# PHYLOGENY AND RELATIONSHIPS IN THE ASCOMYCETES[1]

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## PART I. ARGUMENT

Perhaps there is no other large group of plants whose origin and phylogeny have given rise to such diametrically opposed hypotheses as the fungi. The presence of chlorophyll and the synthesis of carbohydrates from inorganic materials are such general and dominant characteristics of plants, that many students regard them as the fundamental traits which primarily marked the divergence of plant from animal life. According to this hypothesis all plants possess chlorophyll or were derived from chlorophyll-bearing ancestors.

No one questions the origin of the chlorophylless seed plants from chlorophyll bearing ones by the loss of chlorophyll and reduction of photosynthetic organs.[2] What is more natural then, than the hypothesis that the fungi have been derived from chlorophyll-bearing ancestors? It is not my purpose to discuss the question as to whether or not the *Phycomycetes,* or lower fungi, had an independent origin, or were derived from one or several different groups of the green algae. I wish to consider some of the evidence which points to the origin of the *Ascomycetes* from fungus ancestry, rather than from the red algae.

[1] The first part of this paper is the abstract or argument as read at the anniversary proceedings. Because of the brief character of the abstract which renders many of the statements more or less categorical, while some therefore will appear dogmatic, the subject is further elaborated, and illumined by examples in a series of *Notes* which follow as an appendix in Part II.

[2] The chlorophylless seed plants constitute comparatively small, isolated groups of separate origin from different families or orders of the spermatophytes. They do not constitute a phylum. The situation is quite different with the *Ascomycetes*, which make up a great phylum with ascending and diverging lines, as well as descending branches. They do not give evidence of many isolated groups derived by degeneration from many separate families of the red algae.

In this abstract the statements must be more or less categorical, and some will therefore appear rather dogmatic.

*1. The phylogenetic relation of the oöblastema filaments of the red algae, and the ascogenous threads of the sac fungi.—* The nuclear history in the two structures is very different. In the red algae there is a single fusion of one pair of sex nuclei in the egg, forming a true diploid nucleus which multiplies by division in the oöblastema filament providing the primary nucleus for each cystocarp. The oöblastema filament fuses with vegetative auxiliary cells to furnish attachment and base for food supply of the cystocarp, but the diploid and haploid nuclei of the fusion cell repel each other. The attempt to show a phyletic relation between the copulation of short oöblastema filaments with cells of the procarp, or the fusion of the procarp cells, after the union of haploid gametic nuclei, in some groups of red algae, and the communication of functional archicarp cells of certain sac fungi, as well as entertaining the notion that fusions of approximate cells of the ascogenous hyphae are phyletically related to the fusion of oöblastema filaments and auxiliary vegetative cells, introduces additional confusion into a doctrine already overburdened with questionable hypotheses. The oöblastema filaments and ascogenous threads are parallel developments. They present an example of morphological homology or analogy, not of phylogenetic affinity.

*2. The phylogenetic relation of the ascus and carpospore, or tetrasporangium* (see Part II, Notes II and III).—There are two horns to the dilemma here, and either one requires several additional supporting hypotheses. The origin of the ascus from a coenocytic zygote, in some cases by reduction, in others terminating a progressive splitting of the same, is far more comprehensible. The nuclear fusion in the ascus is not vegetative (see Note III). It takes place in all forms thus far investigated and is to be considered the final stage of the sexual act, however modified this may be. Were it merely vegetative fusion there would be no need of conjugate division in the ascus hook to avoid the union of sister nuclei. The nucleo-cytoplasmic relation, or balance, would be just as easily at-

tained by fusion of sister nuclei, or even by contemporaneous growth of nucleus and cytoplasm, such as is well known to occur in many other cases, for example in sexual cells, gonoto-konts, etc.

*3. The phylogenetic relation of the ascocarp and cystocarp.* —If this principle of the resemblance between different types of cystocarp and ascocarp has any force, it would mean that the sac fungi had as many points of origin from the red algae as there are points of resemblance between their fruit structures. I presume no one at the present time holds any such view of the polyphyletic origin of the *Ascomycetes*.

*4. The phylogenetic relation of the trichogyne and sexual apparatus of the Ascomycetes and those of the red algae.*— The sexual apparatus of some of the *Ascomycetes,* particularly the trichogyne, and the so-called spermatia, is generally conceded to be the strongest evidence in support of their phyletic relation to the red algae. This theory, however, requires a jump from the simple trichogyne, a continuous prolongation of the egg of the red algae, to the complex, multiseptate one of the *Ascomycetes*. It requires further the reduction of this trichogyne to a unicellular one, and then to the simple gamete. It also requires the transition from free antheridia, or spermatia, to fixed ones, and from this specialized condition to the simple gamete, thus finally attaining the generalized condition of the copulation of simple gametangia. This appears to me to be a rather strained backward reading of the evidence.

### ORIGIN OF THE ASCOMYCETES FROM FUNGUS ANCESTRY

Although Sachs' suggestion of the relation of the *Ascomycetes* to the red algae was received with favor by many students at that time, and the doctrine has received a fresh impetus in recent years, it was not accepted by some of the foremost students of the fungi at that time (Winter, '79; deBary, '84). DeBary plead for the application of the theory of descent which had come to be used as the basis of classification for the higher plants. As a result of his extensive studies of development in the *Phycomycetes* and *As-*

*comycetes* he was led to the conclusion that the *Ascomycetes* were derived from the *Phycomycetes*. This doctrine is based chiefly on the evidence of a phyletic relation between the sexual organs of the two groups. In spite of the persistence of the belief in the origin of the sac fungi from the red algae, deBary's doctrine of their descent from the *Phycomycetes* has had many adherents. Nowhere in deBary's writings have I been able to find any statement which can be construed as favoring the origin of the sac fungi from the red algae. The esteem in which his judgment is held, even at the present day, has led to the republication of a rumor of an *ante mortem* statement by deBary to the effect that he was inclined to the view that the procarps of the two groups pointed to the origin of the *Ascomycetes* from the *Rhodophyceae!*

Our present knowledge of the cytology of the ascus would not perhaps favor such close contact between the *Ascomycetes* and *Phycomycetes* as would appear from the knowledge possessed in deBary's time. Unfortunately we are not yet in possession of any cytological knowledge of spore production in the zygote of the *Phycomycetes* which we can use for comparison. But at any rate, the difficulties in this relation are no greater than are met with in attempting to derive the ascus from the carpospore or tetrasporangium of the red algae.

*Origin of the ascogenous threads.*—The ascogenous threads are outgrowths of the zygote or oögonium and represent one method of splitting up and proliferation of the same in accordance with recognized principles of progression in the same direction of increase in the output of spores following the sexual process, or its equivalent, and terminating the diploid phase.

One of the most instructive forms suggesting a mode of transition from the *Phycomycetes* to the *Ascomycetes,* is *Dipodascus*. Its sexual organs are strikingly like those of certain *Mucorales* or *Peronosporales* in their young stages. The sexual organs, which can be recognized as antheridium and oögonium, arise either from adjacent cells of the same thread, or from different threads. After resorption of the wall at the point of contact, the fertilized oögonium (or zygote) grows

out into an elongate stout "ascus" or zygogametangium with the production of numerous spores. While all phases of the nuclear phenomena have not yet been made clear, the gametes are multinucleate, and multiplication either of the sex nuclei, or of the fusion nucleus, takes place in the generalized "ascus." This so-called ascus is an outgrowth of the undifferentiated oögonium or ascogonium. The splitting up of such a generalized ascus by filamentous outgrowths, the ascogenous threads, which branch and produce terminal asci containing fewer spores, would be a very natural course in progressive evolution, specialization, and increase in spore output.
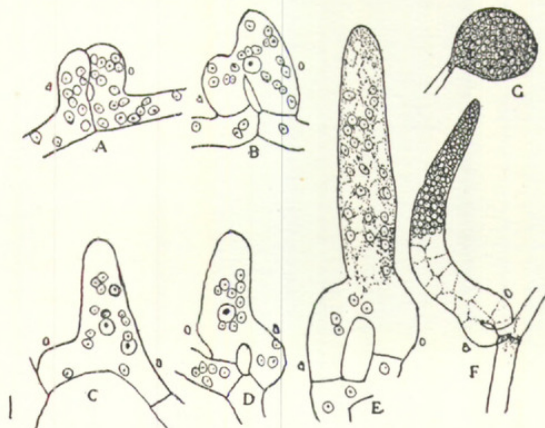


Fig. 1. *Dipodascus albidus:* *A*, copulation of gametangia; *B*, communication established between antheridium and oögonium; *C*, the two sex nuclei approaching each other; *D*, fusion nucleus large, vegetative nuclei small; *E*, growth of generalized ascus from oögonium side of copulating gametes, early stages of, in *C* and *D; F*, generalized ascus with numerous spores; *G*, spore mass crowded out of end of ascus. *a*, antheridium; *o*, oögonium.—*A–E*, after Juel; *F* and *G*, after Lagerheim.

*Origin of the ascus in the Endomycetaceae.*—The tendency of generalized forms to split up in different directions, often giving rise to divergent lines or series, is a well founded principle in the doctrine of descent. These series are often of different character in respect to numbers and diversity of forms, as well as to progression or reduction in one or more structures. One of the directions in which descent from such a generalized, coenocytic, germinating zygote (or ascus) as represented by *Dipodascus* has taken place is that of reduction in size of the generalized ascus and in the number of spores. Evidence of this reduction is furnished by *Dipodascus* itself; for, as the culture ages the asci become smaller and smaller and the spores fewer in number. In this way by reduction in number of spores to 8 and 4, just permitting the meiotic nuclear divisions, forms like *Eremascus* and *Endomyces* have

arisen.   Further reduction of one of the gametes, or of the
vegetative stages, would result in apogamous forms of *En-
domyces,* the *Exoasceae,*[1] the *Saccharomycetes,* or yeasts, etc.
By reduction and loss of one of the gametes without reduction
in size of the generalized "ascus," such forms as *Ascoidea,
Protomyces, Taphridium,* etc., may have arisen.

*Origin, progression and sterilization of the so-called tricho-
gyne.*—There is no well developed trichogyne-like structure in
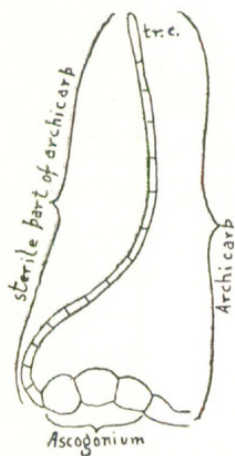any of the known *Phycomycetes.*   But there is evidence in a
few of the forms, like certain species of
*Cystopus,* of a tendency of the oögonium,
probably under chemotactic stimulation and
a softening of the wall, to develop a short
process directed toward the antheridium.
This has been suggested by a number of stu-
dents (Lotsy, '07, p. 468) to be an indication
of the origin of the trichogyne in the *As-
comycetes.*   It does not mean that *Cystopus*[2]
is to be regarded as an ancestral form of the
*Ascomycetes,* though certain species do pos-
sess a number of peculiarities which may be
attributed to such a hypothetical form.   This
peculiar feature of the oögonium of some
species of *Cystopus* is, however, of impor-
tance as it indicates one probable method
of origin of the trichogyne in the *Ascomy-
cetes.*   The trichogyne is not a character
possessed by all *Ascomycetes,* even of those
which still retain two functional gametangia.



Fig. 2.  Diagram-
matic representation
of the archicarp of
lichens  a n d  many
o t h e r *Ascomycetes.*
The fertile part is
the ascogonium; the
sterile  portion  i s
the so-called "tricho-
gyne"; *tr.c,* tricho-
gyne cell.

This, I believe, is strong evidence of the independent origin of
the trichogyne in the *Ascomycetes.*

It arose as a copulating process or beak from the oögonium

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[1] Such an origin for the *Exoasceae* is more comprehensible than the theory
that their mycelium may represent ascogenous hyphae which have migrated from
the condition of parasitism in the vegetative portion of a former ascocarp, to
parasitism on their present hosts, as suggested by Harper ('00, p. 392).

