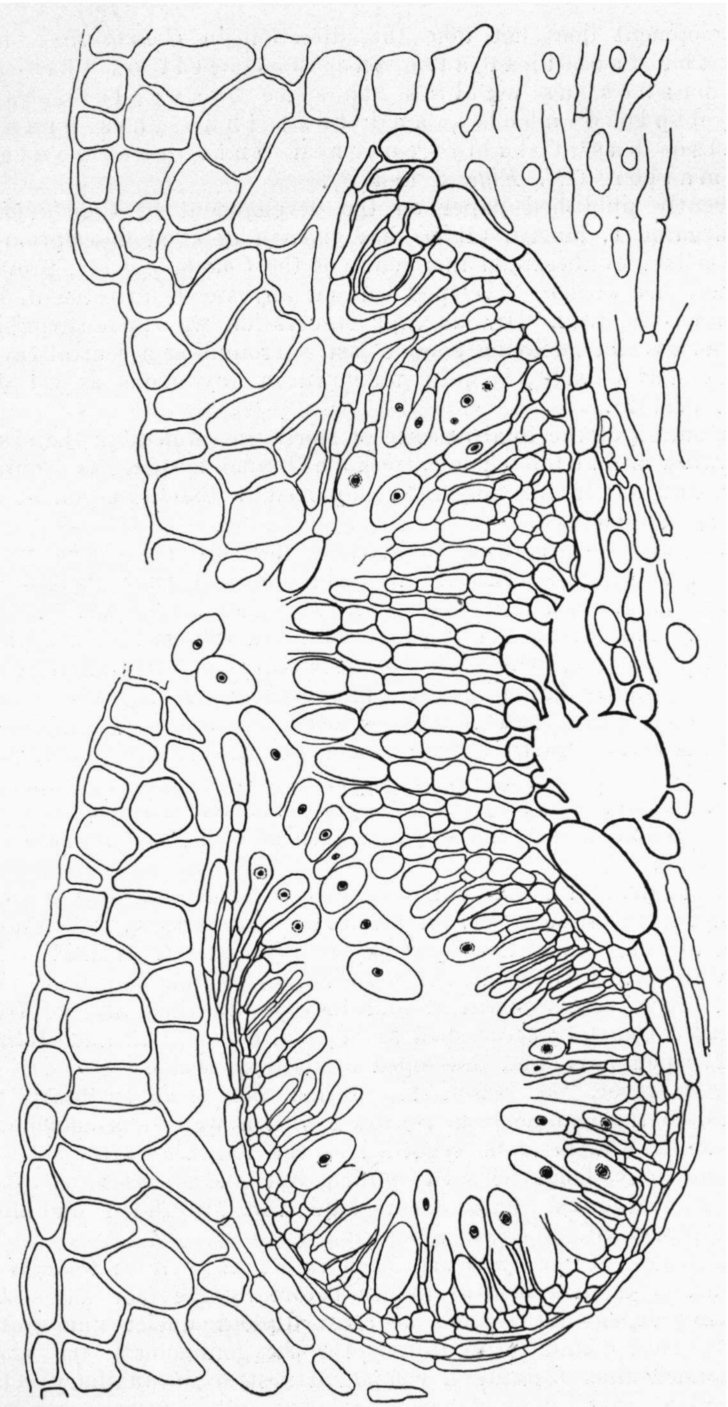

Fig. 3. *Galaxaura Diesingiana* Zanard., mature cystocarp with the primary gonimoblast and the large fusion cell in the centre, and horizontally creeping gonimoblast filaments forming secondary gonimoblast centra (to the right). To the left, a cystocarpic cavity with ripe carpospores.

The development does not take this direction in *Galaxaura*; this is due to the fact that also the first cell of the carpogonial branch, as well as its side branchlets, have acquired diploid nuclei, and that thus this branch system also has totally entered into the gonimoblast formation (Cf. *Figs 2 and 3*).

