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Some recent work on the cytology of fungus reproduction. I.

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(Schluß.)

In the *Pyrenomycetineae* Winge (1911) has published a paper under the very appropriate title "Encore le *Sphaerotheca Castagnei*". de Bary (1863) was the first to find what he considered to be the sexual organs in this species. Two erect protuberances arise simultaneously from different branches; one of these branches is the unicellular ascogonium and the other consists of two cells, the terminal one of which is the antheridial cell. The antheridial branch is always closely applied to the ascogonium. Much controversy took place concerning whether a true fertilisation occurred or not. In 1895 Harper worked at the species with modern cytological methods. He announced that the antheridium and ascogonium are both uninucleate and that when the antheridial cell becomes closely applied to the ascogonium, the walls between the two organs break down to allow the male nucleus to pass into the ascogonium and fuse with the female nucleus. Dangeard (1897) denied that there was ever any open communication between the cells. He often found two nuclei at a later stage in the ascogonium but these he held arose by a division of the ascogonial nucleus probably by amitosis. Blackman and Fraser (1905), while preparing some slides of *Sphaerotheca Castagnei* for class purposes, came across stages which seemed to prove the correctness of Harpers views, and published a short note with figures to that effect. Winge states that Dangeard's interpretation is the correct one and restates many of the latters arguments. He criticises Harper's figures, saying that they represent all the nuclei as being globular, whereas this is only true for the male nucleus. The principal points of his paper are as follows: The ascogonium seems to have an attraction for the antheridial branch, probably as a reminiscence of former times still emitting a substance which attracts the antheridium. No fusion was ever observed between the two cells; they are always separated by a gelatinous layer formed by the walls of the two organs. At a later stage two nuclei occur in the ascogonium. These are usually of different sizes. The smaller nucleus has a similar structure to the larger one, and it is obvious that they have arisen from the division of the original ascogonial nucleus, although, unfortunately, this division has not been seen. Very often at the stage when two nuclei are present in the ascogonium one finds the remains of the degenerated male nucleus in the antheridium, and several times a well preserved male nucleus has been found. The two nuclei in the ascogonium do not fuse. Their further divisions have not been clearly seen, but the ascogonium becomes three-septate. The penultimate cell possesses two nuclei which fuse to form the primary ascus nucleus. This fusion nucleus divides but the divisions have not been carefully studied. From the meagre account given however, it seems as if brachymeiosis may occur, eight chromosomes being present in the first two divisions and "nous croyons avoir vu quatre chromosomes à la dernière division". Winge draws attention to the fact that whereas Harper, and Blackman and Fraser hold that the ascogonium divides into from four to six cells, Dangeard and he find that it always becomes three-septate. He suggests that this difference may be due to the fact that they have been working at different species. In considering this suggestion however one must note that all obtained their specimens from the Hop with the exception of Winge who obtained his specimens from *Melampyrum*. If Winge's suggestion were true it would mean that two different species of *Sphaerotheca* attack the Hop and that one of these is also present on *Melampyrum* the two only being distinguishable by cytological methods [1]). In spite of his suggestion however, he holds that Dangeard and he are correct and that some of Harper's figures are certainly wrong "En effet, nous trouverons assez souvent dans les coupes au microtome, des figures correspondantes aux dessins de cet auteur, mais les explications qu'il en a données sont fausses. Naturellement, quand on coupe en différents sens une ascogone, qui est courbée, qui a trois cellules, dont celle du milieu a deux noyaux, les autres un seul noyau chacune, il est possible de voir les coupes qui, par orientation erronée, donnent des résultats fautifs-et c'est ce qui est arrivé pour Harper." But nothing is said of the figures of Fraser and Blackman who had knowledge of Dangeard's criticisms when they wrote their note.

Vallory (1911) has published a preliminary note (without figures) on the cytology of *Chaetomium Kunzeanum* var *chlorinum*. He records, as did Oltmanns and Dangeard, the presence of an ascogonium, unaccompanied by an antheridium. The ascogonium becomes rolled up on itself and divides into portions eventually forming a mass of false tissue from the cells of which arise the ascogenous hyphae.