[2] One of these features is the generalized character of the sexual organs,
which are polyenergid, but particularly the great variation in number of func-
tional egg nuclei in different species as described by Stevens ('99, '01).

under chemotactic stimulation, combined with a transverse splitting of the oögonium or archicarp.

The failure of the antheridium to perform its function in the sexual process, its reduction or loss, are well known features in the life history of a number of *Ascomycetes*. In many cases where the antheridium or its supposed equivalent, the spermatium, is to all appearance potentially functional, its failure to function appears to be due to the sterilization of the terminal portion of the archicarp.[1]

Analogous situations are known in the seed plants. I need only cite the case of *Elatostoma acuminatum* (see Strasburger, '09). The nucleus of the embryo sac mother cell enters the preliminary phases of the heterotypic division. After synapsis the further stages of the heterotypic division are inhibited, and by typic or "vegetative" division the eight-nucleated embryo sac is formed. The egg, therefore, ripens with a diploid nucleus, and, without fertilization, develops the embryo. The walls of the inner integument grow together at the micropylar end of the ovule and harden, thus forming an effectual barrier to the entrance of the pollen tube (Treub, '05; Strasburger, '09). While great disturbances occur in pollen development and most of the pollen grains are empty or undeveloped, some pollen is formed which appears normal. In some cases the mother cell, which usually forms the diploid embryo sac, undergoes a true reduction division forming a row of four cells, the lower one of which forms a normal embryo sac with a haploid egg. The few male plants of this species, Strasburger thinks, result from fertilization of such

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[1] While the "trichogyne" or terminal portion of the archicarp assumed vegetative characters in an increasing degree, it seems that it did not in every case lose all of the features appropriate to a receptive organ. It appears in a few cases at least to still respond to chemotactic or analogous stimuli, seeking the fixed spermatia as in *Collema pulposum* (according to Bachmann, '13) and *Zodiomyces vorticellarius* (Thaxter, '96). In a number of cases there seem to be receptive areas on the trichogyne where the free sperms become fixed, where fusion of sperm and trichogyne takes place. The perforation of the transverse walls of the trichogyne, which is said to occur after fusion with the sperm, also appears to be another example of the retention of an ancestral character of the archicarp which primarily permitted the passage of sperm nuclei through the terminal segment, or the association of nuclei of different segments as parthenogenesis or apogamy was introduced.

haploid eggs by sperms from the normal pollen.

This sterility of the archicarp, I believe, has been brought about by its assumption more and more of a vegetative character. The formation of septa at the base of the "trichogyne" in such forms as *Pyronema* and *Monascus,* which primarily may have been the beginning of a transverse splitting of the oögonium, would make more difficult the fertilization of the basal portion of the archicarp. In *Aspergillus repens* the so-called "trichogyne," or terminal cell of the archicarp, sometimes gives rise to ascogenous hyphae[1] (according to Miss Dale, '09). The basal portion of the two-celled archicarp, or the basal or central portions of the several-celled archicarp, seem to be the portions which have retained the function of ascogenic cells where that function still resides in the archicarp. As the archicarp becomes longer, the sterile portion, which is non-ascogenic, becomes longer and more septate. This only increases the difficulties of the passage of the sperm nuclei.

The increasing vegetative character of the terminal portion of the archicarp has given rise to the long, simple, multiseptate "trichogyne" of the lichens and many *Pyremomycetes* and *Discomycetes,* as well as to the profusely branched multiseptate trichogyne of certain *Laboulbeniales.*[2] It is an interesting fact that in many of the cases of the extraordinary vegetative development of the terminal portion of the archicarp (the "trichogyne"), antheridia and spermatia are entirely wanting.[3]

The degeneration changes of the sterile portion of the archicarp (multiseptate and often also much branched "trichogyne") which are described as taking place after connection of the spermatium with the receptive terminal cell (for lichens see

[1] It is worthy of note in this connection that Olive's studies ('05) of *Monascus* led him to regard the "trichogyne," or terminal cell of the archicarp, as the ascogonium, and the second cell, or ascogonium according to others, as a nurse cell.

[2] Thaxter ('96) says that when the spermatia do not become attached to the receptive cell of the trichogyne the vegetative growth of the trichogyne is greatly increased.

[3] (*Lachnea cretea,* according to Fraser, '13; in *Teratomyces actobii,* Thaxter, '96, was not able to find antheridia.)

Stahl, '77, Baur, '98, Bachmann, '13; for the *Laboulbeniales,*
Thaxter, '96, p. 225), may be classed as secondary or accom-
panying sexual phenomena. It does not necessarily follow
that the sperm nucleus reaches the egg or fertile portion of
the archicarp. The trichogyne changes taking place after
the entrance of the sperm into, or its connection with the re-
ceptive terminal cell, are not dependent on the final fate of the
sperm, i. e., whether it reaches the egg or not. They are ante-
cedent phenomena and in no sense a proof that fertilization
has taken place. These disintegration changes, initiated, it
would seem, by the influence of the sperm on the receptive cell
of the archicarp, terminate the vegetative growth of the archi-
carp and thus the reflex upon the fertile portion at the middle
or base releases the ascogenic cells from the inhibiting influ-
ence of the vegetative phenomena, and they then proceed with
the modified sexual process among the ascogonial nuclei which
may be now associated in sexual pairs, or this pairing be post-
poned to some period in the development of the ascogenous
hyphae.

*Origin of spermatia in the Ascomycetes.*—The presence of
the so-called spermatia in many lichens and other *Ascomy-
cetes,* associated at the same time in numerous instances with
the trichogyne-like termination of the archicarp, is one of the
major pieces of evidence brought forward in supporting the
doctrine of the red algal origin of the sac fungi. If we accept
this doctrine, then in the *Ascomycetes* we must read the his-
tory of the antheridia in the following order: They appeared
first as free structures, spermatia, abjointed from spermatio-
phores, large numbers of which were crowded in highly spe-
cialized receptacles.

At the next step there were few, imbedded, isolated anther-
idiophores to which a few spermatia remained attached, until
finally the stage was reached where spermatium and anther-
idiophore were merged into the simple antheridium. This
doctrine also requires that along with the change from free
spermatia to the simple antheridium, there was a transition
from the condition in which the spermatia do not function to

that where the sperm nuclei of the simple antheridium are functional.

Notwithstanding this interesting course of evolution of the antheridium and of sexuality which we trace if the red algae are accepted as the source of the *Ascomycetes,* I believe, just as in the case of the archicarp and trichogyne, the evidence warrants us rather in reading it in just the opposite direction; and that in the last stages of progressive development of the sexual apparatus in the *Ascomycetes,* the resemblances to the sexual apparatus of the red algae are merely those of morphological homology and analogy, not phylogenetic homology and affinity.

According to this view, then, the ancestral forms of the *Ascomycetes* were fungi with well developed, simple but generalized gametangia. This condition is retained in a number of existing *Ascomycetes,* in many of which true sexuality exists.[1]

In connection with the specialization of the antheridium and the origin of the spermatia of the *Ascomycetes, Monascus* is an extremely interesting form. The antheridium is an elongate terminal cell of a hypha. The archicarp arises as a branch below the septum. It curves closely against the antheridium, bending it over more or less at right angles, and copulates at any point along the side of the antheridium, there being no portion of the latter especially selected as a copulation place. The conidia in *Monascus* are formed in chains by constriction and septation of terminal portions of hyphae similar in diameter to the antheridium. The archicarp sometimes copulates with a conidium of the chain before their final separation (Barker, '03). A chain of conidia is thus homologous with the antheridium, and a conidium with any section of the antheridium. It would be but a step from this condi-

[1] Examples of generalized, simple (non-septate) gametangia are found in *Dipodascus* and *Gymnoascus.* Examples of simple specialized gametangia, i. e., uninucleate gametangia, are found in the powdery mildews (*Erysiphaceae*) and *Eremascus.* A second stage is presented in forms where the antheridium remains simple and generalized, but there is a beginning of specialization in the archicarp where it is split transversely into two cells, the terminal one (trichogyne) functioning as a copulating organ and migration tube for the sperm nuclei. Examples are found in *Pyronema* and *Monascus.*

tion to the copulation of the archicarp with free conidia. The situation in *Collema pulposum* (Bachmann, '13), *Ascobolus carbonarius* (Dodge, '14), and *Zodiomyces vorticellarius* (Thaxter, '96), is sim-
ilar where the tricho-
gyne copulates w i t h
spermatia (conidia) still
attached to the sperma-
tiophore. These cases
are very strong evidence
suggesting the homology
of conidia (or pycno-
spores as the case may
be) and spermatia[1] in
the *Ascomycetes*.

Progression in the di-
rection of multiplication
of antheridia, or sper-
matiophores, and their
association in groups
followed from the sim-
ple and more or less
isolated situation, pro-
gressing along the same
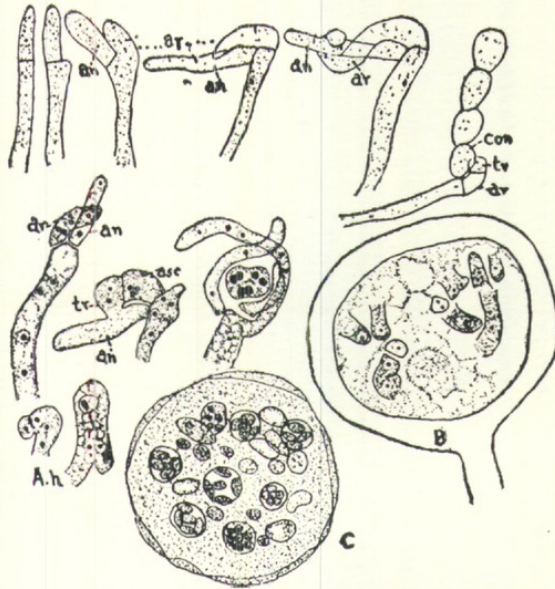course which is recog-
nized in the association



Fig. 3. *Monascus*, showing development of sexual organs and fruit. *an*, antheridium; *ar*, archicarp; *tr*, trichogyne; *asc*, ascogonium; *con*, conidium with which trichogyne is cop-ulating; *A.h*, ascus hooks or croziers; *B*, young fruit showing ascogenous hyphae within, at left is a very young fruit body showing ascogonium becoming surrounded by the enveloping fila-ments; *C*, mature fruit body with asci and ascospores.—Upper row of figures after Barker; lower group after Schikorra.

and massing of conidiophores into bundles, cushions, or pycnidia. It is the same course which is universally recog-nized as a striking indication of progression in other groups of plants, a *cephalization* of fruiting or reproductive struc-tures, as in the bryophytes, lycopods, conifers, and angio-sperms. In the latter it has given us the flower, and further cephalization of the flower has resulted in the head of the com-

[1] Their function in the ancestral or early forms may have been generalized enough to permit of their performing as conidia or sperms, as in the case of *Ectocarpus, Prostosiphon, Ulothrix*, etc. Strasburger ('05, p. 25) has expressed the idea that the pycnospores of the *Ascomycetes* might have been spermatia, and that the process of fructification now presented by these fungi is a secondary adaptation in place of the erstwhile fertilization by spermatia.

posites, the highest stage of phyletic evolution in the plant world.

In conclusion, the *Ascomycetes* present a very rich variety of form, structure, and adaptation with very marked diverging series. Some of these series present evidences of progression from simple, generalized forms to highly specialized forms, while others indicate descent by reduction. The evidences of progression are of the same kind and value as are generally recognized in other groups of plants.
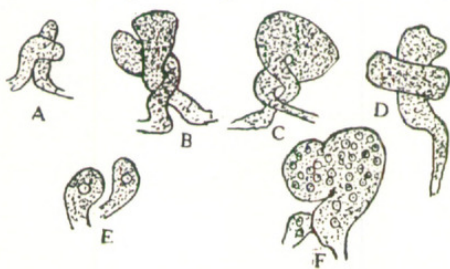
Fig. 4. *Gymnoascus Reessii:* A–D, formation of sexual organs, fusing at *C;* *E,* sexual organs in uninucleate condition; *F,* fusing sexual organs in multinucleate stage.—After Dale.

