THE ORIGIN AND EVOLUTION OF THE ARCHEGONIUM *

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Introduction

Perhaps the greatest gap which we find in the evolutionary study of the plant kingdom, is the one that exists between the Thallophytes and those groups of higher plants which are collectively called the Archegoniatae. [1] Not long ago a similar gap was supposed to exist between the Bryophytes and the Pteridophytes because of the difference in the relative degree of development of the X and the $2X$ generation and other reasons. This gap has now been greatly bridged by the discovery of the group Psilophytales, [2] which in some respects

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[1] The term Archegoniatae has been employed throughout this paper to include the Gymnosperms also.

[2] Kidston, R. and Lang, W. H. (1917-21): On Old Red Sandstone Plants, showing structure, from the Rhynie Chert-bed, Aberdeenshire. Parts I-V, *Trans. Roy. Soc., Edinburgh*, Vols. 51, 52.

presents intermediate characters. The problem in regard to the Thallophytes and the Archegoniatae chiefly concerns the presence of a well defined sporophytic generation in the Archegoniatae and the relation of the sexual organs in the two groups. The presence of a well defined sporophytic generation gives less difficulty because in recent years, studies of the Thallophytes have indicated the possibility of a very general tendency towards the development of a sporophyte in this group. But the problem of the relation of the sexual organs in the two groups, or more precisely the origin of the archegonium and antheridium of the Bryophytes is still unsolved, because these organs have no clear parallel in the sexual organs of the Thallophytes. Views, however, have been expressed from time to time suggesting the possible derivation of these organs from the sexual or asexual reproductive organs of different members of the Thallophytes, but so far no conclusive statement seems to have been made on the subject. In the following pages the writer has attempted to review in brief the most important views expressed by different authors on the origin of the archegonium, and a suggestion has been made to derive this organ from the oogonium of *Coleochaete*. A further attempt has been made to discuss the evolutionary changes that are observed to have taken place in this organ in different groups of the Archegoniatae, of which it is so characteristic a feature. The evolution of the archegonium, as will presently be shown, probably means largely a process of retrogression directly dependent upon the land habit.

The Origin of the Archegonium : Previous Views

Before attempting to elaborate any original idea on the subject, it seems advisable to summarise critically the two most important views, expressed respectively by Götz and Davis.

Götz's View.

In *Chara* there are certain small cells called by Götz Wendungszellen which are cut off from the egg before maturity. The significance of these cells, was not fully known before Götz [1] put forth his view that "they stand for the walls of a reduced archegonium," thus "regarding" the female sex organ "as a degenerate archegonium plus the enveloping whorl of filaments that surround the egg and forms the crown." Davis, however, differs from him and has expressed his opinion, with which I agree that, "This is a very interesting suggestion, although objections present themselves in the complexity of the process required to bring about the degeneration of

[1] Götz, (1899) : Ueber die Entwickelung der Eiknospe bei den Characeen. *Bot. Zeit.* lvii. 1.

such a well-established organ as the archegonium and its displacement by an equally elaborate envelope of filaments.[1] '. About the accessory cells (Wendungszellen), he says that, "they may be nothing more than the final and somewhat irregular expression of the vegetative activities of a growing point that is about to become transformed into a sexual organ."

Davis' View.

Davis, however, derives the archegonium from the multicellular gametangia found in a number of the lower members of the Phaeophyceae, e.g. *Ectocarpus.* He thinks that two sets of factors, one influencing the structure, the other influencing the sexual character of the cells, must have acted to bring about the required change.

Regarding the structural modifications of the gametangium, according to Davis, the most important one which would be effected concomitant with the adoption of the terrestrial habit would be the sterilization of the outer layer of gamete-mother-cells, forming an enclosing capsule. While, on the other hand, as regards the character of the sexual cells he considers that the first step would be the establishment of heterogamy and then the development of the differentiation of activity, and finally the retention of the egg within the gametangium [2].