When a spore germinates it gives rise to a mycelium which is septate and plurinucleate. The nuclei are very small and show a nucleolus but no visible limiting membrane or chromatin. In the hyphae pairs of nuclei are very frequently seen which resemble in every particular what Blackman and his followers described in the ascogonia of various *Ascomycetes* (*Humaria granulata*, *Lachnea stercorea*, *Ascophanus carneus* etc.) and which they considered were female nuclei fusing in pairs. In the case of the mycelium Vallory thinks that it cannot be a case of fusing nuclei and that the only plausible explanation of the phenomena is that the pairs of nuclei are different stages of amitoses where the nuclei are more or less separated. This, he states, is shown by the following facts. The pairs of nuclei are present in the young actively growing mycelium where there is a great increase in the number of nuclei, whereas on the

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1) *Sphaerotheca Castagnei* var. *fuliginea* occurs on *Melampyrum*. It is quite distinct.

other hand pairs of nuclei are much fewer in number or totally absent in the older parts of the mycelium. No other nuclear phenomenon was observed which might explain this increase in the number of nuclei. Again, the pairs of nuclei reappear in the rapidly-growing investing hyphae which arise on the old mycelium and they are present in the wall of the perithecium already well developed. Pairs of nuclei, identical in appearance with those observed in the other parts of the fungus, were found in the young ascogonium and in the various cells produced by the septation of the ascogonium. These pairs of nuclei therefore cannot be stages in the fusion of female nuclei as has been previously thought but are stages of amitotic division. The study of the nuclei of the ascogenous hyphae and of the asci was not carried out. This further work will be awaited with interest.

Though BROWN and VALLORY agree in considering the pairs of nuclei in various ascogonia as division stages, the former, as we have seen, considers that the division is karyokinetic, whereas the latter holds it to be amitotic.

It is a noteworthy fact that in no case where this fusion of pairs of female nuclei has been recorded has there been described a nuclear division in the ascogonium, although the nuclei increase greatly in number. Especially noticenble is a case like *Ascobolus furfuraceus* where the ascogonium is described as being uninucleate when first formed.

The phenomenon was first observed in *Humeria granulata* (BLACKMAN and FRASER, 1906). The nuclei, which are rather small, show no nuclear network but exhibit a nuclear membrane and a deeply staining nucleolus. "As development proceeds the nuclei increace only slightly in size but enormously in number . . . . . Female nuclei were observed fusing in pairs in the ascogonium. These fusions ars to be observed in ascogonia of various ages . . . . . No data were obtained as to the number of nuclei in the ascogonium at its first inception, but judging from the size of the organ at that stage and from the relatively small number of nuclei in the vegetative cells, very numerous divisions must take place. It is curious that such divisions were never observed in the ascogonium; it is probable that they are intermittent in occurense; possibly they take place only at night." It would seem from these extracts that the authors must have considered the case for nuclear division and decided against it.