Sachs, in his later writings, agreed with deBary in recognizing the *Ascomycetes* as a distinct phylum, with an ascending series from simple and generalized forms to complex and specialized ones. He never mentioned the trichogyne as evidence of their phyletic relation to the red algae. But his theory was based on the presence of a *procarp* whether with or without a trichogyne. He selected *Gymnoascus,* where the sexual apparatus consists of simple copulating gametangia, as the simplest ascomycete known at that time. It is only in recent years that the trichogyne has been seized upon as evidence of the phyletic relation of the two groups and has forced this anomalous backward reading of the history.


PART II.  ELUCIDATION

NOTE I

The red algae are remarkable for the great constancy in the form of the procarp (procarpic branch, carpogonial branch, etc.) and the very great divergence in the processes subsequent to the fertilization of the egg (terminal cell of the procarp, carpogonium) and ending in the production of the carpospores. The general character of this divergence may be shown by a brief presentation of several types, as follows:

1. The simplest type of cystocarp development occurs in the *Nemalionales* where the carpogonium, or egg cell, after fertilization, gives rise to several branched sporogenous threads in a compact cluster, bearing terminally the carpospores (*Nemalion, Lemanea,* etc.), or in some species the sporogenous threads are more widely extended in the thallus, the branches producing separated clusters of carpospores (*Dermonema dichotomum,* see Schmitz and Hauptfleisch, '97). Fertiliza-
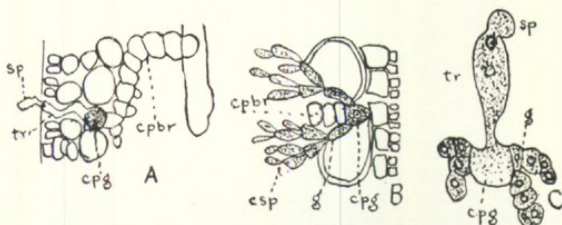


Fig. 5.   *A* and *B, Lemanea; C, Batrachospermum: cpbr,* procarp or carpogonial branch; *cpg,* carpogonium or egg; *tr,* trichogyne; *sp,* spermatium; *g,* gonimoblast; *csp,* carpospores. —*A* and *B,* after Atkinson; *C,* after Davis.

tion by the fusion of a sperm nucleus with the egg nucleus after entrance into the trichogyne and migration down into the carpogonium has been described in *Nemalion* (Wolfe, '04) and in *Batrachospermum* (Schmidle, '99; Osterhout, '00).

2. In *Polysiphonia* (*Rhodomeniales*) the procarp branch of four cells is curved around so that the carpogonium is in contact with an auxiliary cell lying between the carpogonium and the pericentral cell which gave rise to the procarp. After fusion of the sperm and egg nucleus in the carpogonium, the fusion nucleus divides once. The carpogonium now connects with the auxiliary cell mentioned, which fuses with the pericentral cell. The two diploid nuclei migrate into the pericentral cell, the carpogonium separates from the auxiliary cell, while it and the remaining cells of the procarp degenerate. The pericentral cell now fuses with several other auxiliary cells, which arose from it as a branch, forming the central cell. The diploid nuclei remain in the upper part of the central cell, while the haploid nuclei from the auxiliary cells, some having divided, now degenerate (Yamanouchi, '06).

3. A somewhat different situation exists in *Erythrophyllum delesseroides* (*Gigartinales*). The oöblastema filament from the fertilized egg connects with the auxiliary cell which is the basal cell of the seven or eight-celled pro-

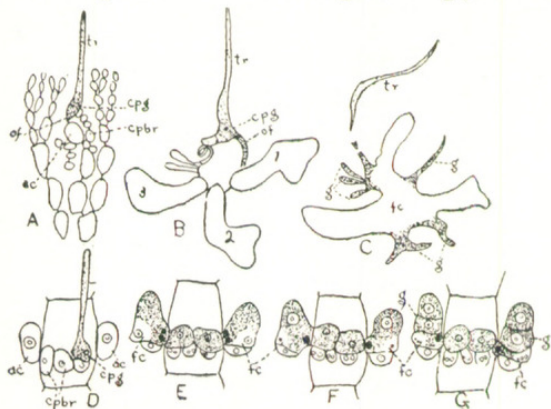carp. This in turn fuses with the two other large cells of the basal portion of the procarp, thus forming the large fusion cell from which t h e gonimoblasts, or sporogenous threads a r i s e (Twiss, '11).



Fig. 6. *A, Harveyella mirabilis; B* and *C, Erythrophyllum delesseroides; D, E, F,* and *G, Callithamnion corymbosum: cpbr,* carpogonial branch; *cpg,* carpogonium; *tr,* trichogyne; *of,* oöblastema filament; *ac,* auxiliary cell; *g,* gonimoblast; *fc,* fusion cell. *1, 2,* and *3* are the three large basal cells of the procarp in *Erythrophyllum* which fuse with the oöblastema filament to form the fusion cell. Shaded portions are diploid; note that in the fusion cell of *Callithamnion* the vegetative nucleus (haploid) remains at a distance from the diploid nucleus.—*A,* after Sturch; *B* and *C,* after Twiss; *D, E, F,* and *G,* after Oltmanns.

4. In *Harveyella mirabilis,*[1] a large cell which gives rise to the four-celled procarp is t h e auxiliary cell. A short oöblastema filament from the egg connects with the latter, which becomes the central cell.

5. In *Callithamnion* (*Ceramiales*) the fusion (diploid) nucleus in the egg divides into two. Two short oöblastema filaments proceed from the carpogonium, each containing a diploid nucleus, and fusing with an auxiliary cell at the side of the base of the procarp. Each of the two auxiliary cells now contains two nuclei. A wall divides each cell into two. The upper daughter cell contains the diploid nucleus and becomes the central cell, giving rise to the sporogenous threads, while the haploid nucleus in the lower cell degenerates (Oltmanns, '04).

6. The most complicated type may be represented by *Dudresnaya purpurifera* (*Cryptonemiales*) where several oöblastema filaments arise from the sterilized egg cell. These fuse with auxiliary cells which are either certain cells of the procarp branch, or terminal cells of its branched system, or of more distant "secondary procarp branches." An oöbla-

[1] *H. mirabilis* is parasitic on certain species of *Polysiphonia,* and is devoid of chlorophyll. For this reason it is regarded by some as indicating a step in the direction of an ascomycete.

stema filament after fusing with one auxiliary cell may grow forward and fuse with another and so on. The diploid nucleus formed in the egg multiplies by division in the oöblastema filaments. In the fusion cell, resulting from the union of the filament and auxiliary cell, the diploid and haploid nuclei repel each other so that the former lies on the filament side while the latter lies in the base of the auxiliary cell. An outgrowth
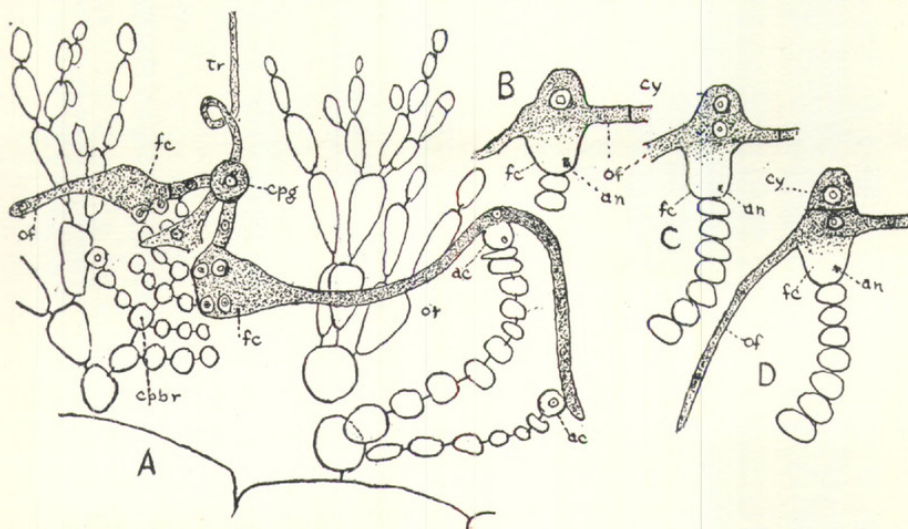


Fig. 7. *Dudresnaya purpurifera:* *A*, oöblastema filaments fusing with auxiliary cells; *B*, *C* and *D*, outgrowth from the fusion cell to form the central cell; *C*, diploid nucleus dividing; *D*, central cell of cystocarp separated by a wall. Note that the nucleus of the auxiliary cell remains distant from the diploid nucleus of the oöblastema filament. Shaded portions are diploid. *cpbr*, carpogenic branch; *cpg*, carpogonium; *tr*, trichogyne; *of*, oöblastema filament; *fc*, fusion cell; *ac*, auxiliary cell; *an*, auxiliary cell nucleus; *cy*, central cell of cystocarp.—After Oltmanns.

arises from the oöblastema filament at the point where the diploid nucleus lies. The latter divides, one nucleus migrating into the outgrowth, while a wall separates it from the fusion cell. This new cell with its diploid nucleus becomes the central cell (Oltmanns, '04).

7. In *Cruoriopsis cruciata* the situation is similar. The oöblastema filament by coursing widely through the thallus, fuses with the terminal cell (auxiliary cell) of "secondary procarp branches." Each of these fusion cells, or auxiliary cells, then gives rise to one or two simple rows of 2–4 spores (Schmitz, '79, '83), or a single 2–4-celled spore chain (Oltmanns, '04).

*Relation between the fusions of procarp and auxiliary cells,
and those of archicarp cells.*—Several persons have made the
interesting suggestion that certain similarities between the
events which take place in the fusion of one or more of the
middle or basal cells of the procarp with an outgrowth from
the carpogonium, either direct, or through the medium of an
auxiliary cell, as represented in *Erythrophyllum, Harveyella,
Callithamnion,* etc. (third, fourth and fifth types mentioned
above), and those occurring in the fusion among themselves of
the middle or basal cells of the archicarp prior to the forma-
tion of the ascogenous threads, may be evidence of a phylo-
genetic relationship between the red algae and *Ascomycetes.*
Thus Baur ('98) suggests that the first fertile cell of the sev-
eral-celled ascogone of *Collema crispum* may be the egg cell,
that this may be fertilized by the entrance of the sperm nu-
cleus and its fusion with the egg nucleus.  This fusion nucleus
may now divide.  The other cells of the ascogone below the
egg are conceived of as auxiliary cells into each one of which
a nucleus resulting from the division of the fertilized egg
nucleus migrates after pore formation in the intervening
walls.

In an interesting paper on the morphological relationships
of the *Florideae* and *Ascomycetes,* Dodge ('14) emphasizes
this theory by pointing to a number of cases in the lichens
and other *Ascomycetes* where fusion, or pore connections, are
known to occur between the ascogenous cells of the archicarp
where more than one cell gives rise to ascogenous hyphae.
Examples among the lichens are *Collema crispum* (Baur, '98),
*Physcia pulverulenta* (Darbishire, '00), *Anaptychia ciliaris*
(Baur, '04), and *Collema pulposum* (Bachmann, '13), while
among the other *Ascomycetes* may be mentioned the follow-
ing: *Ascobolus* (Harper, '96.  Here there is but one asco-
genous cell which gives rise to the ascogenous hyphae, but pore
formation in intervening walls permits intercommunication
between several adjacent cells in the middle of the archicarp.
The species is not given), *Ascophanus carneus* (Cutting, '09),
*Lachnea cretea* (Fraser, '13), *Polystigma rubrum* (Nienburg,
'14).