Dr. Church, however, differs from Mr. Davis and has remarked in his book "Thalassiophyta," "The analogy of an archegonium with a plurilocular sporangium was considered by Davis (1903) with very imperfect data, and little progress seems possible along these lines." [3] He is of opinion that the origin of the archegonium must be sought for in the transmigrant phyla, as the result of the transition to the new environment. The following few lines quoted from his book give a summary of his view about the origin of the archegonium. "It may be granted that the archegonium, so long regarded as the distinctive attribute of the "Archegoniatae" is clearly an end product of oogamic evolution, the limiting term of something quite unknown, probably originating in something quite different from any recent archegonium, and if we saw it, scarcely recognizable as such. Very probably again of polyphyletic origin, arising in phyla of marine algae of quite diverse descent, and convergent in general factors, as the limiting term of a

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1 Davis B.M., (1903): Origin of Archegonium, *Ann. of Bot.* Vol. 17, p. 477.

2 For a series of diagrams illustrating the possible evolution of the archegonium and antheridium from the plurilocular sporangia, see Davis, B.M. (1903).

3 Church, A. H., (1919): Thalassiophyta and the Subaerial Transmigration, pp. 12-14. *Oxford.*

special mechanism; at bottom no necessary guide to affinity, but merely indicating that the "Archegoniatae" may be the expression or a number of phyla at the same physiological horizon in this particulaf respect.'

Apart from Dr. Church's criticism, it may be remarked that there has been a general tendency among botanists to regard the Chlorophyceae rather than the Phaeophyceae or the Rhodophyceae, as helpful in tracing the evolution of the higher plants. Among the green algae, the greatest plasticity of form and structure is found in the Isokontae which according to West and others includes the progenitors of the higher plants.[1] Even Davis seems a little sceptic about his view when he says that, "The lower Phaeophyceae" with plurilocular sporangia "can hardly be supposed to have given direct origin to the Bryophytes although this is conceivable."[2] In fact he derives the Bryonhytes from a hypothetical extinct group of Chlorophyceae with plurilocular sporangia. Therefore while searching for a type which would possess a female sexual organ nearly resembling an archegonium, it is natural to look for it among the green algae with special reference to Isokontae.

A Suggestion to Derive the Archegonium from the Oogonium of Coleochaete.

A searching study of the Chlorophyceae seems to show that the female sex organ of *Coleochaete* is more suggestive of an archegonium than any which we have studied so far. Although it is true that the procarpium of *Callithamnion* has some resemblance to the archegonium, but we will not hold discussion on that organ any further and would reject it on the same ground as the plurilocular gametangium of the Pheophyceae. The female sex organ of *Coleochaete* is known as the oogonium. It is a unicellular flask-shaped body with a long neck which opens at the tip when mature, to allow the entrance of spermatozoids. The egg is situated in the lower swollen part of the oogonium. In general appearance the oogonium looks very much like an archegonium and if we compare it with a mature archegonium of the Liverworts the lowest evolved group among the Bryophytes—the most striking difference is seen in the absence of a multicellular wall.

The development of the multicellular wall can very well be attributed to an adaptation to the terrestrial habitat, that is to meet a demand for protection against desiccation. Besides the multicellular wall we have a varying number of neck-canal cells and a ventral-canal cell, in the archegonium of a Liverwort, while the oogonium

[1] West, G. S., (1915): Algae (Cambridge University Press), p. 158.

[2] Davis, B. M. (1903): Origin of the Archegonium, *Ann. of Bot.* Vol. 17, p. 492.

of *Coleochaete* is a unicellular structure. We know that when the archegonium becomes mature its neck-canal and ventral-canal cells degenerate and their contents becoming mucilaginous exude out of the neck and diffusing in the water present outside, exert an attractive stimulus on the spermatozoids. Not only in the Liverworts but even in the Bryophytes as a whole and also the Pteridophytes, the ventral-canal and the neck-canal cells have the same function. Thus it seems quite clear that the ventral-canal and the neck-canal cells have no other function to perform in the process of fertilization except ultimately of serving to attract the spermatozoids after being converted into some sort of chemotactic mucilaginous substance. It will be shown in the following paragraphs that the development of these extra cells besides the oosphere (egg) in an archegonium, has been a direct result of an adaptation to the terrestrial habitat.

When the migration from water to land took place the chances for the act of fertilization naturally became less, as for example in the case of amphibious plants (*viz.* the Bryophytes, etc.) the fertilization had to be carried out in the presence of only a little amount of water and that also was not always available, so there was less chance of the spermatozoids reaching the egg. In order to meet this deficiency in the chance of fertilization, some means had to be evolved by the migrating plants. This deficiency might be said to have been met by the production of some chemotactic substance through the disintegration of the neck-canal and ventral-canal cells of the mature archegonium.