In the *Laboulbeniaceae* (considered by THAXTER and FAULL as belonging to the *Pyrenomycetineae*) FAULL (1911) has published an introductory account of the cytology of the group. The female organ (procarp) consists of three distinct parts. The uppermost portion is the trichogyne and may be unicellular or more complicated in structure; the middle portion is in all cases unicellular and uninucleate and is termed the trichophoric cell; the lowest portion, unicellular and uninucleate, is termed the carpogonium, being the portion of the procarp which is fertilised. Except in the case of *Laboulbenia chaetophora*, the author is uncertain as to the origin of the pair of nuclei which appear later in the carpogenic cell. This species is interesting because of the lack of antheridia or of any organs that might function as antheridia. The nucleus of the carpogonium divides and the lower of the two daughter nuclei is cut off to form the inferior supporting cell. The nucleus in the trichophoric cell also divides. The septum between the trichophoric cell and the carpogonium now temporarily dissappears and one of the daughter nuclei passes into the carpogonium. After this, a septum reappears. The pair of nuclei present in the carpogenic cell now undergo division and a transverse wall is formed which separates off a binucleate ascogonium from a binucleate supporting cell. Presumably the nuclei in the ascogonium again divide to provide the nuclei for a binucleate secondary inferior supporting cell which is sometimes cut off from the lower end of the ascogonium. The binucleate ascogonium may at once begin to bud off asci but it usually first divides by a nearly vertical wall into a pair of binucleate ascogenic cells. The nuclei of the ascogenic cells divide conjugately and mitotically. A daughter of each nucleus passes into the young ascus and a fusion takes place between them. The fusion nucleus unters upon a long period of growht finally undergoing three successive mitoses. „The first exhibits cleerly the phenomena said to be characteristic of meiosis, except that neither here nor in the two subsequent divisions is there any change in the number of chromosomes.“ Spore formation occurs in the same manner as in the ordinary *Ascomycetes*. Speaking of the *Laboulbeniaceae* as a whole, Faull finds that the cells of the thallus are typically uninucleate and that the nuclei divide mitotically. The spermatia are uninucleate in all the forms studied. Spermatia have been seen attached to trichogynes but their entrance into, or fusion with them has not been detected. Neither has the spermatium nucleus been detected migrating down the trichophoric cell although the carpogonium in every case studied became binucleate as also did later the ascogenic cells. No evidence of a nuclear fusion in the carpogenic cell or in the ascogonium has been seen, "though the possibility of the occurrence of such a fusion is not precluded". Faull points out that the phenomenon of conjugate nuclear division, and the presence in *L. chaetophora*, of a reduced type of sexuality, suggest similar phenomena in the rusts and in certain *Ascomycetes*. Also the "uninucleate antheridium, the possibility of proliferation of spermatia from the same antheridium, and the exogenous type of spermatium organisation, suggest similar phenomena in the rusts, many *Ascomycetes* and the *Florideae*". It seems rather unfortunate in many ways that a form which is lacking in spermatia should have first been chosen for cytological investigation instead of one of those forms in which Thaxter states that he has observed spermatia fused with the trichogynes. When such forms have been studied it will be possible to see whether the nuclear occurrences in *L. chaetophora* are normal or not, and whether the nucleus which migrates from the trichophoric cell into the carpogonium is to be regarded as a vegetative nucleus and thus comparable with the migrating nucleus described in *Phragmidium violaceum*.

In the *Uredineae* the nuclear phenomena seem now to be fairly well known but it seems extremely probable that there is much more variation in this group than was at first thought likely. By the work of various investigators, especially of Sappin-Trouffy, it was clearly shown that in the majority of cases, there is an alternation of a binucleate condition with a uninucleate one. The binucleate condition arises at the base of the aecidium. The two nuclei divide conjugately and the vegetative and reproductive cells in the life cycle up to the mature teleutospore stage are binucleate. In the mature teleutospore the two nuclei fuse. The teleutospore on germination gives rise to a promycelium which bears uninucleate sporidia. The sporidium produces a uninucleate mycelium. The process by which the uninucleate mycelium becomes binucleate was first described by Blackman (*Phragmidium violaceum*, 1904). He found that in the young aecidium the uninucleate hyphae arranged themselves in parallel rows perpendicular to the surface of the leaf. The end cells were sterile but the penultimate cells became binucleate by the migration of a nucleus from a sub-adjacent cell of a neighbouring hypha. Christman (1905) showed that in *P. speciosum* the binucleate condition arose by the breaking down of the cell wall between two adjacent penultimate cells. Further work has shown that the method described by Christman is much the more frequent. Olive (1908) tried to harmonise the two results but certain investigators hold that where migration takes place, as described by Blackman, the phenomenon is purely pathological.

Maire (1911) in an interesting paper on the biology of the *Uredineae*, incidentally mentions that on re-examining his slides of *Puccinia Bunii* he finds that the binucleate condition seems to arise by Christman's method. The cells are so intricate, however, that it is impossible to distinguish details.