Now as to the suggested relationship between the phenomenon of broad or narrow pore formation in the walls of certain cells near the middle or base of the archicarp in certain lichens and other *Ascomycetes,* and that shown in the communications taking place between the carpogonium and auxiliary cells (often including one or more of the other procarp cells), it may be said (1) that in the red algae this communication of the carpogonium (terminal procarp cell) with other procarp cells when it does take place is not direct, but by a roundabout method, either through a distinct outgrowth from the carpogonium, or through the medium of one or more auxiliary cells, or by a combination of both, to form the central cell; (2) no evidence of any similar roundabout method has been observed in the archicarp of the sac fungi. The intercommunication between the middle or basal cells of the archicarp is always direct, and no communication in the multicellular archicarp occurs by means of which either a fertilized nucleus, or a sperm nucleus has been observed to migrate from the terminal cell to the middle or basal cells; (3) that in a number of the fungi where pore formation occurs between cells of the fertile portion of the archicarp, the "trichogyne" is either absent, or admittedly degenerate, or the antheridium is absent. Examples are: *Ascobolus,* studied by Harper ('96), antheridium and trichogyne absent; *Ascophanus carneus,* antheridium absent, trichogyne doubtful or degenerate; *Lachnea cretea,* no antheridium observed, trichogyne not functional; *Polystigma rubrum,*[1] trichogyne not functional, from a multicellular cell at base of archicarp one nucleus migrates into the adjacent uninucleate archicarp cell, which is regarded as the ascogonium (Nienburg, '14). In none of the lichens has a sperm or other nucleus been observed to move down into the fertile part of the archicarp. Pore formation in the archicarp of the *Ascomycetes* has no phyletic relation to the fusions of auxiliary cells among themselves or with a short oöblastema thread or the egg cell. It occurs in-

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[1] Blackman and Welsford ('12), who earlier investigated the cytology of *Polystigma rubrum,* are of the opinion that the "spermatia" as well as the archicarps degenerate, and that certain vegetative cells become transformed into ascogones.

dependently in different groups of the fungi as a means of permitting the association of nuclei, often in conjunction with the association of sex nuclei or their equivalent modified sex nuclei (see the situation in *Basidiobolus,* Eidam, '86; Raciborski, '96; Fairchild, '97; Olive, '07; Woycicki, '04).

*Relation of oöblastema filaments and ascogenous hyphae.*— In the *Ascomycetes* the processes in the growth of the zygote or ascogenic cell present to a certain extent a somewhat analogous course of progression to that of the carpogenic cell of the red algae. In the less complicated process, as shown in the *Laboulbeniales,* the carpogenic cell may undergo a few divisions, the subterminal cell of the series forming the ascogonium. The ascogonium then usually divides to form two or four ascogenic cells, or without division forms the single ascogenic cell (Thaxter, '96; Faull, '12). The ascogenic cells give rise directly, by budding, to the asci. They are, therefore, somewhat comparable or analogous to the gonimoblasts of the red algae. In *Sphaerotheca* (Harper, '95[a], p. 475) there is a single short ascogenous thread of a few cells (arising from the one-celled oögonium or ascogonium) forming a single ascus from the subterminal cell. Where the process is more complex, as in *Pyronema* (Harper, '00; Claussen, '12), several long ascogenous hyphae arise from the large single-celled zygote or ascogonium, giving rise ultimately to numerous terminal asci. In other forms the ascogonium is several-celled, a number of the cells developing ascogenous hyphae (*Collema,* Stahl, '77; Baur, '98; Bachmann, '12, '13; *Anaptychia ciliaris,* Baur, '04; *Physcia pulverulenta,* Darbishire, '00; *Ascophanus carneus,* Cutting, '09; *Lachnea cretea,* Fraser, '13; etc.).

Some of the chief objections in the way of accepting the theory of a phylogenetic relation between the oöblastema filaments of the red algae and the ascogenous threads of the sac fungi are as follows:

1.   The fusion of a free sperm and the egg nucleus in the single uninucleate oögonium or carpogenic cell. So far as we know this is universal in the red algae. In the *Ascomycetes* the oögonium is usually multinucleate or multiseptate. In no

case has fertilization by a free sperm been determined, and in forms with a multiseptate "trichogyne," or oögonium, the so-called spermatia, or antheridia, do not, so far as we know, play the usual rôle in fertilization, not even a modified rôle by association with the oögonial nuclei.

2. The individual nuclei of the oöblastema filaments are of the usual diploid character, and there is no fusion of these nuclei prior to the formation of the carpospores. The individual nuclei of the ascogenous threads, or ascogenic cells, are probably haploid in character, and sooner or later form the so-called synkarion, an association of two nuclei, together equivalent to a diploid nucleus. Fusion of the paired nuclei takes place before the formation of the ascospores.

3. It has been suggested that the complex processes in the extensive migration, branching and fusions of the oöblastema filaments with auxiliary cells as is known to occur in the *Cryptonemiales* (as in *Dudresnaya, Cruoriopsis, Gloeosiphonia*, etc.), may furnish still more important evidence of the ancestry of the *Ascomycetes* than that suggested in the fusions of procarp and auxiliary cells on the one hand, and archicarp cells on the other (Dodge, '14). The fusions of the oöblastema filaments with auxiliary cells and the production of sporogenous threads from the central cells thus formed, are supposed to be represented by the fusions which are known to occur between the ultimate and antepenult cells of the ascus hook prior to the formation of additional asci. The processes in both groups result in the multiplication of spore origins and consequently in an increase in spore output. Perhaps the nearest analogue to the process in the *Ascomycetes* which results in the formation of the ascus with its four to eight spores, is found in *Cruoriopsis,* where one or two spore chains of two to four spores each are produced as a result (Schmitz, '79, '83; Oltmanns, '04). The theory of "second sexual fusions" in the red algae was founded on the discovery of these fusions of the oöblastema filaments with auxiliary cells, since it was supposed that a fusion occurred between the nucleus of the oöblastema filament (derived from the diploid nucleus of the fertilized egg) and the nucleus of the vegetative auxiliary cell

(Schmitz, '83).   Recent cytological work on the red algae has
not confirmed this theory, but, on the other hand, has discred-
ited it, since in the cases examined the diploid nucleus of the
oöblastema filament and the haploid nucleus of the auxiliary
cell are said to repel each other and no fusion between them
occurs.   It should be emphasized that the fusion of the oöbla-
stema filament and the auxiliary cell is a fusion of a diploid
structure with a haploid one, that it is probably of a nutritive,
or parasitic, nature comparable to the fusion of the moss
sporogonium with the tissue of the gametophyte, a physiolog-
ical, nutritive requirement in the absence of other means of
nourishing the moss sporogonium.   The fusions occurring be-
tween cells of the same ascogenous hypha are fusions between
cells of the same phase and serve to bring into association
nuclei of more or less remote ancestry, but each endowed with
the same number of chromosomes (probably the 1x number).

Thus, while there are somewhat analogous variations in the
splitting up of the ascogonium in the sac fungi, and of the car-
pogonium in the red algae, with progress in the direction of
increasing the output of spores, it seems fair to conclude, that,
so far as the evidence at present in hand is concerned, the rela-
tion between the fusion of oöblastema filaments and auxiliary
cells in the red algae, and those between the ultimate and an-
tepenult cells of the ascus hook (of the ascogenous hyphae),
however interesting it may be, has no phylogenetic signifi-
cance, and is at best a rather strained parallel.

Ascogenous hyphae, gonimoblasts, oöblastema filaments, the
several fertile cells of certain ascogonia which communicate
by resorption of the intervening septa, the fused procarp, may
be considered as morphological equivalents, as suggested by
Dodge ('14, p. 174), but there is no evidence of a phyletic rela-
tion between the ascogenous hyphae and fusing ascogonial
cells, and their morphological equivalents in the red algae.
They illustrate different modes of increase of spore output by
splitting up of the oögonium.

### NOTE II

The fundamental difference in the method of development of
ascospores and carpospores is one of the great barriers in the

way of the descent of the *Ascomycetes* from the *Florideae*. Some (Bessey, E., '13, p. 151) have attempted to overcome this difficulty by suggesting the homology of the ascus and tetrasporangium.  But this effort leads to so many suppositions and supporting hypotheses because of the fundamental difference between the process of spore formation in the ascus, and the processes of carpospore or tetraspore formation, that the descent of the ascus fungi from the red algae would require a far more labyrinthian course than would be necessary in deriving them from the *Phycomycetes*.

<div align="center">NOTE III</div>

<div align="center">IS NUCLEAR FUSION IN THE ASCUS OF A VEGETATIVE OR SEXUAL NATURE?</div>

It is unfortunate that there is such great divergence of opinion in the interpretation of the nuclear phenomena in the archicarp and ascogenous threads.  These conflicting results are probably, in a large measure, due to the difficulties presented in the minute size of the nuclei.  The divergence of opinion relates primarily to the question as to whether the fusion nucleus of the ascus is the result of two successive nuclear fusions, the first taking place in the ascogonium and the second in the ascus, or whether the nuclear fusion in the ascus is the only one.

The principle of a single nuclear fusion, that in the ascus, interprets this act as the final stage in the process of fertilization, by the fusion of two nuclei of more or less remote ancestry.  At some time prior to ascus formation these two nuclei may possibly become associated in pairs into a synkarion and multiply in the ascogenous threads by conjugate division, or the synkarion and conjugate division may be postponed to the ascus hook and the complicated series of fusions between the ultimate and antepenult cells of the crozier, or proliferations of the young ascus with accompanying conjugate divisions of the synkarion.

Dangeard ('94) first described the presence of two nuclei in the young ascus, and their fusion, in several species (*Borrera ciliaris, Peziza vesiculosa, Helvella ephippium, Geoglossum*

*hirsutum, Acetabula calyx, Exoascus deformans,* and some lichens).  The origin of the ascus was correctly described in a number of cases, but in the majority of cases at that time he thought the young ascus arose by the copulation of two unicellular gametes according to a method similar to the formation



Fig. 8.  *Pyronema confluens: A*, section of mature discocarp; *B*, group of archicarps copulating with antheridia by means of the slender prolongation (trichogyne) of the ascogonium which is separated as a distinct cell; *C*, pair of sexual organs copulating by means of the trichogyne cell, ascogonium at left, antheridium at right; *D*, showing multinucleate condition of sexual organs and communication of antheridium and trichogyne.  *a*, antheridium; *b*, trichogyne; *c*, ascogonium. *E*, older stage of a similar group of sexual organs after the antheridial nuclei have entered the ascogonium and the trichogyne nuclei have degenerated; also showing early stage of growth of ascogenous hyphae from the ascogonium; *F*, showing relation of ascogonia, ascogenous hyphae, asci, and paraphyses in mature fruit body.—After Harper.

of the ascus in *Eremascus,* so that the ascus appeared to be supported on two stalks. Frequently, however, in *Peziza vesiculosa* and *Helvella ephippium* he observed the origin of the ascus from a single hypha curving at the end in the form of a hook or crozier. The four nuclei resulting from the division of two were so situated in the crozier that after the formation of two cross walls the ultimate and antepenult cells each contained one nucleus, while the penult cell contained two nuclei. The association of two nuclei in the young ascus and their fusion he interpreted as a sexual act, and the young ascus was looked upon as an oögonium. Later, Dangeard found that the crozier method of ascus formation was the usual one in the forms studied and that in no case in these higher forms did the ascus arise immediately from the conjugation of two different hyphae.

This important pioneer work by Dangeard was a great stimulus to further studies which has led to a more or less clear knowledge of the history of the nuclei from the archicarp through the ascogenous hyphae to the ascus, while the origin of the ascogenous hyphae from the fertile cells of the archicarp was first described by Janczewski ('71) in *Ascobolus,* and later by Kihlman ('83) in *Pyronema confluens.* Harper first demonstrated the origin of the ancestral ascus nuclei in the archicarp of *Sphaerotheca castagnei* ('95[a]) and *Pyronema confluens* ('00) and their migration in the ascogenous hyphae, though he does not give the nuclear history in the ascogenous hyphae, except the later stages at the time of formation of the ascus. Their archicarp origin has been abundantly confirmed by several investigators in a number of different forms, both among the lichens and other *Ascomycetes.*

The different opinions in regard to the significance of nuclear fusion in the ascus rest upon the interpretation by different investigators of the behavior of the nuclei in the archicarp, or ascogenous cells, before they begin to move into the ascogenous hyphae. Some maintain that there is a fusion, in pairs, of the sex nuclei (1) in the archicarp when fertilized

by an antheridium (Harper in *Sphaerotheca castagnei*,[1] '95ª, '96; *Erysiphe*, '96; *Pyronema confluens*, '00; *Phyllactinia*, '05; Blackman and Fraser in *Sphaerotheca*, '05; Claussen in *Boudiera* [=*Ascodesmis*], '05); or (2) in the archicarp where the antheridium is functionless or absent (Blackman and Fraser, '06, in *Humaria granulata;* Fraser, '07, in *Lachnea stercorea*). In *Aspergillus herbariorum* Miss Fraser (07, p. 420) finds that the antheridium often degenerates and did not observe disappearance of the intervening wall when fusion with the trichogyne took place. She *nowhere* describes or figures fusion in pairs of the ascogonial nuclei. She merely assumes it, for, in the summary ('07, p. 428) she says: "It seems probable that normal fertilization occurs in some cases, and that in others it is replaced by a fusion of ascogonial nuclei in pairs"; Welsford ('07) in *Ascobolus furfuraceus;* Dale ('09) in *Aspergillus repens;* Cutting ('09) in *Ascophanus carneus* believe in the fusion of archicarp nuclei in pairs; or (3) of nuclei in vegetative cells where the archicarp is wanting or functionless (Fraser, '07, '08, in *Humaria rutilans,* fusion of the nuclei said to take place soon after entering the ascogenous hyphae; Carruthers, '11, in *Helvella crispa;* Blackman and Welsford, '12, merely found evidence of nuclear fusion in vegetative cells of *Polystigma rubrum*).