We also know cases where the egg and the ventral canal cell cannot be distinguished one from the other in a mature archegonium, at least so far as size is concerned, for example in *Fossombronia longiseta,* [1] *Porella Bolanderi* [1] *Anthoceros,* [1] *Notothylas sp.,* [2] *Notothylas orbicularis,* [1] *Ophioglossum pedunculosum,* [1] *Marattia Douglasi,* [1] *Pinus Laricio,* [3] etc. And in *Pinus Laricio,* it is interesting to note that they are not distinguishable until after fertilization. In abnormal cases the ventral-canal cell in an archegonium may even behave as an egg in addition to the normal one already present. Then there are also cases known in which the egg, ventral-canal and neck-canal cells may all be alike in size *e.g.* in *Porella Bolanderi* [1]. Besides all these evidences from the mature

[1] Campbell, D.H., (1918): Mosses and Ferns. p. 93. fig. 44; p. 108, fig. 54 F.; p. 127, fig. 66 A & p. 134; p. 150, fig. 81 A. & p. 151, fig. 82 D.; p 235, fig. 125 F.; p. 280, fig. 153 C.

[2] Mottier, D.M., (1894): Contribution to the Life-history of Notothylas. *Ann. of Bot. Vol.* 8, *p.* 399.

[3] Coulter, J. M. and Chamberlain, C.J., (1925); Morphology of Gymnoperms, p. 267.

archegonia represented from different circles of affinity, we have the developmental study of the archegonium in which it is clearly seen that in every case all the cells whether ventral-canal or neck-canal are cut off from a single one. With these data before us, it will not be unnatural to regard the neck-canal and ventral-canal cells to have probably been formed in phylogeny by being cut off from an ancestral egg when the migration to land was taking place. If we agree to what has been said above we can derive the archegonium from the oogonium of *Coleochaete* by encapsulation in order to meet the demand for protection against desiccation, and by the cutting off of neck-canal and ventral-canal cells from the egg, these cells on disorganisation forming some mucilaginous substance which exerted an attractive force on the spermatozoids, to meet the deficiency of water for the act of fertilization.

In support of the view put forth the writer has to offer the following arguments :—

(1) "The Confervoideæ among the Green Algæ are for good reasons considered to be among living forms, the nearest to the progenitors of the Archegoniatæ. Among the Confervoideæ, *Coleochaete* most nearly approximates to the condition found in the lower Bryophytes." [1] If the Coleochaetes are nearest to the progenitors of the Archegoniatae as stated above by Campbell then the writer's view as to the derivation of the archegonium from the oogonium of *Coleochaete* will probably not appear unwarranted.

(2) As we approach nearer and nearer to the siphonogamic mode of fertilization, we find that the motility of the sperms is gradually lost and that they are bodily carried to their destination (the egg) by the pollen-tube. Concomitant with this feature the neck-canal and the ventral-canal cells being no longer needed (after disintegration) to attract the spermatozoids, decrease in number till all of them are eliminated as we see in some Gymnosperms *e.g.* *Podcarpus.* Thus it is quite clear that the ventral-canal and the neck-canal cells are chiefly concerned with the attractive movements of the spermatozoids.

(3) That the development of the multicellular wall of the archegonium is chiefly to meet the demand for protection against desiccation, is shown by the fact that in those plants in which the archegonium lies embedded in the prothallus and consequently has a secure position it loses the identity of its walls and may be said to have no wall at all as there is no difference between the cells surrounding the egg cell and the cells of the prothallus.

[1] Campbell, D.H., (1918): Mosses and Ferns, p. 563.

The Evolution of the Archegonium

Comparative Study of the Archegonium

We shall now attempt to trace the general tendency in the evolution of the archegonium. The most important characters in this connection are, the variation in the number of the neck-canal cells, the ultimate elimination of the ventral-canal cell and lastly the position of the archegonium on the female gametophyte. We shall therefore take up the consideration of these three characters group by group. The chart given below contains a summary of the more important characters of the archegonia in nine genera selected from the Bryophytes.

A. Bryophyta.

Genera	Ventral C. Cell	Neck C. Cells	Neck Cell	Position on the prothallus
Targionia ...	1	8	60–80	Projecting on the prothallus
Fossombroni ι..	1	4–6	many	do.
Porella ...	1	5	do.	do.
Aneura ...	1	4–6	do.	Partly embedded.
Riccia ...	1	4	do.	Situated in a cup-shaped cavity.
Sphaerocarpus	1	2–4	do.	do.
Anthoceros ...	1	4	do.	Embedded.
Funaria ...	1	5	do.	Projecting.
Sphagnum ...	1	many	do.	do.