In a recently published paper on the development of *Chaetangium saccatum*, Margaret T. Martin (1939) has given a detailed description of the structure of the cystocarp in this genus of the *Chaetangiaceae*, proving that the gonimoblast is here developed without any sterile investment, i. e. the cystocarp has no wall. Dr. Martin's observation was then surprising news. "The massive interweaving gonimoblast, surrounding a central cavity and devoid of sterile 'wall', is quite unknown in any genus as yet described". (l. c. p. 142).

The explanation of the total absence of sterile investment in the cystocarp in *Galaxaura* is that the whole carpogonial branch system has acquired diploid nuclei and has in this way been employed in the formation of the spore-producing gonimoblast.

In *Chaetangium* — according to Martin's description — some particular gonimoblast branches are able to assimilate and have therefore a nutritive function, at least for some time. Her statement (l. c. p. 131) "that the carpospores are actually produced by development from these so-called 'wall filaments', which do not show any differentiation whatever", seems to prove that probably even branches from cells of the carpogonial branch other than the hypogynous one are included in the gonimoblast. However, Martin's paper does not make this point quite clear. It is to be observed that *Chaetangium* is a haplobiont like *Scinaia*, with reduction division occurring in the hypogynous cell. Thence, there are in any case no diploid nuclei in the gonimoblast of *Chaetangium*, as is the case in *Galaxaura*.

Oltmanns has defined a floridean cystocarp as constituted by a gonimoblast and a sterile investment, *i. e.* an involucre; that is to say, cystocarps are, according to him, "umhüllten Sporophyten" (Handb. 2. Aufl. II, 1922, p. 380). According to this definition, neither *Chaetangium* nor *Galaxaura* could claim to have real cystocarps, and they would thus diverge from other investigated *Chaetangiaceae* such as *Scinaia, Gloiophloea* and *Actinotrichia*, all of which have well developed cystocarpic walls.

There is, however, no reason to confine the term cystocarp, as Oltmanns does, to the gonimoblasts provided with a wall — so much the less so as Schmitz, who is to be regarded as the founder of the modern Floridean terminology, holds no such opinion, but characterises the cystocarp of the *Florideae* as "bald nackt, bald von Hüllfäden umhüllt". (Schmitz, 1883, p. 228).

The development of the cystocarp, such as we know it in *Galaxaura*, differs from all types of *Florideae* known before by the fact, firstly, that the whole carpogonial branch acquires diploid nuclei immigrated from the carpogonium, and forms initials for the gonimoblast, the whole carpogonial branch thus forming a compound system of auxiliary cells; and secondly, that stoloniferous elongated cells form secondary gonimoblastic centres which, however, finally become so compressed that they disperse their carpospores through one and the same ostiole in the calcified cortex.

Thus, we can here distinguish between primary and secondary gonimoblasts developed from the same carpogonial branch, the primary one being that which has arisen directly in connection with the central fusion cell, and the rest being secondary ones — those developed later.

Comparison with other types of Nemalionales.

As it has now been shown that, as regards the gonimoblastic development, *Galaxaura* holds a unique position amongst the *Florideae*, it will be a very interesting task to compare this type with other, nearly related genera, and particularly with such as belong to the order of *Nemalionales*. This group, which according to all algologists is the most primitive among the *Florideae*, shows a great variation of types in respect of the development of the gonimoblast. On the other hand, the higher orders of the *Florideae* show a much greater stability and uniformity in this respect. I venture to say that certain fixed evolutionary types of the gonimoblast in the higher orders are established in such a way that the variability of these higher *Florideae* is more evident in other respects than that of the development of the cystocarp.

The most primitive types of *Nemalionales* are to be found within the family of *Helminthocladiaceae*, the species *Chantransia, Batrachospermum, Sirodotia* and *Cumagloia*, all of which are distinguished by having their gonimoblasts growing out directly from the carpogonium without any fusion whatever between the carpogonium and any other cells, either in or outside the carpogonial branch. Wilke and Ziegenspeck (1929) have named these ”*Florideae anauxiliatae*“, as they do not even show any trace of auxiliary cells or of auxiliary cell-systems.