[1] Dangeard ('97) claims that the antheridium is functionless and that the single nucleus in the oögonium divides into two. After his study of *Pyronema* Claussen ('12) is inclined to question the fusion of the two sex nuclei in the oögonium of *Sphaerotheca, Erysiphe, Phyllactinia,* and *Pyronema* as described by Harper ('95ª, '96, '00, '05), and by Blackman and Fraser ('05) in *Sphaerotheca* as well as in the case of *Boudiera* (=*Ascodesmis*) studied by him in 1905. In respect to his work on *Boudiera* he now says: "My own statements upon the nuclear fusion in the ascogone of *Boudiera* (*Ascodesmis*) are clearly wrong." He points out that in none of these cases is the history of the nuclei in the ascogenous hyphae known, and thinks that a reinvestigation will show paired nuclei here. A question to be considered, says Strasburger ('05, p. 24), is whether the chromosomes of the nuclei united in the oögonium do not remain in separated groups in the ascogenous hyphae, in order to fuse as individual nuclei in the ascus. Lotsy ('07) has expressed a somewhat similar view in an attempt to harmonize the situation in the *Ascomycetes* and *Basidiomycetes.* The fusion nucleus in the oögonium remains for a time a 2x nucleus but some time prior to ascus formation the 2x nucleus separates into two individual 1x nuclei in the ascogenous hypha, forming a synkarion. Conjugate division now takes place with ascus formation occurring immediately or after several successive conjugate divisions.

Others maintain with equal assurance that there is no fusion of the sexual nuclei in the archicarp. There is merely an association of sex nuclei.

(1). In forms with a functional antheridium and archicarp may be mentioned *Monascus*[1] (Schikorra, '09) and *Pyronema confluens* (Claussen, '07, '12).

(2). In forms where the antheridium is absent or functionless may be mentioned *Pyronema confluens* (Brown, W. H., '09, antheridium functionless), *Lachnea scutellata* (Brown, W. H., '11, antheridium absent). In both of these examples, cases of division of the nuclei in the ascogonium were observed which might be mistaken for fusion. Since no divisions of nuclei in the ascogonium have been described by authors in the forms where they believe sexual fusions of nuclei to take place, W. H. Brown ('11) suggests that they may have had before them division stages. In



Fig. 9. *Pyronema confluens: A, B,* and *C,* conjugate division of nuclear pairs in the ascogenous hyphae; *D,* conjugate division in ascus hook; *E,* tips of branched ascogenous hyphae with ascus hooks, young asci, and beginning of conjugation of the ultimate and antepenult cells of the ascus hooks; *F,* completed conjugation of the ultimate and antepenult cells of the hook and association of their nuclei as a pair. *Ascog,* ascogonium; *asc. h,* ascogenous hyphae with paired "sexual" nuclei.—After Claussen.

*Ascophanus carneus* and *Ascobolus immersus* the antheridium is absent, but association of the nuclei in several of the multinucleate ascogonial cells occurs after pore formation in the walls. Most of these nuclei become paired and remain paired as they migrate in the ascogenous hyphae to the ascus hooks, where conjugate division takes place. The only fusion of nuclei is that in the ascus, except in badly fixed preparations or in degenerating nuclei in the ascogonium (Ramlow, '14). In *Leotia* (Brown, W. H., '10) the ascogenous hyphae
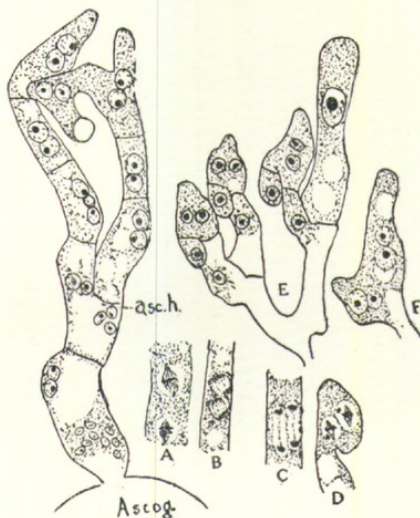
[1] Barker ('03) ascribed his failure to find a fusion of nuclei in the ascogonium of *Monascus* to the absence of proper stages in his material.

are supposed to arise from an ascogonium in the base of the ascocarp, but the nuclei are believed to arise from a haploid nucleus. Conjugate division occurs in the ascus hooks, the majority of which are formed by proliferation of the binucleate penult cell and from fusions of the ultimate and antepenult cells of croziers, so that many conjugate divisions of the haploid nuclei take place, and the first nuclear fusion is in the ascus. In *Laboulbenia chaetophora* and *L. Gyrinidarum* (Faull, '11, '12) fusion of nuclei does not occur in the ascogonium, the mature binucleate ascogenic cell develops the asci by budding, each ascus bud being preceded by a conjugate division of the nuclear pair. In *Polystigma rubrum* (Nienburg, '14) no fusion in the ascogonium occurs. In *Collema pulposum* (Bachmann, '13) the nuclei in the ascogenic cells were often found in pairs, but no cases of fusion were observed.

(3). Forms in which an archicarp is absent or functionless, and certain vegetative cells take on the function of ascogenic cells, in which the authors believe nuclear fusion does not take place except in the ascus: *Gnomonia erythrostoma* (Brooks, '10); *Helvella elastica* (McCubbin, '10) in which the "ascogenous hyphae" form an intricately interwoven subhymenial layer of threads each with two nuclei in the end. The ends of these hyphae form croziers with conjugate division of the two nuclei followed by about six repeated proliferations of the young ascus and crozier formations, accompanied by fusions of the ultimate and antepenult cells and crozier formation, resulting in many successive conjugate divisions of the haploid nuclei, with fusion first in the ascus. In *Xylaria tentaculata* (Brown, H. B., '13) the ascogenic cells which appear to be derived by the separation of the cells of "Woronin's hypha" are uninucleate and soon become multinucleate by nuclear division. The nuclei multiply also in the ascogenous hyphae.

The theory of a vegetative fusion in the ascus arose from the belief on the part of some students that sexual fusion of the nuclei occurred in the ascogonium, that the nuclear fusion in the ascus must be a second fusion with no relation to the

sexual process, and, therefore, it must be of a vegetative nature. If a second fusion of the nuclei occurred it would call for a triple division of the fusion nucleus in order that the haploid condition should be again reached.

The universal occurrence of the triple division in the ascus in the formation of the spores is by some ascribed to a "quadrivalent character" of the chromosomes in the fusion nucleus, and rendered necessary in the return to the univalent condition (Harper, '05; Overton, '06), and Overton states, "that all these divisions persist, no matter how many spores are to be produced, which shows their necessity in the process of reduction."[1] *Eremascus* controverts this statement since there is certainly but one fusion (Stoppel, '07; Guilliermond, '09) and yet triple division occurs in the ascus.

The results of cytological investigations by different students in connection with the triple division show considerable variation. Thus Harper ('00, '05) finds the same number of chromosomes in all three divisions (10 in *Pyronema*, 8 in *Phyllactinia*). The two ascus nuclei "fuse with all their corresponding parts" (Harper, '05, p. 67), so that the quadrivalent nature of the chromosomes in the fusion nucleus is not to be seen, though he conceives it to exist. Synapsis occurs in the first division.

Miss Fraser ('07, '08) describes *Humaria rutilans* as having 16 chromosomes in the first division where synapsis occurs (heterotypic) which split transversely and the daughter nuclei have each 16 chromosomes which appear on the nuclear plate in the second division. In the second division the chromosomes split longitudinally (homöotypic) and 16 chromosomes pass to each daughter nucleus. In the third division the 16 chromosomes are supposed to separate at the nuclear plate without division, 8 going to each daughter nucleus. This division she terms "brachymeiotic". A similar situation is described by Fraser and Welsford ('08), Fraser and Brooks ('09), and Carruthers ('11). Faull ('05) finds the same num-

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[1] Polysporous asci resulting from several to many nuclear divisions may be the retention of an ancestral character, the number of divisions being reduced to three in most forms.

ber of chromosomes in all three divisions, in some species 4
or 5 (*Hydnobolites*), in others 8 (*Neotiella*).

More recently Claussen ('12) after a very thorough study
of *Pyronema confluens* finds the same number of chromosomes
(about 12) in all three divisions. The first division is hetero-
typic accompanied by synapsis, diakinesis and a splitting of
the chromosomes. The second is homöotypic, while the third
is typic. Faull ('12) in a recent study on *Laboulbenia* also
finds that the two first divisions in the ascus agree with the
usual phenomena accompanying reduction in spore mother
cells, the first being heterotypic, while the second follows
"very swiftly on the heels of the first." He concludes that
"probably the only nuclear fusion in the life cycle is that in
the ascus," and that conjugate divisions of nuclei are an im-
portant phase in the sexual phenómena of the *Ascomycetes*.

The evidence from recent investigations, therefore, supports
more and more the interpretation of nuclear fusion in the
ascus as a process of exactly the same significance as the
nuclear fusion in the basidium of the *Basidiomycetes,* and in
the teleutospore of the *Uredinales,* i. e., it is the fusion of a
pair of nuclei of a longer or shorter history of conjugate divi-
sions from a pair of ancestral nuclei of more or less remote
association. This association of nuclei arises in a variety of
ways and at different periods in the ontogeny just as it does
in the *Basidiomycetes* (Maire, '02; Ruhland, '01; Harper, '02;
Nichols, S. P., '04; Kniep, '13), and *Uredinales* (Sappin-
Trouffy, '96; Maire, '99, '01; Blackman, '04; Christman, '05,
'07; Blackman and Fraser, '06; Olive, '08; Hoffmann, '12;
Werth und Ludwigs, '12). The association is accomplished
in some cases through the copulation of two gametangia
(*Pyronema, Monascus, Gymnoascaceae,* and the *Erysipheae*).
Such an association represents nearly, if not quite exactly,
the true type of sexuality. The other methods of association
represent a variety of modified types of sexuality (see Note 1)
where the archicarp is present and the antheridium absent, or
functionless, or where the archicarp is absent and vegetative
cells, either with or without the migration into them of nuclei

from adjacent vegetative cells, give rise to the ascogenous threads.

The results of recent work tend more and more to show that there is no fusion of the associated nuclei in the ascogonium, or ascogenic cells, whether certain of the nuclei have been derived from an antheridium (*Pyronema,* Claussen, '12; *Monascus,* Schikorra, '09), or not. Conjugate division in the ascogenous threads has been abundantly proven, though in some cases it may occur only one or a few divisions prior to the formation of the ascus.

