Original Articles.

ON ALTERNATION OF GENERATIONS IN THE THALLOPHYTES.

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The discovery of the fact that an alternation of generations, comparable to that already known in the case of certain animals, takes place in the life-history of certain plants, is due chiefly to the labours of Hofmeister.* So far back as 1849 he pointed out that the prothallium of the Vascular Cryptogams is morphologically equivalent to the Moss-plant; that a Fern, a Lycopod, or a Rhizocarp, is the homologue of the Moss-fruit; and further, that in both Mosses and Ferns the asexual is interrupted by a sexual reproduction, this interruption occurring at an earlier stage in Ferns than in Mosses, and that the sexual and asexual generations regularly alternate.

So soon as these views were generally accepted, attempts were made to apply them to the life-histories of the Phanerogams on the one hand, and of the Thallophytes† on the other. Such an application is rendered difficult in the case of the former group, by the very intimate connexion of the two generations in the ovule, which makes their exact distinction a matter of some uncertainty; in fact, in spite of the considerable recent additions to our knowledge of the structure of the ovule and of the process of fertilisation, this question is still under discussion: in the case of the latter group it is rendered difficult by the more or less complete independence of the two generations, and by the frequent repetition of the one before the recurrence of the other. Some Thallophytes, however, viz. the *Conjugatæ*, *Fucaceæ*, and *Characeæ*, are generally considered not to exhibit any alternation of generations. It is the object of this paper to discuss the application to the Thallophytes of this doctrine, and to inquire in how far such an application is justifiable.

Before proceeding to do this it will be well to give a brief sketch of the life-history of a Moss, which may serve in some sort as a standard for comparison. Calling the sporogonium (the asexual generation or sporophore) the first generation, we find that

* Ueb. die Fruchtbildung und Keimung der höheren Kryptogamen, 'Bot. Zeit.,' 1849, No. 45.—Vergl. Unters. 1851. On the Higher Cryptogamia, 'Ray. Soc.,' 1862. Zur Uebersicht der Geschichte von der Lehre der Pflanzenbefruchtung, 'Flora,' 1857, p. 120.

† For instance, Pringsheim, Ueb. die Befruchtung und den Generationswechsel der Algen, 'Monatsber. der Berl. Akad.,' Mai, 1856:—Braun, Ueb. Parthenogenesis bei Pflanzen, 'Abhandl. d. k. Berl. Akad.,' 1856.

it is developed from a sexually-produced reproductive cell, the oospore, and that it bears asexually-produced reproductive cells, the spores, from which the second generation, the Moss-plant (oophore), is derived: in other words, the spore *always* gives rise to an oophore, and the oospore *always* gives rise to a sporophore.

The following account of the current views on alternation of generations in the Thallophytes is taken mainly from Sachs' 'Lehrbuch,'* where they are clearly and fully stated. Beginning with the *Zygosporeæ*, and taking *Mucor Mucedo* as an example of the Fungi belonging to that Class, we find that the zygospore is regarded as the equivalent of the fertilised oosphere (oospore) of the Moss, and that consequently the product of its development is the homologue of the sporogonium. According to Brefeld's very complete account † of the life-history of this plant, the zygospore gives rise, on germination, to a simple mycelium bearing a single sporangium: this mycelium is then the sporophore of the plant. When the spores (conidia) developed in this sporangium germinate, they usually give rise to mycelia which bear only conidia, and several generations of these may be produced before the recurrence of a sexual mycelium bearing zygospores. It is evident that these conidia-bearing generations are not the equivalents of repeated Moss-sporogonia, for it is the peculiarly modified generation developed directly from the zygospore which is considered to be the sporophore: under these circumstances, the successive conidia-bearing mycelia must be regarded as being *potentially* sexual, that is, as being capable of producing zygospores under certain favourable conditions, but in the absence of those conditions they produce only conidia. Comparing this life-history with that of a Moss, it appears that the mycelium, developed from the germinating zygospore and never producing zygospores, is the asexual generation or sporophore, and is equivalent to the sporogonium: the spores (conidia) which it produces give rise to a generation which, unlike the corresponding generation of the Moss, may or may not be sexual according to the conditions under which it exists.

If we take *Pandorina* as an example of the algal forms of this Class, we find the sporophore represented only by the zygospore; from it, swarm-spores are liberated, which are considered to correspond to the spores of a Moss. In this case the mode of development of the spores from the zygospore is much simpler than in *Mucor Mucedo;* no vegetative organs whatever are developed, but the zygospore is itself the sporangium in which the spores are formed. These two modes of development have been distinguished by Pringsheim as "*mycelienkeimung*" (*Mucor*) and "*sporangienkeimung*" (*Pandorina*).‡ Each of these swarm-spores gives rise to a cœnobium, which, like the mycelium of *Mucor Mucedo*, is either

* '4te Auflage,' 1874, pp. 231, 238, &c.