Already in *Nemalion*, however, a fusion is found between the carpogonium and the primary cells of the carpogonial branch, which together form what G. M. Smith (1938, p. 318) calls the ”placental cell“.

In *Scinaia*, the four lateral cells of the hypogynous cell of the carpogonial branch are especially developed into a hypogynous disc (”hypogyne Scheibe“, Schmitz), which after fertilization gets the diploid nucleus that migrates down here. In these cells densely filled with protoplasm and finally fused together, the zygote nucleus undergoes the reduction division. Afterwards the gonimoblast grows up again and presses itself out from the base of the carpogonium. These cells, which receive and house the diploid nucleus during the reduction division, and which form initials for the gonimoblast, are real auxiliary cells, and as they derive from the actual carpogonial branch, they can, as Wilke and Ziegenspeck (1928) have proposed, be called ”Karpogonauxiliarien“, *i. e.* carpogonium auxiliaries.

Dermonema (Svedelius, 1939, p. 39) shows fusion between the carpogonium and the supporting cell of the carpogonial branch, much the same as in *Atractophora* (Kylin, 1928).

Asparagopsis (Svedelius, 1933, p. 27) shows fusion between the carpogonium and the hypogynous cell, in which, just as in *Scinaia*, the reduction division takes place, and from which the gonimoblast originates. In *Asparagopsis,* however, there are, besides, numerous nutritive, or nurse cells at the disposal of the gonimoblast. The cells of the carpogonial branch have formed a branch system, rich in plasma and food, the so-called "sterile filaments", in the gonimoblast. This proves a higher organization in *Asparagopsis.* The same is also the case in *Bonnemaisonia* (Kylin, 1915, and Svedelius, 1933), the organization of which resembles that of *Asparagopsis* in several respects, with food-storing sterile nurse cells. Contrary to the case in *Asparagopsis,* the gonimoblast in *Bonnemaisonia* is developed direct from the carpogone.

Of all more closely examined types of the *Nemalionales, Chaetangium* (Martin, 1939) seems to follow the course of development most nearly like that of *Galaxaura,* though with the fundamental difference that *Chaetangium,* like *Scinaia,* is haplobiontic, while *Galaxaura* is diplobiontic. Common to the organization in *Chaetangium* and *Galaxaura* is the absence of any special sterile wall round the gonimoblast. The branch system that, in other nearly related forms, constitutes the wall of the cystocarp is here required for the formation of carpospores. Protection is already superfluous here, at any rate in *Galaxaura,* since the cortex becomes calcified and the gonimoblast lies wholly depressed beneath this firm covering layer.

The number of chromosomes.

Regarding the number of chromosomes in the species of *Galaxaura* examined by me, I will in this connection only give the approximative numbers that I have found. I hope to have the opportunity in my further detailed paper of treating this question precisely.

In *G. Diesingiana* I have found, in the female nucleus of the carpogonium as well as in the growing point of the female plant, the number of 10 or 12 at most. In spermatia I have with certainty counted at least 8 chromosomes. In very young gonimoblasts I have found up to 17—18. The nuclei being very small, all certain counting is difficult, but, approximately, one might be able to assume that the number of chromosomes is 10 and 20, possibly somewhat less.

The chromosome number in *G. corymbifera* seems to be the same as in *G. Diesingiana.* Observations of the number of chromosomes in haploid nuclei of *G. corymbifera* (♀) have yielded the results of 10, 12, and in young gonimoblast branches I have found 19—20 chromosomes. Thus, *G. corymbifera* also have approximately the numbers 10 and 20. In any case, it is quite certain that the reduction division does not take place in the carpogonium, and that the whole gonimoblast is diploid. This also explains the existence of particular tetrasporic individuals in *Galaxaura.* Here in this connection I will only state that I have also observed that the reduction division occurs in the tetrasporangia. I shall, however, return to their cytology in another connection.