What the peculiar features of nuclear fusion in the ascus are which characterize it as vegetative, seem to rest more on an *ex parte* judgment of a fusion of nuclei in the ascogonium than upon any well established idea of the nature of vegetative nuclear fusion. Thus, Miss Fraser ('08, p. 37) states that in *Humaria rutilans* the two nuclei in the ascus enter independently upon the prophases of the first division, fusing in the spirem stage. This she regards as evidence in disproof of the sexual nature of the fusion of nuclei in the ascus ('08, p. 44). Harper ('05) raises a similar objection. On the other hand, it seems to me that it is excellent evidence that it is not of a vegetative nature. It is well known in a number of cases that the egg and sperm nuclei, lying side by side in the egg, undergo the prophase stages of division up to the formation of the chromosomes before fusion of the two takes place. I cite certain examples in the *Abietineae: Pinus sylvestris* (Blackman, '98); *P. strobus* (Miss Ferguson, '01, '04); *Tsuga canadensis* (Murrill, '00).

In support also of the supposed vegetative nature of the fusions in the ascus Miss Fraser ('13, p. 559) cites "vegetative nuclear fusions" in the quadrinucleate ascus of *Humaria rutilans* and her work on this plant in 1908. But she nowhere describes or figures the fusion of the four nuclei in such asci. She says ('08, p. 41) "trinucleate (Fig. 50) and quadrinucleate (Fig. 51) asci are sometimes formed; their fate could not be determined." It is very likely that such tetranucleate young asci found by Miss Fraser in *Humaria* result from further conjugate division prior to the prolifera-

tion of the young ascus to form branches and further croziers resulting in an increase of asci as shown to take place in *Pyronema confluens* by Claussen ('12, p. 25, fig. 6, III).

It has been suggested by some who regard the fusion in the ascus as a second fusion of nuclei (Harper, '05; Overton, '06) that if the synkaryophytic condition of the terminal portion of the ascogenous hyphae in *Pyronema,* and far back in those of *Galactinia succosa* (Maire, '03, '05), could "work back until the egg cell was reached," an apogamous condition might result similar to that in the *Hymenomycetes.* Certainly those who have suggested this theory have not thought far enough ahead, for how would the univalent condition of the spore nucleus pass to the bivalent condition of each nucleus prior to the paired (= quadrivalent) condition in the ascogenous hyphae of the next generation unless this were preceded by a nuclear fusion. Such a condition would not be apogamy. The quadrivalent character of the fusion nucleus of the ascus, or of the synkarion in the ascogenous threads, demands two successive nuclear fusions, if the triple division in the ascus brings about the reduction of a quadrivalent nucleus to a univalent one as maintained by the adherents of this theory. As to such an apogamous condition being similar to that in the *Hymenomycetes* it must be remembered that there are only two divisions in the reduction process in the *Hymenomycetes,* so that when two univalent nuclei become associated in cells of the mycelium or basidiocarp the bivalent condition of these cells is attained.

In a very interesting and scholarly argument Harper ('05) has attempted to explain the inclusion and fusion of two nuclei in the young ascus on the basis of the nucleo-cytoplasmic relation or balance in the cell. The abundance of food material in the tips of the ascogenous hyphae inhibits cell wall formation so that two nuclei are enclosed in one cell. Rapid growth of the ascus and cytoplasm follows in order to balance the relation of the latter with the nuclear mass. The fusion of the nuclei and growth of the fusion nucleus again overbalance the cytoplasm, which then by growth increases again

in mass. The process is thus a reversible one, and by a sort of see-saw growth of nucleus and cytoplasm the ascus cell is pushed up to the large size characteristic of spore mother cells.

It is very true that the "regulative function is a reversible one," that an active cell with a large amount of cytoplasm demands a correlative amount of nuclear substance, that the increase in one may result in the increase of the other. Also it is very true that the ascus belongs to the category of spore mother cells, which are characterized by relatively large nuclei and cytoplasmic mass compared with most vegetative cells, but this does not explain why, when ascus or spore mother cell formation is about to take place, cell division does not occur at a period when the food relation would permit the formation of young uninucleate asci if these nuclei are bivalent in nature. The regulative functions accompanying growth and maturity of such a young gonotokont would assure sufficient size, sufficient food material, and the necessary equilibrium. The fact that asci in different species and groups vary so greatly in size shows this, and also that there is no general standard of mass in relation to surface area which would demand two nuclei at the origin of the ascus.

In fact it is very clear, from the morphological processes which take place in the tip of the ascogenous hyphae of most of the forms studied, that cell division, or cell wall formation, is more likely governed by the last division of the two nuclei so that the cell walls are laid down between the daughter nuclei. If the inclusion and fusion of two nuclei in the young ascus were controlled entirely by nutritive and cyto-regulative processes, why are not sister nuclei included? Surely the purely cyto-regulative functions would be just as well satisfied. It appears that in rare cases sister nuclei may be included in the ascus (Brown, W. H., '10, in *Leotia chlorocephala*).

Of the four nuclei resulting from the two successive divisions of the zygote nucleus in *Spirogyra,* Chmielewski ('90) states that two fuse to form the nucleus of the single germling which is usually formed in the *Zygnemaceae*. Harper inter-

prets this as a vegetative fusion in support of his interpretation of vegetative fusion in the ascus. Karsten ('08) describes the divisions of the zygote nucleus into four nuclei in *Spirogyra jugalis,* but does not state the relation of the nuclei to the germling (second division sometimes omitted). Tröndle ('07) interprets the process in *Spirogyra Spréeiana* as presenting but a single division of the zygote nucleus. Results of this nature, so divergent from expectations based on the normal history in many other organisms in widely separated groups, are usually received with considerable reserve, particularly where they are pioneer investigations in a group not yet studied. Recently Kurssanow ('11) in a thorough study of nuclear division and germination of the zygote in two species of *Zygnema* (*Z. cruciatum* and *Z. stellinum*) has shown that the process is normal, there being two successive divisions, three of the nuclei usually degenerating, while one becomes the nucleus for the single germling characteristic of the *Zygnemaceae.* Occasionally only two of the nuclei degenerated, but then two germlings were formed, an interesting case showing a tendency to retain what is believed to be the ancestral condition where four germlings are formed as in the *Mesotaeniaceae,* while in the desmids two germlings are regularly formed.

Other cases cited as examples of vegetative nuclear fusion and classed with nuclear fusion in the ascus, are those of the endosperm nucleus with the second sperm nucleus in seed plants (Harper, '05), and (Fraser, '13) nuclear fusions in paraphyses and in hairs of the excipulum of certain discomycetes. Such cases, however, cannot be legitimately compared to fusion in the ascus, since those nuclei are shut off from further participation in the line of successive ontogenies.

The example cited by Harper of Boveri's ('88) experiment in shaking sea urchin's eggs after fertilization, resulting in the production of an abnormally large larva with 72 instead of 36 chromosomes, is in a different class from most of the other examples of vegetative fusion given. This is equivalent to a true double fertilization and it is quite within the bounds of possibility that among many such larvae some

might under favorable conditions be the starting point of a new ontogeny which would be similar to certain mutants. The case of *Oenothera gigas* (see De Vries, '03, '13) a mutant from *Oe. Lamarckiana* with double the number of chromosomes is similar.[1] Other tetraploid mutants are known (see Gates, '13), the diploid gametophyte and tetraploid sporophyte of the mosses produced experimentally by Marchal ('09, '11) is interesting in this connection.

Now, the possibility of a similar double fertilization in an ascomycete is not, a priori, excluded. There might be an isolated example. But the normal expectation is that it would have afterward a nuclear history in its ontogeny similar to others with one nuclear fusion and one reduction from 2x to 1x. But it is not likely that the entire group of sac fungi is founded on such a mutation, followed by a double reduction with triple division and then double fertilization again and so on. The several cases where it has been quite well established that there is no nuclear fusion prior to the ascus, together with the great uniformity of the ascus nuclear phenomena in the group, controverts the idea of any such origin for the sac fungi.

All of these facts go to prove that the inclusion and fusion of two nuclei in the young ascus is of a very different and far greater significance than a vegetative one. The process of nuclear fusion in the ascus does not comprise in itself the entire series of events generally accepted as belonging to the process of fertilization, for in most organisms nuclear fusion occurs in the same cell where nuclear association takes place. It is generally conceded that before the haploid condition of the nucleus is again established important processes take place which we call reduction phenomena, the full significance of which we perhaps are as yet ignorant of. These processes, including synapsis, cannot take place unless nuclear fusion has occurred, and some students see in

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[1] Just how the doubling arose in this instance is of course difficult to determine. Stomps ('12) suggested that it arose through the union of two unreduced diploid gametes, while Gates ('09, '13) thinks it arose through "suspended mitosis of a megaspore mother cell" having (4x) 28 chromosomes, and its apogamous development.

them the real act of fertilization (Strasburger, '00, '04, '05).

*Remarks on the origin of the specialized ascus.*—In the direction of progression from the generalized ascus by splitting up of the zygote, the diploid phase has been prolonged and the number of spores multiplied. The filamentous outgrowths of the zygote, or its equivalent, provide numerous terminal cells of restricted size suitable for the production of a small number of spores in each, following the meiotic divisions of the fusion nucleus which terminate the diploid phase.

The situation in species with polysporic asci, where the spores result from numerous divisions of the fusion nucleus, is interpreted by some as a germination phenomenon (Overton, '06), but it seems to me more comprehensible to regard it as a retention of a primitive feature existing in certain phycomycetous ancestors, and characteristic also of primitive *Ascomycetes* like *Dipodascus*.

The formation of internal non-motile spores through free cell formation in the zygote, under conditions adapted for dispersion by ejection from either the generalized or specialized ascus, may be sufficient to account for the distinctive processes of spore formation in the sac fungi. In the oögonium of *Saprolegnia,* functional nuclei in the oögonium are very similar to the nuclei of the ascus preceding ascospore formation. The nucleus is provided with a prominent central body at its pointed end from which kinoplasmic radiations extend (Hartog, '95; Claussen, '08; Mücke, '08).

In most of the *Ascomycetes* the cytoplasm in the ascus is differentiated into epiplasm and spore plasm, the former assisting in the ejection of the ascospores. This separation of the plasm may have been one of the direct causes of the peculiar method of ascospore formation.

## NOTE IV

### THE PHYLOGENETIC RELATION OF THE TRICHOGYNE AND SEXUAL APPARATUS OF THE ASCOMYCETES AND THOSE OF THE RED ALGAE

The sexual apparatus of the *Ascomycetes,* particularly the trichogyne and the so-called spermatia, is generally conceded to be the strongest evidence in support of their phylogenetic

relation to the red algae. The analogy at least between the trichogyne of the red algae and that of the *Ascomycetes* is very striking. The evidence brought forward by Stahl ('77) and others of the relation of the trichogyne to the ascogonium in the lichens, together with the fusion of spermatia to the trichogyne, followed by the gradual and peculiar degeneration of the latter and the subsequent development of the ascogenous threads, was generally accepted as proof of fertilization in the ascogonium by a spermatium. Also the early studies of *Polystigma rubrum* (Fisch, '82; Frank, '83) and *Gnomonia erythrostoma* (Frank, '86) in which similar structures and phenomena were observed at that time, were generally accepted as indicating a well developed condition of sexuality. These studies gave a great impetus to the theory suggested by Sachs ('96) that the *Ascomycetes* had their origin from the red algae, or that the two groups had ancestors in common. This theory has taken very deep root and probably is accepted by a majority of botanists even at the present time, especially by those who are not special students of the fungi. It should be stated also that a number of our foremost students of the fungi, perhaps a majority of them, are firm disciples of this theory.

Recent investigation, however, including a cytological study of several of the now classic types, including *Collema* (Bachmann, Miss F. M., '12, '13), *Polystigma rubrum* (Blackman and Welsford, '12; Nienburg, '14), *Gnomonia erythrostoma* (Brooks, '10) have failed to furnish any evidence of a real sexual function on the part of either the trichogyne or spermatia in any of the species of fungi possessing these two structures. Pairing of nuclei in the oögonium, or the pairing of these with nuclei from adjacent cells of the ascogonial branch or archicarp, furnish the synkaria, or the synkaria are organized at different stages in the development of the ascogenous hyphae (see Note III). In some quarters these results have led to a loss of confidence in the sexual significance of the trichogyne and spermatia of the *Ascomycetes*. Some have therefore attributed to the trichogyne a physiological significance of another kind, that of a respiratory organ for

example (Brooks, '10), or a boring organ, a terebrator
(Lindau, '99). Zukal ('89) interpreted the trichogyne of
*Pyronema confluens* as a haustorium to provide food for the
large ascogonium with its numerous ascogenous threads.