† 'Bot. Unters. üb. Schimmelpilze,' Heft I., 1872.

‡ Ueb. den Generationswechsel der Thallophyten etc., 'Jahrb. f. wiss. Bot.,' Bd. XI., p. 42.

actually or potentially an oophore; the cells of the cœnobium divide and give rise to motile cells which, according to circumstances, either conjugate in pairs and form zygospores, when they are termed gametes,* or simply divide and form new cœnobia, when they are termed zoogonidia.

The oospore of the *Oosporeæ*, like the zygospore of the preceding Class, is regarded as the sporophore. Its development may resemble that of the zygospore of *Pandorina*, swarm-spores being formed within it which either give rise to potentially sexual individuals reproducing by means of spores (conidia, gonidia), or at once to sexual individuals; or it may resemble that of the zygospore of the *Mucorini*, and form a mycelium (*e.g.*, *Peronospora Valerianellæ*)† which, in this case, does not differ materially from the mycelium produced by a germinating conidium. It is of interest to note that both modes of development are exhibited by closely allied plants in the *Peronosporeæ*, and by the same plant‡ in the *Saprolegnieæ*.

In the *Carposporeæ* it is the cystocarp which is regarded as the sporophore, and the plant developed from the carpospore is the actual or potential oophore. The cystocarp varies much in structure; in *Coleochæte* it is not very different from an oospore or a zygospore, but in the *Ascomycetes* and in the *Florideæ* it is an organ of considerable complexity.

These views may be conveniently tabulated as follows:—

	Sporophore.	*Oophore.*
Moss	Sporogonium.	Plant.
Fern	Plant	Prothallium.
Zygosporeæ.		
Mucor . . .	Zygospore and rudimentary mycelium. .	Mycelium.
Pandorina . .	Zygospore.	Cœnobium.
Oosporeæ.		
Peronospora. .	Oospore	Mycelium.
Œdogonium. .	Oospore	Thallus.
Carposporeæ.		
Ascomycetes. .	Cystocarp (apothecium)	Mycelium.
Florideæ . . .	Cystocarp	Thallus.

This interpretation of the life-history of Thallophytes has been recently criticised by Pringsheim.§ He lays it down as a fundamental axiom, that the generations of Thallophytes, like those of Cormophytes, begin in all cases with a free cell, the spore, but that, unlike those of Cormophytes, the generations are distinct and

* See Strasburger, 'Befruchtung und Zelltheilung,' p. 9.

† De Bary, 'Beitr. z. Morphol. u. Physiol. d. Pilze,' Heft II., p. 40.

‡ Pringsheim, 'Jahrb. f. wiss. Bot.,' Bd. IX.

§ Ueb. d. Generationswechsel der Thallophyten, &c., 'Jahrb. f. wiss. Bot.,' XI.

do not remain in organic connexion; consequently, it is impossible to regard the "fruits" of Thallophytes as representing an entire generation. In illustration of this he points out that the zygospores of the *Mucorini* are not fructifications comparable to the sporogonium of a Moss, but that they are, like those of the *Conjugatæ*, the initial cells of a new generation, and he regards the rudimentary mycelium developed from the zygospore as the "first neutral generation," which differs from the succeeding neutral generations in the very slight development of its vegetative organs. He does not mean to imply that no alternation of generations occurs in the life-history of the *Mucorini;* on the contrary, he endeavours to show that there is an alternation, not indeed between the zygospore with its rudimentary mycelium and the sexual mycelium, but between dimorphic sexual and asexual mycelia. He deduces an argument against the current views from Brefeld's observations upon *Mucor dichotomus.** Brefeld has found that the zygospore of the *Mucorini* does not give rise in all cases to a simple asexual mycelium as in *Mucor Mucedo:* in *Mucor dichotomus*, when the zygospores germinate under appropriate culture, they produce well-developed mycelia which bear a number of zygospores. Here then is a case in which the sexually-produced reproductive cell of an oophore gives rise at once to a new oophore, a fact which is obviously irreconcilable with the Moss-type of alternation of generations. Although this fact affords some support to Pringheim's objections to the current views, it is of no positive value as evidence in favour of his own views of the alternation of generations, as will be shown hereafter. In the other group of the *Zygosporeæ*, the *Pandorineæ*, the alternation, according to Pringsheim, is not of a motile sexual cœnobium and a resting zygospore, but of sexual and asexual cœnobia.