On the auxiliary cells within the order of the Nemalionales.

Fr. Schmitz (1883), the founder of the modern taxonomy of the *Florideae,* laid the main stress on the development of the gonimoblast in characterising the chief Floridean groups, and the foundation he thus laid for the system of the *Florideae* is still valid, even though later investigations, as for instance those of Oltmanns (1922), have revised his system in several respects. Kylin (1928, 1935), who has also modified Schmitz's system in several of his papers, has in particular sought to stress the occurrence or non-occurrence of auxiliary cells as a systematic character of a very high degree for the diagnoses of the orders of the *Florideae.* However, he has hereby altered the original conception of the auxiliary cell proposed by Schmitz, and restricted the term in such a way that a so-called ”typical auxiliary cell“ must always be the starting-point for the gonimoblast (Kylin, 1935, p. 141). He further claims that the typical auxiliary cell cannot belong to the proper carpogonial branch. ”A typical auxiliary cell never occurs in the carpogonial branch“ (Kylin, 1935, p. 140). Thus, if fusion takes place between the carpogone and the fertilized female nucleus on one side, and between other neighbouring cells in the carpogonial branch or its supporting cell on the other, then Kylin does not designate such cells typical auxiliary cells unless the gonimoblast also originates directly from these. I have already in another connection (Svedelius, 1933, p. 49) pointed out that I cannot possibly share this opposing view, and what I have now found in *Galaxaura* strengthens me in the opinion that this restriction of the comprehension of the auxiliary cell is arbitrary and apt to obscure the evolutionary relation between the different types among the *Florideae.* Nor does it help to give a clear picture of the origin and evolution of the strange organization in the *Florideae* which we know under the term of ”auxiliary cell“.

In my opinion, it is a matter of secondary importance whether or not an auxiliary cell belongs to the carpogonial branch proper, and also whether the gonimoblast is developed directly from the latter or not. It should instead be pointed out that all such cells that fuse directly or indirectly with the carpogonium and that, though only temporarily, have received and housed future gonimoblast nuclei, must be designated auxiliary cells. When Schmitz chose the term ”auxiliary cell“, he certainly had in mind the fact that these cells were supporting, not only as food-storing cells but also as housing the fertilized nucleus. An auxiliary cell must have received and housed the fertilized female nucleus or nuclei originating therefrom. This quality distinguishes the auxiliary sharply from the cells that are only food-storing, which often accompany the carpogonial branches, the so-called ”sterile cells“ in the carpogonial branch system. Such cells are to be regarded as storage tissue and are easily distinguishable from auxiliary cells. *Bonnemaisonia asparagoides,* for instance, shows an example of such storage cells developed from the carpogonial branch.

Wilke and Ziegenspeck (1929, p. 417) have in their paper on a system of the *Florideae,* founded on the auxiliary cells, covered with the term auxiliary cells all cells — independent of provenance — which are formed by the mother plant and where a fusion of plasma and nuclei, a so-called ”Mixogalle“, from different generations takes place, leading to the development of the gonimoblast. They say further: ”Werden von der

Tragpflanze besondere Fäden abgeliefert, die ihre Reservestoffen an den Gonimoblasten abgeben, so reden wir von Nährfäden". This broader limit for the conception of the auxiliary cells, with which I agree, leads to a clearer comprehension both of the origin and of the evolution of this organization, so characteristic for the *Florideae.* If the conception of the auxiliary cell is strictly limited to so-called typical auxiliaries, and only such cells as do not belong to the carpogonial branch but still function as starting-points for the gonimoblasts are accepted as auxiliaries, then only the differentiated special cases of a more general organization will be termed auxiliary cells. In that way, the evolution will become obscure.