Recent investigations on *Collema pulposum* (Bachmann,
F. M., '13) have revealed an interesting departure in the rela-
tion of the trichogyne and spermatia from that thus far found
in other lichens, and is in strong contrast with the condition
found by Stahl in *Collema*. The "spermatia" are not free
and are not formed in large numbers in superficial receptacles,
but are imbedded in the thallus and remain attached to the
supporting hypha. The trichogyne does not extend to the
surface but migrates through the interior of the thallus, seeks
the spermatia and fuses with one. Then the trichogyne un-
dergoes the usual deterioration, but no evidence was obtained
of the migration of the nucleus of a spermatium to the as-
cogonium, although a nucleus supposed to be the sperm
nucleus appears to have been observed in the terminal cell of
the trichogyne.

In the red algae the only variations and progression in the
trichogyne is in variations in length to meet the requirements
of thin or thick cortex, some more or less sinuous or spirally
wound, and a few stout and blunt. It is universally a con-
tinuous, enucleate,[1] prolongation of the oögone, i. e., not sep-
tate nor a separate cell. So far as we know the sperm always
functions in the red algae. In the sac fungi, there is great
variation and marked morphological progression from an
oögone without a trichogyne through short one-septate
trichogynes to long, simple, several-celled ones, and also to
profusely branched, multi-septate trichogynes. It is more
comprehensible to regard this progression and variation in the
light of evolution from the simple to the complex, in the as-
comycete phylum, independent of the red algae, than to con-

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[1] Davis ('96) describes the trichogyne of *Batrachospermum* as having a
nucleus of its own, but it is not separated from the egg nucleus by a wall until
just prior to the development of the gonimoblasts from the egg. He also states
that the sperm nucleus never passes out of the trichogyne into the egg. How-
ever, Schmidle ('99) and Osterhout ('00) find no trichogyne nucleus and describe
a real fertilization by fusion of sperm and egg nucleus.

ceive the long septate trichogyne of the highly specialized *Collema* to be derived directly from the simple trichogyne of the red algae, and then degenerate to the simple gamete of lower more generalized *Ascomycetes*.

<div align="center">NOTE V</div>

<div align="center">MODIFICATION OF SEXUAL PROCESS ALONG WITH STERILITY OR LOSS OF THE ANTHERIDIUM AND STERILIZATION OF THE ARCHICARP</div>

*Sterility or loss of the antheridium.*—Several species are known in which the antheridium, though present, does not function. In such cases sexuality is modified in such a way that sex differentiation occurs among the nuclei in the as-cogonium or in the ascogenous hyphae. Several examples may be cited as follows: In *Pyronema confluens* (Brown, W. H., '09) the antheridium sometimes fuses with the trichogyne but there is no migration of its nuclei; in other cases it may not connect with the trichogyne. The antheridial nuclei degenerate. In still other cases the antheridium is absent. In *Lachnea stercorea* the antheridium fuses with the terminal cell of the archicarp but its nuclei degenerate (Fraser, '07). In *Aspergillus herbariorum* (Fraser and Chambers, '07) and *A. repens* (Dale, '09) a similar situation exists. In those numerous examples where spermatia (mostly free "antheridia") are present it is very likely that the sperm nuclei no longer play a rôle in fecundation due to such exten-sive sterilization of the terminal segments of the archicarp, but the cytology of only a few species has been determined. They no longer perform the function of fecundation in *Poly-stigma rubrum* (Blackman and Welsford, '12; Nienburg, '14), *Gnomonia erythrostoma* (Brooks, '10), and in *Collema pul-posum* (Bachmann, '13) the sperm nucleus has not been traced through the long succession of sterile segments of the archicarp, and it is very probable that it does not reach the ascogonial cells. The spermatia are entirely absent in a num-ber of species where archicarps are present, as in *Laboul-benia chaetophora* (Thaxter, '96; Faull, '12).

*Sterilization of the terminal portion of the archicarp and differentiation of sex nuclei in the ascogonium or ascogenous*

*hyphae.*—A moderately large number of species, in which more or less extensive sterilization of the terminal portion of the archicarp has occurred, have been examined by cytological methods and in most cases a reduced or modified sexual condition has been found.

In *Pyronema confluens* great variations occur in the sexual nature of the ascogonium. In what may be called normal cases, antheridial nuclei enter and become associated with the ascogonial nuclei (Harper, '00; Claussen, '07, '12). Under cultural conditions the antheridium may be normal, rudimentary or absent, but the ascogonium develops in a normal manner (van Tieghem, '84). Different strains may also behave differently. In some the antheridium does not fuse with the trichogyne, while in others it does (Brown, W. H., '09). In some cases even when the antheridium fuses with the trichogyne, its nuclei do not pass into the ascogonium (Dangeard, '07), but degenerate *in situ* (Brown, W. H., '09). In these cases where the antheridium does not function the sexuality of the ascogonium is modified in as much as its nuclei are differentiated sooner or later so that in pairs they perform the function of sperm and egg nuclei. According to W. H. Brown ('09) in cases where the origin of the pair of nuclei in the ascus hook could be determined, they were sisters. After the one conjugate division in the hook the two nuclei in the ascus, or penult cell, are "cousin" nuclei.

The archicarp of *Lachnea scutellata* (Woronin, '66; Brown, W. H., '11) consists of about nine cells. No antheridial structure has been observed. The penultimate cell functions as the ascogonium (Brown, W. H., '11). It is multinucleate and no fusion of nuclei in pairs takes place here. The nuclei are increased in numbers by division, not only in the ascogenous threads where they do not appear to be paired or show conjugate division, but also in the ascus hook where conjugate division takes place. The numerous fusions of the terminal and basal cells of the ascus hook result in numerous successive conjugate divisions. In *Leotia,* although the archicarp has not been clearly observed, it would appear from the account (Brown, W. H., '10) that the antheridium is absent (or

if present, functionless) and that the ascogonium consists of a single coenocytic cell. Conjugate division takes place in the ascus hook, and the subsequently fusing cells, so that in most cases rather distantly related pairs of nuclei form the fusion nucleus in the ascus. In *L. chlorocephala* (Brown, W. H., '10), it appears that the pair of ascus nuclei are sometimes sisters. This would indicate an extreme case in the modification of sexuality, the distance of relationship between the sex nuclei being reduced to the minimum. It recalls the very close relationship of the sex nuclei in many of the lower algae, particularly in certain diatoms[1] (Oltmanns, '04), and in the species of *Spirogyra* having buckle-joint conjugation (Chodat, '10). In the case of *Spirogyra* it is not known whether the pair of sex nuclei in this type of conjugation are cousins or sisters, or whether now one and then another of these possibilities exists. Such species of *Spirogyra* in which certain threads present scalariform as well as buckle-joint conjugation offer an interesting parallel to the variation in distant relationship of the fusing nuclei in the young ascus.

In some other species where the antheridium is functionless or wanting, sex differentiation is said to take place among the nuclei in the ascogonium. This indicates a sex differentiation much earlier than that which is supposed to occur in the species just cited. This differentiation in sex nuclei has been described in *Humaria granulata* (Blackman and Fraser, '06).

Another species in which similar phenomena are described is *Lachnea stercorea* (Fraser, '07). Here the archicarp consists of several coenocytic large cells and the terminal trichogyne of 4–6 smaller coenocytic cells. The unicellular coenocytic antheridium fuses with the terminal cell of the trichogyne, but its nuclei do not reach the single-celled ascogonium, among whose nuclei sex differentiation is said to take place.

For a number of years *Polystigma rubrum,* a parasite on cherry leaves, as the result of studies by Fisch ('82) was regarded as an example of fertilization of an ascogone coil by

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[1] In *Achnanthes subsessilis,* the protoplast divides into two parts along with nuclear division. The two uninucleate protoplasts now immediately unite in auxospore formation.

sperm nuclei from spermatia after passing through a long succession of cells constituting the trichogyne or sterile portion of the archicarp. The trichogyne, or sterile portion of the archicarp, is very long and branches into two portions, one extending to either surface of the leaf. But according to Nienburg ('14) sex differentiation has occurred between the basal cells of the archicarp and a nucleus from the basal cell migrates into the adjacent cell, which becomes the ascogonium or ascogenic cell, but nuclear fusion does not take place here.

*Loss of function by the archicarp or its disappearance.*— A number of examples are known in which the archicarp has either lost its function as a sexual organ or ascogone, or has disappeared. In such cases differentiation of sex occurs in special vegetative cells, sometimes by the migration of a nucleus from certain cells into adjacent ones. In *Gnomonia erythrostoma,* although Frank ('86) described coiled ascogone-like structures with trichogynes, and believed that the coils were fertilized through the agency of the spermatia, recent cytological work (Brooks, '10) on this species appears to show that the tufts of hair-like structures emerging through the stomates of cherry leaves, on which this species of *Gnomonia* is parasitic, are not now connected with the coiled hyphae deeper in the tissue. It appears also from the same work that the ascogenous hyphae do not arise from the coils, but from one or more slightly differentiated hyphae in the center of each coil.

A similar example is found in *Xylaria polymorpha* (Fisch, '82), where an extensively coiled hypha ("Woronin's hypha") occurs in the early stages of the formation of the ascocarp, but later disappears and certain vegetative cells give rise to the ascogenous hyphae.

In *Humaria rutilans* (Fraser, '08) no archicarp or ascogone coil is discernible, but certain vegetative cells function as ascogenic cells following the migration into them of nuclei from adjacent cells.

#### MORPHOLOGY OF THE ARCHICARP

If the history of the *Ascomycetes* is correctly read from the simpler and more generalized forms to the complex and

highly specialized ones as Sachs ('74, '96), de Bary ('81, '84), and many other students have advocated, the female organ or archicarp first appeared as a "unicellular" or continuous organ, not differentiated into an oögonium or fertile portion, and a trichogyne. The presence of a "procarp," whether consisting of one or several cells, which ultimately gave rise to the asci or ascogenous threads was the predominant character which led Sachs in 1896 to believe in the phyletic relation of the sac fungi and red algae, although earlier he had regarded the morphology of the ascocarp and cystocarp of greater importance in showing relationship. No known red alga possesses a procarp simple enough to represent the prototype of the two groups. *Gymnoascus* was selected by Sachs as representing the simplest *Ascomycetes*. The archicarp of *Gymnoascus* is a continuous structure more or less coiled around the antheridium from which it copulates directly without the intervention of a trichogyne.

After copulation the ascogonium divides into several cells which give rise to the ascogenous hyphae. In some forms the splitting up of the ascogonium by transverse division occurs at an earlier period, before copulation. There is some evidence which indicates that the "trichogyne" in the *Ascomycetes* primarily was a prolongation of the "unicellular" oögone (or carpogone), and that when it was first separated as a distinct cell it was still a fertile part of the archicarp. In *Aspergillus repens* the terminal cell, or "trichogyne," sometimes gives rise to ascogenous hyphae (Fraser, '08).

The terminal cell became merely a trichogyne when it ceased to give rise to ascogenous hyphae, and acted as a transport tube for the sperm nuclei from the antheridium to the ascogonium, as in *Pyronema* and *Monascus*. The septum between the terminal cell and the functional ascogonium was an impediment to the passage of the sperm nuclei, as well as the fact that when they entered the terminal cell of the archicarp they did not meet with functional egg nuclei. This situation very likely favored the assumption of sperm and egg functions by the nuclei of the functional ascogonial cell. The variations in *Pyronema* where the antheridium may or may

not be present, and often when present and fused with the trichogyne its nuclei degenerate and the ascogonium is still functional producing ascogenous hyphae and asci, is in support of this interpretation.

Further sterilization of the terminal portion of the archicarp proceeds as it becomes longer and more septate, the fertile ascogonial cell or cells being near the center or base. All of the sterile portion of the archicarp distal to the ascogonial cells is usually interpreted as the trichogyne. I believe it would be more in harmony with the historical origin of the archicarp, and with the real homologies, if only the terminal sterile receptive cell of the archicarp were called the trichogyne, the other portions to be regarded as sterile portions of the archicarp or ascogonium. This would be in harmony also with Thaxter's ('96) interpretation of the archicarp of the *Laboulbeniales*.[1] In this group the inferior and superior supporting cells are sterile cells of the archicarp derived by a transverse splitting of the ascogonium. Even with this interpretation of the trichogyne of the *Ascomycetes,* it would be a different structure from that of all the red algae where it is merely a continuous prolongation of the egg cell.