In applying his views to the *Oosporeæ*, he rejects the suggestion of Braun † that the oospore is a rudimentary one- or many-spored fruit, and he regards it as the initial cell of the new generation, so that in this Class, as in the preceding, the alternation is that of dimorphic, independent, sexual and asexual plants.

Passing on to the *Carposporeæ*, we find that in the case of *Coleochæte*, Pringsheim considers the mass of cells formed within the cystocarp to be the "first neutral generation" of the plant, which produces a second neutral generation by means of swarm-spores. With regard to the other sexual *Carposporeæ*, the *Ascomycetes* and the *Florideæ*, he considers that the "fruits" are not to be regarded, any more than those of *Coleochæte*, as the direct products of fertilisation, but simply as the female reproductive organs which have been indirectly affected by it, and which resemble, in this particular, the calyptra of Mosses and the cushion on the prothallia of Ferns. The trichophore and the ascogonium, he urges, are to be regarded as an archegonium which undergoes direct fertilisation, the fertilising influence being conveyed from cell to cell of the organ until it reaches the ascospores. If this view be correct,

* 'Bot. Zeitg.,' 1875, p. 848. † *Loc. cit.*, p. 372.

the ascospores must necessarily be regarded as oospores. The alternation of generations in the *Ascomycetes* and the *Florideæ* is then that of independent sexual and asexual plants, and not that of cystocarp and sexual thallus. He considers, partly on account of their structure and partly on account of the products of the germination of the stylospores, that probably the pycnidia are the neutral fructifications. This view derives support from Bauke's observations on *Pleospora herbarum*,* in which the perithecium and pycnidia appear to represent the two generations, though their succession is very irregular.

It cannot be denied that Pringsheim's objections to the accepted interpretation of the life-histories of Thallophytes, according to the Moss-type of alternation of generations, are well-founded. The fact that such groups as the *Conjugatæ* and the *Fucaceæ* exist, which exhibit no such alternation, is presumptive evidence against it; this is supported by the above-mentioned development of a sexual mycelium from the zygospore of *Mucor dichotomus:* moreover it must not be overlooked that in *Peronospora*, where the oospore produces an ordinary mycelium, there cannot be an alternation of generations according to the Moss-type; and finally, it will be readily granted that a great part of the fructification of the sexual *Carposporeæ* belongs, as Pringsheim states, to the parent-plant, so that the "fruit" cannot be regarded as constituting a distinct generation, and the view that the carpospores are really oospores is at least not contrary to our knowledge of the mode of fertilisation in these plants.†

Admitting then that it is not possible to interpret the life-history of Thallophytes in the same way as that of a Moss, the question arises whether or not there is any ground for continuing to use the expression "alternation of generations" with reference to Thallophytes as Pringsheim does. Nearly all the arguments brought by Pringsheim against the Moss-type theory are equally valid against any theory of alternation of generations whatsoever; and when it is also borne in mind that in certain of these plants, such as *Ulothrix zonata* ‡ for instance, the differentiation of sexual and asexual reproductive cells is so slight, that if the former fail to conjugate and to form zygospores they germinate like ordinary zoogonidia, there seems to be good reason for answering this question in the negative. It seems to be more in accordance with fact to say simply that a sexual Thallophyte may reproduce itself either sexually or asexually, the mode of reproduction depending more especially upon the external conditions. Speaking generally, it is not possible to say of a spore (conidium, gonidium) of any given Thallophyte that the product of its germination will necessarily be a sexual plant, nor is it possible to say of the oospore (zygospore, carpospore) that the product of its germination

* Zur Entwickelungsgeschichte der Ascomyceten, 'Bot. Zeit.,' 1877.

† See Thuret and Bornet, on the fertilisation of the *Florideæ*, 'Ann. d. Sci. Nat.,' 1855 and 1867; also Stahl, Ueb. die geschlechtliche Fortpflanzung der Collemaceen, 1877.

‡ Dodel, Ueb. *Ulothrix zonata* , Prings. 'Jahrb. f. wiss. Bot.,' X.

will be necessarily an asexual plant, conditions which are accurately fulfilled in those plants (*Bryophyta*, *Pteridophyta*) in which an alternation of generations undoubtedly takes place. Since this is so, it appears to be quite unnecessary and even unwarrantable to introduce the idea of an alternation of generations into our general conception of the life-history of Thallophytes.