Several species with incomplete life cycles have been studied. One of the most interesting cases is that of the genus *Endophyllum* which does not possess teleutospores. Hoffmann (1911) has worked at a species of this aberrant genus, *E. Semperviri*. Maire (1900) had previonsly investigated this species as well as *E. Valerianae-tuberosae*, while Sappin-Trouffy (1896) had worked at *E. Euphorbiae silvaticae*. In the first and last of these species the process described was identical. Binucleate aecidia are formed. These germinate and the nuclei divide to form the four nuclei of the promycelial cells. The nuclei pass into the sporidia and there divide previous to germination. The account given for *E. Valerianae-tuberosae* is different. The aecidiospores are at first binucleate but one of the nuclei degenerates and disappears. When the aecidiospore germinates a very short promycelium is formed. The remaining nucleus passes into this and there divides, and a wall is formed between the two daughter nuclei. The nucleus of the lower cell either degenerates at once, or divides, in which case both daughter nuclei degenerate. The nucleus of the remaining cell passes into the single sporidium.

It was difficult to see how these results could be made to fit in with the results obtained in so many other genera. Hoffmann's account however shows that in the case of *E. Sempervivi* at least, the phenomena are not so anomalous as was previously thought. A binucleate basal cell arises in the young aecidium by the breaking down of the cell wall between two adjacent cells in the manner first described by Christman in *Phragmidium speciosum*. The two nuclei divide in the usual conjugate manner, forming a series of alternate binucleate aecidiospores and intercalary cells. The two nuclei fuse in the ripe aecidiospore. The fusion nucleus undergoes reduction either in the spore or in the promycelium which arises from it. The promycelium consists generally of four uninucleate cells, from each of which arises a uninucleate sporidium. The sporidium on germination gives rise to a uninucleate mycelium which produces spermatia (of which the fate is unknown) and the aecidia. There is thus a well marked alternation of generations, but the sporophyte is considerably reduced.

It is probable from this study that the homology of the spores in *Endophyllum* will be considered to be with the aecidiospores in the other genera as suggested by de Bary and not with teleutospores as Dietel holds, although the additional fact of the fusion of nuclei in the ripe spore lends some support to Dietel's view.

An interesting case where apparently there is not a binucleate sporophytic stage has been studied by Moreau (1911). The observation was made on an *Aecidium* parasitic on *Euphorbia silvatica.* The aecidia have the usual appearance but when cytologically examined it is seen that all the cells are uninucleate. The elongated cells which support the chains of aecidiospores are uninucleate as are also those of the subaecidial mycelium. At no period is there a doubling of nuclei. In each of the cells at the base of the aecidium the single nucleus divides. A wall forms between the two daughter nuclei separating off at the summit a uninucleate aecidiospore-mother-cell. The second nucleus remains in the basal cell and contributes by the same procedure to the formation of a second mother cell and so on. The nucleus of each mother cell divides in its turn into two and a wall forms which separates the mother cell into two uninucleate cells, the upper larger one of which is a young aecidiospore, the lower smaller one an intercalary cell. Thus chains are formed. The aecidiospores grow, ripen and detach themselves, while the intercalary cells disappear. Thus everything occurs as ordinarily except that the cells are uninucleate and not binucleate. Moreau was unable to germinate the aecidiospores and therefore could not determine whether she was working with *Endophyllum* or not. Plowright (Brit. Ured., p. 229) however, speaking of *E. Euphorbiae* says. — "The spores of this species germinate freely in water". If the fungus is a species of *Endophyllum* we have a further type to add to the three referred to above. Whatever the genus, the point of interest is that this is the first record of parthenogenetically formed aecidiospores.