If we now look at *Galaxaura* from the above points of view, the following facts can be established:

1) Either the fertilized nucleus immigrates immediately into the hypogynous cell of the carpogone, or a first division occurs already in the carpogone, whereafter the daughter nuclei move down;

2) after a repeated division of nuclei, an immigration of diploid nuclei to all the cells of the carpogonial branches takes place, resulting in an active formation of the new branches, i.e. the gonimoblast;

3) these gonimoblast filaments are primarily developed from the hypogynous cell, whereby certain branches can grow up and out direct through the carpogonial basis, later from all the cells of the carpogonial branch. These latter cells grow out laterally at first, and are able to form so-called secondary centres of gonimoblasts.

Thus we find that practically the whole system of carpogonial branches is required as starting-points for the formation of the gonimoblast, whence no cystocarpic wall whatever can develop. We see, then, that *Galaxaura* — even with Kylin's definition (from 1928) of the auxiliary cell — must be characterised as provided with auxiliaries, as the hypogynous cell as well as the other cells of the carpogonial branch are the starting-points for the gonimoblast.

I have earlier proved (Svedelius, 1933) that *Asparagopsis,* which likewise belongs to the *Nemalionales,* must also be considered to have a typical auxiliary cell in the hypogynous cell, into which the fertilized nucleus immigrates and whence the gonimoblast also derives its origin. According to Kylin's interpretation of 1935, however, it still does not meet the claims to be classed as a typical auxiliary cell, since it belongs to the carpogonial branch proper. Kylin's conception of auxiliary cells has changed somewhat since 1928, when he says about them that investigations have proved that we must distinguish at least two different kinds: "Einerseits gibt es nämlich Auxiliarzellen die nur als Nährzellen dienen, anderseits aber auch solche, die nicht nur Nährzellen sind, sondern auch die Ausgangspunkte der Gonimoblastbildung. Nur diese letzteren Auxiliarzellen sind typische Auxiliarzellen und ich werde zuerst diese besprechen und zwar deshalb, weil die Charaktere dieser Zellen die wichtigsten Grundlage der Florideen-systematik darstellen". At this time, the purely food-storing cells were — in my opinion quite rightly — eliminated from the conception of the auxiliary cell, which was then characterised as starting-point for the gonimoblast. Later, when *Asparagopsis* (Svedelius, 1933) proved to have a typical auxiliary cell according to this definition, a further demand on the typical auxiliary cell was added in Kylin's paper of 1935: it must not belong to the carpogonial branch proper.

I find it difficult to understand this further restriction of the conception of the auxiliary cell, if it is not to be interpreted as an attempt to retain for the *Nemalionales* the absence of auxiliaries as a distinct systematic character. In his work "Entwicklungsgeschichtliche Florideenstudien", Kylin (1928) outlines a revised system of the *Florideae.* From his description of the *Nemalionales* is here quoted the following: "Typische Auxiliarzellen sind in der Ordnung nicht vorhanden. Die Gonimoblasten entwickeln sich deshalb direkt aus dem Karpogon...". This, however, does not hold good of either *Asparagopsis* or *Chaetangium,* nor, as I have now proved, of *Galaxaura.* Still, they are all typical genera of *Nemalionales.*

I will remark, though, that the conception of the auxiliary cell that I have tried to advance, and that accords closely with that presented by Wilke and Ziegenspeck, has also been supported by other algologists. Thus, for instance, Martin (1939, p. 139) writes of Kylin's establishing of the Floridean system chiefly on the occurrence of typical auxiliaries: "In this classification the *Nemalionales* and *Gelidiales* are characterized by absence of 'typical auxiliaries'; Kylin refuses to apply the term to any of the genera investigated in *Nemalionales.* This interpretation, however, is difficult to understand". And the same author goes on to say: ... "But in *Asparagopsis armata* (and now in *Chaetangium*) where the gonimoblast undoubtedly arises from the hypogynous cell, the term 'typical auxiliary c ll' would seem, on Kylin's own definition, to be directly applicable. This is the view taken by Svedelius for *Scinaia,* and he considers that in *Asparagopsis armata* the case is even more clear, and that this species has a typical auxiliary cell in Kylin's more limited sense also (1933). I should entirely agree with this interpretation; if we adhere to Kylin's definition of a 'typical auxiliary cell' it is difficult to understand his rejection of the term for *Asparagopsis armata,* where he states that 'according to my opinion this cell ought not to be called a typical auxiliary cell' (Kylin, 1935)."