Discussion : A general survey of the archegonium in the Bryophytes shows that most members of this group have superficial archegonia. This character is naturally regarded as a primitive one. In *Aneura* the base of the archegonium is confluent with the thallus and in this respect it offers an easy approach to the condition found in *Anthoceros*, where the sterile cells of the archegonia being embedded lose their identity in the tissue of the gametophyte. Besides these few variations, the general structure of the archegonium is quite constant throughout the phylum. The number of the neck-cells is very variable and is more numerous in the Mosses than in the Liverworts. It will be seen later that no phylogenetic stress can be laid on this character.

The two most important points, which deserve mention in this connection are, firstly, the variation in the number of the neck-canal cells, and secondly, the position of the archegonium in relation to the female gametophyte. It will be shown in the succeeding pages that the reduction in the number of the neck-canal cells and the embedded condition of the archegonia in the gametophyte, are criteria of higher evolution. If these be granted for the time being we would see that *Anthoceros*—with 4 neck-canal cells (with the exception of the *Sphaerocarpus*) and the embedded condition of its archegonia—among the Bryophytes would be the most nearly related to the Pteridophytes. In fact its partially independent sporophyte is selected as illustrating a possible ancestral condition of the vascular plants at the level of the Bryophytes.

Further Dr. Campbell, in a recent paper on the sporophyte of *Anthoceros fusiformis*, Aust.[1] has brought out certain very interesting points which in addition to other facts show similarity of certain recondite characters in common with the Devonian Rhyniaceae, thus binding the Bryophytes and the Pteridophytes in a closer bond of relationship. For the sake of clearness a summary from Dr. Campbell's papers is reproduced below :—

"The discovery that the sporophyte of *Anthoceros fusiformis* under certain conditions, may become practically independent and the ability of these plants to develop photosynthetic and conducting tissues commensurate with their needs, is a very strong argument in favour of the antithetic theory of alternation of generations in the Pteridophytes". [1], [2].

"The very close resemblance between the large sporophytes of *Anthoceros fusiformis* and the Devonian Rhyniaceae warrants the assumption of a real relationship between the latter and the Anthocerotales."[3]

"The existing Pteridophytes are almost certainly of polyphyletic origin, but all might be traced back to similar, but not necessarily closely related ancestors. The ancestral forms had sporophytes similar in structure to that of *Anthoceros*."[3]

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[1] Campbell; D.H, (1924): A Remarkable Development of the Sporophyte in Anthoceros fusiformis, Aust. *Ann. of Bot.* Vol. 38, pp. 472-483.

[2] Campbell, D.H., (1925): The Relationship of the Authocerotaceae. *Flora order Allgemeine Botanische Zeitung*: *Neue Folge*, 18 and 19 Band; (der ganzen Reihe 118 und 119 Band) S. 62-74.

[3] Campbell, D.H., (1925): The Relationship of the Anthocerotaceae. *Flora order Allgemeine Botanische Zeitung*: Neue Folge, 18 and 10. Band; (der ganzen Reihe 118 und 119 Band). S. 62-74.

B. Pteridophyta.

Thirteen types have been examined, the result of which is summarised in the chart given below:

Genera	Ventral C. Cell	Neck-Canal Cells	Neck Cells	Position on the prothallus.
Equisetum ...	1	*E. debile* 1; other spp. 2	4; 4	Projecting.
Psilotum ...	1	...	24	do.
Lycopodium.	1	many	10–16	do.
Selaginella ...	1	one	2	Embedded.
Isoetes ...	1	one with 2 nuclei	4	Partly embedded.
Ophioglossum.	1	do.	4	Embedded.
Botrychium ...	1	do.	4	Projecting.
Marattia ...	1	do.	3–4	Embedded.
Onoclea ...	1	do.	5–7	Projecting.
Osmunda ...	1	one or two	6	do.
Gleichenia ...	1	...	...	do.
Marsilia ...	1	one very small	2	Embedded.
Pilularia ...	1	do.	2	do.