Sharp (1911) has published a preliminary note on *Puccinia Podophylli.* A binucleate condition prevails in the mycelium that gives rise to aecidia and spermagonia. The nuclei even before there is any indication of aecidium formation are associated in pairs and divide conjugately. This condition is not however constant as a uninucleate mycelium is sometimes observed. The young aecidium arises in a dense tangle of hyphae beneath the epidermis of the host. Certain cells in this tangle enlarge and become "basal cells" giving rise to aecidiospore chains of the usual type but containing two, three or four nuclei according to the number of nuclei present in the basal cell. In older chains only two of these basal cell nuclei continue to function so that binucleate spores usually far outnumber the others. It is not known how the basal cells arise. Spermatia formation has also been studied. Two facts recorded by the author with regard to these are very interesting in connection with the generally accepted view that the spermatia are male cells viz: 1. the spermatia are sometimes binucleate; 2. "the spermatia vary in length, some of them being more than three times as long as the diameter of the nucleus, so that they contain much besides nuclear material". When the author's complete account of these phenomena is published it will be possible to decide whether in *P. Podophylli* we have the opposite phenomenon from the one described by Moreau i. e. a binucleate condition throughout the life history instead of a uninucleate one. The presence of large basal cells containing three and four nuclei seem against this view as also does the presence at times of a uninucleate mycelium and of tri- and tetra-nucleate aecidiospores. Such a range in the number of nuclei is certainly rather surprising.

In the *Basidiomycetes* Kniep has given an account of results obtained in cultures of *Armillaria mellea.* He sowed various parts of the fungus and always obtained a uninucleate mycelium. On this mycelium arose aërial outgrowths which, from their structure and appearance, were obviously basidia. The basidia were always uninucleate. The nucleus increased in size. This increase in size was not due to a fusion of two nuclei, all possibilities of such being the case having been carefully considered. This large nucleus underwent two successive divisions which were identical in all their stages with the two divisions which occur in normal basidia and are generally supposed to constitute reduction divisions. The two bodies which wander to the poles during the two divisions Kniep considers, with a certain amount of reserve, not as chromosomes but as chromatin bodies which have been described as occurring also in certain other thallophytes. In the second division the nuclei remain close together. Unfortunately the fate of the basidiospore could not be followed. From the stages observed during the divisions in the basidium Kniep considers that the nucleus in that organ is of diploid nature. He therefore thinks that during the life history of the fungus there must have been a fusion of nuclei which gave rise to a series of diploid nuclei but unfortunately this fusion was not seen by the investigator.

In connection with this it is interesting to note the occurrence of uninucleate basidia in *Hygrophorus conicus.* Fries (1911) has worked at *f. sulphurea* of this species. The work of several authors has shown that in the majority of cases the young basidium is binucleate. The two nuclei fuse later, the fusion nucleus increases in size and then undergoes two divisions which resemble the reduction divisions observed in many plants. The four resulting nuclei pass into the spores. Species with only two nuclei have been studied (*Dacryomyces* spp. *Amanita bisporigera* etc.) but in these cases there has been observed a nuclear fusion and two successive divisions, two of the nuclei passing into the spores, the other two remaining in the basidium. It is true that Dangeard thinks there is only one division, and that apparently an indirect one in the case of *Dacryomyces deliquescens* but Istvánffi, Juel and Maire believe that there are the usual divisions in this genus. Maire holds that in this species there is a second crop of spores which utilise the second pair of nuclei but from Buller's work on the morphology of basidia this seems very unlikely.

Maire (1902) had previously worked at *Hygrocybe* (*Hygrophorus*) *conica* and *H. ceracea.* He found the cells of the subhymenium and the young basidia constantly uninucleate[1]). He founded a new genus for the reception of these species. — *Godfrinia* which he diagnoses as characterised “surtout par ses basides ventrues et constamment bisporiques, uninucléées a l'état jeune, ainsi que les cellules du subhymenium”.

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1) Mr. Carleton Rea, Hon. Sec. of the British Mycological Society, informs me that the red form of *H. conicus* in England, always possesses four sterigmata and four spores. I. R.