In my opinion, the order of *Nemalionales* is a very instructive illustration of how the auxiliary cells, so characteristic for the *Florideae,* have originated and developed from the very beginning. Entirely anauxiliate are the genera *Chantransia, Batrachospermum, Sirodotia* and *Cumagloia* (*"Anauxiliatae"*). Of these, *Sirodotia* occupies a quite distinct position by reason of its far-reaching, self-nourishing gonimoblast.

Nemalion holds an intermediate position between the anauxiliate and the auxiliate types of the *Nemalionales.* Fusion takes place between the hypogynous cells of the carpogonial branch and the carpogonium, from which, however, the gonimoblast grows out. This fusion cell is called "placental cell" by G. M. Smith (1938, p. 318), and "Karpogonauxiliare" by Wilke and Ziegenspeck, and *Nemalion* is designated as the original type for the *Nemalionales* genera with carpogone auxiliaries, *i. e.* such auxiliaries as belong to the carpogonial branch proper — the so-called "primäre Karpogonauxiliaren", primary carpogonium-auxiliaries.

Scinaia shows a fusion between the carpogonium and its hypogynous cell as well as its lateral cells which, already before fertilization, are curiously developed, and which fuse together. Here the reduction division occurs, after which the gonimoblasts make their way out again through the basal part of the carpogonium. As the auxiliary cells are here daughter cells to a carpogonial branch, Wilke and Ziegenspeck name them "primärogene Auxiliaren".

Dermonema (Svedelius, 1939) shows a large, strongly developed supporting cell for the carpogonial branch, which cell becomes the auxiliary one with which the carpogonium fuses. The carpogonial branch thus being fixed on the auxiliary cell, Wilke and Ziegenspeck designate such types "*Auxiliofixatae*". It seems, however, as if this fusion does not necessarily take place in *Dermonema*. *Dermonema* is characterised, just as *Sirodotia* is, by a creeping and far-extending gonimoblast.

Asparagopsis shows fusion with the hypogynous cell in which the reduction division takes place just as in *Scinaia*. The gonimoblast grows out from the hypogynous cell; but here more food-storing cells further appear, the contents of which are consumed at the increase of the gonimoblast (Svedelius, 1933).

Galaxaura and *Chaetangium* show the peculiarity that not only one single cell but the whole carpogonial branch system receives and houses the nuclei that are to enter into the gonimoblast. The whole carpogonial branch is here an auxiliary cell-system. However, a marked difference exists between them: *Chaetangium* is a haplobiont, while *Galaxaura* is a diplobiont. Otherwise the development seems to agree.

The order of *Nemalionales* shows how we must imagine the auxiliary cells, so characteristic of the *Florideae*, to have originated.

The most primitive forms (*Chantransia*, *Batrachospermum*) develop their carpospores direct from the carpogonium; if the food does not suffice, the assimilating (*i. e.* self-nourishing) gonimoblast extends into the tissue of the mother plant, though at first without fusions (*Sirodotia*).

Some types have later developed in such a direction that the cells, richer in food, of the carpogonial branch receive directly and house the fertilized nucleus (*Scinaia*). In others (*Dermonema*), on the other hand, the supporting cell of the carpogonial branch is particularly adapted to receive the fertilized nucleus. Hence, by a fusion of nucleus and plasma, greater possibilities arise for the fertilized nucleus quickly to build up a gonimoblast able to produce a greater number of carpospores than would have been possible without fusion, and the more so as the gonimoblast is not, or has ceased to be, assimilating. In this lies the origin of the auxiliary cell.