Discussion: The number of ventral-canal cells is always one and that of the neck-canal cells never goes higher than four except in the case of Lycopods in which there are many neck-canal cells and in this respect they resemble the Bryophytes. In the Filicales the number of the neck-canal cells is reduced to one, the nucleus of which sometimes divides into two but no wall is formed between them. Thus we see that the general tendency among this group has been to reduce the number of the neck-canal cells and among the Filicales the reduction has reached the stage of a single uninucleate cell. (In the Gymnosperms even this has disappeared). The number of neck cells varies from about two to sixteen. The heterosporous members of the group have reached the two-celled-neck stage which is generally seen among the Gymnosperms. In most of the cases considered, the archegonia are embedded in the tissue of the gametophyte as we saw in *Anthoceros*. It is remarkable that the heterosporous members of Pteridophytes have the archegonia on the climax of reduction. Among the species of *Equisetum*, *E. debile* [1] seems in this respect, to be the most advanced one, there being only one neck-canal cell as against two in the other species. Among the species of *Lycopodium*, *L. cernuum* occupies a similar position, with only one neck-canal cell.

C. Gymnosperms.

Genera or Families	Ventral Canal Cell	Neck Canal Cells	Neck Cells	Position on the prothallus.
Cycas ...	Only nucleus	nil	2	Embedded.
Ginkgo ...	one small cell	do.	2	do.
Abietineae ...	one cell or only a nucleus	do.	2-8	do.
Taxodineae ...	Only ephemeral nucleus	do.	2-8	do.
Cupressineae ...	do.	do.	2-8	do.
Taxineae ..	Even nucleus may not be cut off	do.	2-25	do.
Podocarpineae ...	do.	do.	2-6	do.
Ephedra ...	Only nucleus	do.	32	do.

• *Discussion*: The above chart dealing with the more important characters of the archegonia amongst the Gymnosperms, brings forth the conclusion that the general tendency among the Gymnosperms

[1] Kashyap. S. R., (1914): Prothallus of Equisetum debile. *Ann. of Bot.* Vol. 28, pp. 163-181. *Postscript.*—Since the above was written Sethi (Ann. of Bot. Vol. 42 p. 732 figs. 7-8) has shown that the number of neck-canal cells in this species is two, and not one as reported by Kashyap.

seems to be to eliminate the ventral-canal cell. Among the living forms so far known, a walled ventral-canal cell is retained only in the *Abietineae* and *Ginkgo*. In the other living groups the wall has disappeared altogether and the ventral-canal cell is represented only by a free nucleus. In certain forms even this nucleus has disappeared *e.g.*, in some members of the Taxaceae. The neck-canal cell has been completely eliminated from the Gymnosperms. The number of neck-cells shows a good deal of variation. In *Ephedra*, the neck is the longest known among the Gymnosperms, the minimum number of neck-cells being 32. Next lower in the scale come some member of the Taxineae which may have as many as 25 neck-cells and the two-celled neck is an established feature of the Cycadales, the Ginkgoales and some of the Pinaceae. The latter condition at first sight may be regarded as advanced, so far as that character is concerned, but there is so much variation in the number of the neck-cells even within a genus (*e.g.*, in *Torreya taxifolia* there are 2-3 neck-cells but in *T. californica* the number varies from 4 to 6) that no definite phylogenetic importance can be attached to that feature.

We do not find any archegonium in *Welwitschia*, the embryo-sac has two to five-nucleated cells in its micropylar region and all the nuclei in a cell are potential egg nuclei. In *Gnetum* the embryo sac at the time of fertilization contains only free nuclei and each one of them is potentially an egg nucleus. Thus we see that in these two members of Gymnosperms the last traces of the archegonium are being lost and *Gnetum* approximates to the condition found among the Angiosperms.

Summary.

(1) The views put forth by Davis and Götz, on the origin of the archegonium have been briefly dealt with and criticised.

(2) A suggestion to derive the archegonium from the oogonium of *Coleochaete* (by a process of encapsulation) has been put forth and discussed. As far as known to the author, this view is being advanced for the first time.

(3) It is suggested that the multicellular wall and the neck and ventral canal cells were produced in response to the terrestrial conditions, the first as a safeguard against desiccation and the second to meet the deficiency of water for the act of fertilization.

(4) The further evolution of the archegonium has been chiefly a process of reduction and of retrogression of the essential organ, the egg-cell, into the tissues of the gametophyte.

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