There is reason, however, for believing that in two groups of Thallophytes, the *Characeæ* and the *Coleochæteæ*, a distinct alternation of generations, more or less resembling that of Mosses, occurs.* In a previous number of this Journal† I have fully discussed the indications of such an alternation in the life-history of the *Characeæ;* it is therefore unnecessary for me to say anything on the subject in this paper. As regards *Coleochæte*, the oospore becomes divided by the formation of successive walls, so that it is converted into a mass of cells united to form a parenchymatous tissue. This mass of cells is the sporophore of the plant, or, according to Pringsheim's view, the "first neutral generation," which differs but little, excepting in size, from the ordinary thallus.‡ When the wall of the cystocarp ruptures in the spring, the sporophore is set free, and from each of its cells a single swarm-spore escapes which gives rise to an asexual individual. It is only after a long succession of asexual generations, continuing through the whole summer, that sexual plants are produced. Pringsheim, in an earlier publication, § pointed out the homology of the body thus formed in the oospore of *Coleochæte* with the sporogonium of a Moss, a view to which he still adheres. The alternation, in this case, is that of a sporophore with a succession of potential oophores terminated by an actual oophore; it deviates from the Moss-type in the intervention of a number of potential oophores between the sporophore and the true oophore; it is, as it were, a middle term between the fortuitous succession of sexual and asexual generations in Thallophytes generally, and their regular alternation in Mosses and Ferns.

From this point of view, Pringsheim's expression for the sporophore of *Coleochæte*, "first neutral generation," is inadmissible, for it suggests that the sporophore is of the same nature as the succeeding generations, and this, as we have seen above, is not the case. Moreover, it suggests also that the sporophore of *Coleochæte* is of the same nature as the "first neutral generation" of the *Œdogonieæ*, of *Bulbochæte*, *Sphæroplea*, *Hydrodictyon*, *Pandorina*, and *Cystopus*, where it is simply a sporangium, or of *Mucor*, where the vegetative organs are developed to some extent. Now Pringsheim has already pointed out, in the last-mentioned publication, that in those Thallophytes which exhibit "*sporangienkeimung*," the changes taking place in the germinating, or more correctly, the developing zygospore or oospore suggest rather the

* Possibly this may be also true of the *Florideæ:* see Pringsheim, Ueb. Befruchtung und Keimung der Algen; Monatsber. d. Berl. Akad., 1855.

† December, 1878.

‡ At least in *C. scutata*.

§ Die Coleochæteen: 'Jahrb. f. wiss. Bot.,' II.

development of several embryos from a single fertilised oosphere, than the formation of spores in a sporangium; that these are, in fact, cases of polyembryony comparable to those occurring in Gymnosperms.* If this be so, the expression "first neutral generation" is inapplicable to these zygospores and oospores, and the products of their development. Again, it has been shown above that in those Thallophytes which exhibit "*mycelienkeimung*," the product of the germination (here this word is the correct one) of the zygospores and the oospores is by no means always an asexual generation, and therefore it cannot be generally described as a "first *neutral* generation." On these grounds it may be fairly concluded that the phrase "first neutral generation" is of no value as a general expression, and that it tends, therefore, rather to confuse than to make clear our ideas of the life-histories of the different groups of Thallophytes.

The results of this discussion may be briefly summed up as follows:—It appears that it is impossible to detect any distinct alternation of generations in the life-histories of Thallophytes, with the exception of the *Coleochæteæ* and the *Characeæ*. In both these groups the oospore undergoes division whilst it is still enclosed in the oogonium, and gives rise to a mass of cells, combined together into a tissue, which constitute an embryo: in the former, each cell of the embryo, which is the sporophore, subsequently gives rise to a swarm-spore from which a potential oophore is developed; in the latter, the embryo developes into an aposporous sporophore from which the oophore is produced by a process of lateral budding.

ERYTHRÆÆ IN THE ISLE OF WIGHT.

By Fred. Townsend, M.A., F.L.S.

I have been asked by the Editor of the 'Journal of Botany' if I would send a notice of an *Erythræa* which I collected this summer on the chalk downs in the neighbourhood of Freshwater and the Needles, in the Isle of Wight. I have with me few books and no specimens, but an early notice may lead to light being sooner thrown upon the subject by engaging the attention of botanists who have materials ready to hand. After the examination of very numerous specimens, I drew up, on the spot, the following characters:—

Stem usually simple, solitary, or several from the crown of the root; lower leaves ovate, obtuse, 3–5 nerved, shorter than the intermediate, and forming a rosette; intermediate linear-oblong, somewhat narrowed below, uppermost bract-like, often broader below, one or two usually equalling or exceeding the flowers; flowers sessile, numerous, densely corymbose, bracts linear, obtuse but apiculate; calyx equalling or exceeding the corolla-tube; *stamens*

* For a typical instance see Strasburger's account of *Ephedra altissima* in his 'Zellbildung und Zelltheilung.'