The problem of increasing the gonimoblast within the *Nemalionales* by means of fusions with other cells is solved in different ways. In *Galaxaura*, the whole carpogonial branch is demanded for this purpose, and has grown into a compound system of auxiliaries, and certain gonimoblast branches extend laterally in order to increase still more the carpospore production of the gonimoblast system.

It is remarkable that we meet already in the *Nemalionales* this tendency of the gonimoblasts to extend, as well as in the above quoted *Siro-*

dotia also, and particularly in *Dermonema,* and now in *Galaxaura* too. It is, from a systematic viewpoint, very interesting that we can trace this tendency as early as here in the *Nemalionales,* a tendency later on appearing in the higher *Florideae* within the order of the *Cryptonemiales,* which order, as Oltmanns has already pointed out, must be regarded as the one most nearly related to the *Nemalionales.*

Hence, the *Nemalionales* types give us suggestions from several points of view as to how we may imagine the origin of the organization of the auxiliary cells in the *Florideae,* which organization later develops and consolidates in different directions. These organizations later help to form one of the fundamental bases for the taxonomy of the orders of *Florideae.* In the *Nemalionales,* the auxiliary cells are still of a rather varying type. On the one hand, this may afford the taxonomist certain difficulties, but on the other it may also give us some hints regarding the origin of this remarkable organization.

On the systematical position of the genus Galaxaura.

In this connection I should like, finally, to make some remarks on the systematical position of *Galaxaura,* and on haplobiontic and diplobiontic organization in the taxonomy of the *Florideae* in general.

A comparison between the more closely investigated species of the *Chaetangiaceae*: *Scinaia, Chaetangium* and *Galaxaura* shows that the first two species named are haplobionts lacking tetrasporic plants, while *Galaxaura* is a diplobiont with a diploid gonimoblast and special tetrasporic plants. Judging from brief statements in the literature, *Gloiophloea* J. Ag. and *Pseudoscinaia* Setch. are with certainty haplobiontic, whilst *Actinotrichia* Decaisne is a diplobiont. Madame Weber—van Bosse has observed and reproduced tetrasporangia of this genus on separate plants (Weber—v. Bosse, 1928, Pl. VI). This shows, as I have already pointed out in my paper on *Scinaia* (Svedelius, 1915, p. 49), that we must be very careful in using haplobiontic and diplobiontic organization as a systematical main character for the large groups. Even genera that are manifestly quite closely related behave differently in this respect. Different species within the genus *Chantransia* already behave differently, in that *Chantransia efflorescens* has specific tetraspore-forming plants alternating with sexual plants, while the other species are undoubtedly haplobionts (Rosenvinge 1909). Thus, haplobiontic organization must not be made into a fundamental character for the order of *Nemalionales,* even though it is probable that the majority of the genera belonging here are haplobionts. This character seems to me not to be given a higher systematical value than should be given, for example, to the heterospory and the homospory for the taxonomy of *Pteridophyta,* i. e. it can in no case be made the fundamental basis for the distinction of the main subgroups. We may be entitled to maintain that within the order of *Nemalionales* we meet the transition types to diplobiontic organization, *i. e.* to the kind of organization which later becomes predominant in the higher orders of the *Florideae.* This is evident in, for instance, *Galaxaura,* which must be classed among the highest organized and most abounding in species of all genera within the *Nemalionales.*

As to the special taxonomy of the family of *Chaetangiaceae,* it is generally divided, after Schmitz and Hauptfleisch (Engler u. Prantl, 1896, I:2), into the two groups *Scinaieae* and *Chaetangieae.* The former is characterised by these authors by the immersed cystocarp with erect branched gonimoblast filaments, which are surrounded by a thin cystocarpic wall, while in *Chaetangieae* the cavity containing the gonimoblast filaments is said to be covered by a firm wall, in which the gonimoblast filaments form a kind of hymenium, from the beginning penetrated by sterile paraphyses.