Fries' work confirms that of Maire with regard to *H. conicus* The young basidia are uninucleate. The nucleus enlarges and wanders to the point of the basidium. It divides once and immediately rests. In the anaphase only two chromosomes are present. (This Maire also found but he recorded here, as in all the cases he studied, the presence of what he terms protochromosomes). At this stage the sterigmata grow out and give rise to the kidney-shaped spores. The daughter nuclei wander into the spore beginnings and divide, either immediately or somewhat later, so that the spore when it falls always possesses two nuclei. The author concludes that there are in this fungus, no reduction divisions, and that the reduced number of chromosomes holds right through the life history i. e. that the diploid phase is wanting. Thus there is a state of apogamy of the kind which Guilliermond has termed apomixie. These results can be somewhat satisfactorily compared with those recorded by Moreau which are referred to previously in this resumé.

Fries (1911) has also published a continuation of his work on the development of *Nidularia*. He finds, as is usual, that the young basidia are binucleate. The two nuclei increase in size and then fuse. The fusion nucleus rapidly increases in size and then undergoes two successive divisions the details of which are hard to make out. Fries considers, however, that in the first division two bivalent and in the second two monovalent chromosomes are present. The two divisions thus constitute a reduction division. The nuclei, after this second division, pass into the spores through the sterigmata. They are, at this stage, in the prophase of a division which is completed in the spore. The spore therefore is binucleate as in all the *Gasteromycetes* studied. The spindle in the first nuclear division in the basidium is at right angles to the longitudinal axis (Chiastobasidiae of Juel). Maire (1902) has described very similar happenings in *Nidularia globosa* and *Cyathus hirsutus*.

In most *Basidiomycetes* studied the basidium arises from a series of binucleate cells. It is not yet known how this binucleate condition arises, nor at what stage of the life history. It is therefore not yet possible to relate the nuclear phenomena, to what occurs in the Uredineae and to what Claussen has described in *Pyronema confluens*.

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Die neueren Arbeiten betreffend die Chemie der Alcoholgärung.

Von **O. EMMERLING.**

Die Lehre von der enzymatischen Spaltung des Zuckers bei der alcoholischen Gärung ist jetzt wohl allgemein anerkannt, ebenso die Tatsache, daß die BUCHNERsche Zymase allein nicht imstande ist, diesen Prozeß auszulösen, sondern daß dazu ein zweites Enzym, das sog. Co-Ferment, erforderlich ist. Während die Kenntnis der Zymase durch zahlreiche Untersuchungen näher gerückt wurde, weiß man über die chemische Natur des Co-Fermentes und seine Wirkungsweise noch außerordentlich wenig, wenig mehr, als daß es gegen siedendes Wasser widerstandsfähig und dialysierbar ist. Daß außerdem die Phosphorsäure bei dem Zerfall des Zuckers eine Rolle spielt, wird später in dieser historischen Skizze gezeigt werden.

Alle gewonnenen Tatsachen, welche sich auf die Tätigkeit der genannten Faktoren beziehen, erklären aber noch in keiner Weise den eigentlichen chemischen Mechanismus der alcoholischen Gärung, und die mancherlei Erklärungsweisen sind bislang leider nichts als mehr oder weniger plausible Hypothesen geblieben.

Der älteste Erklärungsversuch von BAEYER (1), auf der LIEBIGschen Annahme fußend, daß die Hefe dem Zuckermolecül einen Anstoß zum Zerfall erteile, und darin gipfelnd, daß in diesem Molecül infolge der Abspaltung und Wiederanlagerung von Wasser eine Anhäufung des Sauerstoffes nach der Mitte der Kohlenstoffkette und damit eine Sprengung der letzteren stattfinde, ist zunächst von BUCHNER und MEISENHEIMER (2) acceptiert worden. Daß dabei vorübergehend Milchsäure gebildet würde, wurde von BAEYER nicht angenommen. Die Formulierung des Vorganges, wie sie den BUCHNERschen Annahmen entspricht, und in welcher die intermediäre Entstehung von Milchsäure eine wesentliche Rolle spielt, hat