To the former group belongs of old *Scinaia,* investigated by myself (Svedelius, 1915), and *Gloiophloea,* investigated by Setchell (1914). The organization of these genera is similar in every respect. They have superficial, non-immersed spermatangia, they are haplobiontic, and are so closely related that I find it questionable whether *Gloiophloea* should be counted as a genus of its own.

The group *Chaetangieae* includes, according to Schmitz and Hauptfleisch, *Galaxaura, Actinotrichia* and *Chaetangium.* Martin's investigation of *Chaetangium saccatum* (1939) made it clear that this genus has no sterile cystocarpic wall whatever differentiated from the gonimoblast, the whole carpogonial branch system being instead absorbed in the carpospore formation; and also that the statement regarding the paraphyses is wrong. By my present investigation of *Galaxaura,* it has now also been proved that in this genus the whole carpogonial branch is needed for the gonimoblast after the immigration of diploid nuclei, and that here, also, no special wall is formed round the cystocarp, and there are no paraphyses. It is therefore evident that *Chaetangium* and *Galaxaura* are nearly related systematically by this accordance in the construction of their cystocarps. They should therefore together form the group of *Chaetangieae.* The genus *Actinotrichia,* however, which has been placed here in this group, has a distinctly settled wall of sterile cells, as is clearly evident from Madame Weber—van Bosse's instructive figure. This wall is developed from the lower part of the carpogonial branch, just as in the genera in the *Scinaia* group. Regarding the construction of the cystocarp, *Actinotrichia* does not agree with either *Chaetangium* or with *Galaxaura,* but instead with *Scinaia,* and should therefore be placed within the group of *Scinaieae.* In this group should also, in my opinion, be placed the genus *Pseudoscinaia,* which in its vegetative structure corresponds with *Scinaia* but which, according to Setchell's statement, should have a cystocarpic organization resembling that of *Galaxaura.* In Setchell's figure of *Pseudoscinaia Snyderae* (1914, Pl. 16, fig. 61), the boundary between the gonimoblast and the wall is certainly less distinct than in *Scinaia* and *Gloiophloea;* but that such a boundary really exists is evident, and in any case the lower lateral branches of the carpogonial branch do not enter into the gonimoblast. Thus, *Pseudoscinaia* belongs to the *Scinaia* group, to which probably also belongs *Whitbeyella.* In this case, however, some hesitation is justifiable on account of our imperfect knowledge of this genus.

The classification of the genera in the family of *Chaetangiaceae* should thus be as follows:

I. **Scinaieae**: from the lowest cell of the carpogonial branch an outer sterile involucre or wall is differentiated around the gonimoblast, *i. e.* the cystocarp is provided with an evident wall. Spermatangia as a rule superficial.

A) Haplobionts: *Scinaia, Gloiophloea* and *Pseudoscinaia.*

B) Diplobionts: *Actinotrichia* with the spermatangia superficial or somewhat immersed.

II. **Chaetangieae**: a sterile wall round the cystocarp is not formed from the carpogonial branch, as the gonimoblast is developed from all the cells of the carpogonial branch. Cystocarp thus without special wall. Spermatangia immersed in cavities.

A) Haplobiont: *Chaetangium.*

B) Diplobiont: *Galaxaura.*

The position of *Whitbeyella* must be studied more thoroughly before it is definitively settled in the system.

Through this re-grouping, and through altered characters of the subgroups, it seems to me that the genera of the family *Chaetangiaceae* have now been placed in a more natural way. The group of *Chaetangieae* is characterised both by the peculiar organization of its gonimoblast and by the immersed position of its spermatangia.

That a diplobiontic organization must have arisen on different occasions in the evolution of the family is also evident from the system, which, however, is chiefly founded on the structure and development of the cystocarp.

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