### NOTE VI

The coenocytic character of the mycelium of the *Phycomycetes* has been presented as an obstacle to the derivation of the sac fungi from the sporangium fungi (Bessey, E. A., '13); this character can, however, have very little or no significance, for many of the *Ascomycetes* are coenocytic. As in most of the fungi, cell wall formation is delayed so that new portions of filaments are often multinucleate, the cell walls being laid down subsequently, sometimes enclosing one nucleus, sometimes several in a cell. There are the monoenergid and polyenergid species of sac fungi. In the *Phycomycetes* cell wall formation is usually longer delayed or does not occur except where reproductive cells are formed. In the *Mucorales* old mycelium frequently becomes multiseptate. It should be noted that in *Basidiobolus* (Eidam, '86; Raciborski, '96; Fair-

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[1] Except in the case of the multiseptate branched trichogynes.

child, '97, and others) the cells are uninucleate. The varia-
tion in coenocytic character of mycelium probably is due in
some measure to the usually fundamental difference between
cross wall formation in dividing cells, in the thallophytes and
the higher groups of plants, where the fibers of the inner
spindle play a part and the cell wall development is centrif-
ugal, while in most thallophytes the spindle fibers do not
play such a part, wall formation being centripetal, like a clos-
ing iris diaphragm.

The strong plasma connections between the protoplasts of
the *Laboulbeniales* (Thaxter, '96) present a very striking re-
semblance to those in the red algae. This feature is regarded
by some as very strong evidence of a phylogenetic relation
between the *Laboulbeniales* and the red algae. But intercellu-
lar plasma connections are a common feature in all groups of
plants, though in many plants these connections are very
minute. The single central pore in the wall of the *Laboul-
beniales* is perhaps the result of incomplete closing of the ring-
forming wall, and in the *Laboulbeniales* would seem to be of
physiological rather than of phylogenetic significance. The
firm cell walls which are characteristic of the members of this
group bear a very definite relation to their habit as external
parasites of insects. Standing out free from their bodies and
thus having no other means of support than their own rigidity,
thick cross walls would interfere with transport of food ma-
terial, while the prominent plasma connections permit easy
passage of nutrients.

### NOTE VII
#### BRIEF OUTLINE OF SOME OF THE THEORIES AS TO THE PHYLOGENY OF THE ASCOMYCETES

I. *Descent from the Rhodophyceae.*—Sachs ('74, p. 287)
regarded the resemblances between cystocarp and ascocarp
as the most important character indicating a relationship be-
tween the red algae and sac fungi, although the form of the
sexual organs, particularly the carpogonial branch, was also
believed to point in the same direction. In his 'Lehrbuch der
Botanik' he did not even suggest that the *Ascomycetes* were
derived from the *Florideae*. The relationships were based

on the principle of morphological homology, which he believed were great enough to justify their inclusion in the same class. To justify his arrangement in one large group of plants with such diverse aspects and habitats, he cites the inclusion of the *Lemnaceae* and palms in the great group of the monocots. We could not then interpret his inclusion of the sac fungi and red algae in one class, the *Carposporeae,* as indicating that the former were derived from the latter.

Sachs says ('74, p. 288) that in order to find the relationships between plant divisions one must compare the simplest, not the highest forms. By this method he finds that the *Coleochaetaceae* and *Characeae* are linked, on one hand to the simplest *Florideae,* and on the other to the simplest *Ascomycetes.* Each of these series, he says, has developed in its own peculiar manner to higher forms, so that if one compared the most complete *Ascomycetes* with the coleochaetes only very slight resemblances are to be found. From this it is very clear that Sachs, at that time, had no thought of the derivation of the *Ascomycetes* from the *Florideae.* There is nothing to indicate that he believed the *Ascomycetes* descended from the charas and simplest coleochaetes, to which he says the simplest *Ascomycetes* are most closely related. Nor would his theory require a common ancestor for the two groups. Because of the morphological resemblance between cystocarp and ascocarp, he would have united the *Ascomycetes* and *Florideae* into a higher group even had he believed that the former were derived from the *Phycomycetes.*

It has been said by Sachs ('96, p. 204) that the fungi as a whole cannot be valued as an architype because, as apochlorates, they must be descended from green plants. The bacteria he would derive from the *Cyanophyceae,* the *Phycomycetes* from the *Siphoneae,* and the *Ascomycetes* (or at least the *Discomycetes*) from the *Rhodophyceae.* The predominant feature indicating the descent of the sac fungi from the red algae he now sees in the procarp of both groups ('96, p. 205).

The chlorophylless seed plants have only a slight form-producing power or motive, as Sachs has pointed out ('96, p. 205), since they occur mostly as small plant groups within certain

green leaved families and show very plainly the morpholog-
ical characters of their antecedents. But he says it is quite
otherwise with the fungi. The simplest primitive forms of
the *Ascomycetes, Phycomycetes* and *Basidiomycetes* have
given rise independently to an enormously high state of dif-
ferentiation. Now Sachs in 1896 (and earlier, '74, p. 310)
recognized *Gymnoascus* as belonging to the simplest *Ascomy-
cetes,* the sexual organs of which are a simple carpogone and
pollinode. It is very clear then that Sachs would not derive
the *Ascomycetes* from any primitive form at all like any
known red algae, much less through such forms as the highly
specialized *Collema* or *Polystigma.* This warrants us in con-
cluding that Sachs had in mind a primitive hypothetical an-
cestor of the sac fungi and red algae, which possessed simple
copulating gametes. With the knowledge we possess to-day
of such forms as *Dipodascus, Eremascus,* etc., where the
zygote becomes the ascus (generalized or simple) I believe he
would have recognized in the *Phycomycetes,* as we know them
to-day, a situation very closely approximating an "Urform"
for the *Ascomycetes,* particularly in view of the fundamental
difference in the cytology of the red algae and sac fungi.

But whether the fungi represent one or several architypes
it by no means follows that, because of the absence of chloro-
phyll, they *must* be derived from green plants, or that each
great series must be derived separately from different groups
of algae.

The appearance of the higher fungi (*Eumycetes*) was, in
the opinion of Vuillemin ('12, p. 223), contemporaneous with
the emergence of sea-shore, which abandoned certain red algae
to a terrestrial life. This new environment introduced the
change, which, accompanied by loss of chlorophyll, gave rise
first to the *Pyrenomycetes,* from which the other higher fungi
(*Uredinales, Basidiomycetes*) have originated. The sapro-
phytic forms represent the productive and progressive stock.
Parasitic groups, like the *Uredinales, Laboulbeniales,* lichens,
etc., are composed of highly specialized and uniform members,
their progressive potentialities being suppressed, but they re-
tain their hold on existence because of their specialized hab-

itat.  The first *Pyrenomycetes,* according to his view, were
some of these depatriated red algae, losing their pigments
while preserving the structure, the sexual organs and the gen-
eral evolution.  But he recognized no known member of the
red algae as a prototype of the *Pyrenomycetes.*  Primitive
trichogyne-bearing algae gave rise to the red algae on one
hand, and to the *Pyrenomycetes* on the other, the now known
colorless red algae (like *Harveyella mirabilis, Choreocolax
alba*) being recently reduced forms having no significance in
the origin of the sac fungi.  But the *Pyrenomycetes* with well
developed trichogyne and spermatia are chosen as the primi-
tive forms, the simplest represented by *Polystigma* (in his
"*Polystigmales*") the higher ones (his "*Pyreniales*") giving
rise successively to the *Hysteriales* and *Phacidiales.*  From
the *Polystigmales* three other lines arose, their simplest forms
being represented by first, *Gymnoascus;* second, *Pyronema;*
and the third line represented by the *Laboulbeniales* (see
Vuillemin, '12, pp. 338-341).

Bessey ('14) regards the *Discolichenes* as the most primi-
tive *Ascomycetes.*  This theory is based on the supposed
phyletic relation of the multiseptate trichogyne of the lichens
(*Collema,* for example) to the trichogyne (a mere tubular,
continuous, prolongation of the egg) of the red algae.  Cer-
tain of the red algae became parasitic on blue-green algae and
on simple members of the green algae, forming a lichen
thallus.  It is supposed that this parasitism may have had
its origin while both kinds of organisms still lived in the water,
but finally the lichen assumed the land habit.  The improba-
bility of such a derivation of the sac fungi as suggested in the
above theories has been fully discussed in the preceding pages.

II.  *Descent from the Phycomycetes.*—De Bary ('81, '84,
'87), as already stated in the first part of this paper, be-
lieved the *Ascomycetes* were derived from the *Phycomycetes,*
particularly through such forms as the *Peronosporales.*  The
criterion for the *relationship* is the close homology and mor-
phological resemblance of the sexual organs, though he sug-
gested that *Eremascus* might have been derived from the
*Mucorales* through some such form as *Piptocephalus* where

the zygote is the outgrowth from the fusion point of two equal gametangia.

Brefeld ('89, '91) also derived the *Ascomycetes* from the *Phycomycetes* but interpreted the ascus as the phyletic homologue of the sporangium, the ascus representing a specialized structure derived from the generalized sporangium in one direction, while the conidia were regarded as reduced one-spored sporangia. But the nuclear fusion and reduction phenomena in the ascus are so fundamentally different from any known cytological processes in the sporangium, that its phyletic relation to the sporangium is doubtful.[1] The conjugation of the gametangia he interpreted as ordinary fusion of hyphae which occurs in numerous instances devoid of all sexual significance. *Protomyces, Ascoidea* and *Thelebolus,* with numerous spores in the ascus, were interpreted as representing an intermediate condition between the generalized sporangium of the *Mucorales* and the specialized ascus. In *Thelebolus* it has been found that the development of the ascus follows the type with crozier formation and that it is closely related to *Ascobolus* and *Rhyparobius* (see Ramlow, '06; Dangeard, '07). As for *Protomyces* and *Ascoidea* they probably represent forms with reduced sexuality while retaining the ancestral character of many divisions of nuclei to form numerous spores.

Zukal ('89), influenced by Brefeld, derived the hymenial *Ascomycetes* (like *Ascobolus, Pezizales,* etc.) through *Thelebolus* and *Monascus;* the stromatic *Ascomycetes* (whether *Pyrenomycetes* or *Discomycetes*) from the *Uredinales;* the *Gymnoascales* and others with asci arising directly from the mycelium, from another ancestral type.

Lotsy ('07, p. 469) sees no difficulty in deriving the polyenergid forms like *Pyronema* from the *Phycomycetes.* The forms with spermatia, which are usually monoenergid, it would seem rational, he thinks, to derive from the red algae, and this raises the question as to whether the *Ascomycetes* are of polyphyletic (or biphyletic) origin. The great uniformity of the

[1] The nuclear phenomena in the "germ" sporangium (from the zygote) are not known.

ascus in the entire group is a great obstacle in the way of accepting a polyphyletic origin for the group. All things considered he is inclined to accept de Bary's view of their phycomycetous origin.

The origin of the *Ascomycetes* from the *Phycomycetes* is recognized by Dangeard ('07) through such forms in which there is still a union of gametangia. *Dipodascus* and *Eremascus* represent such forms in his scheme. The generalized ascus resulting from the union of the gametangia of *Dipodascus* he terms a "sporogone." From *Eremascus,* by reduction, forms like *Endomyces* arose, while the *Ascomycetes* with ascogenous hyphae were derived from such forms as *Dipodascus* by delayed nuclear fusion and the proliferation of the gametangium into what he terms "gametophores" (= ascogenous hyphae). The gametes then are formed in the nuclear pair which fuses in the ascus. This terminology arises from his persistent belief that the ascus is the egg. Shorn of the change in terminology and his, perhaps, unfortunate insistence on homologizing the ascus with the egg, his interpretation of the relation which such a form as *Dipodascus* bears to the *Ascomycetes,* has much merit.

Nienburg ('14) suggests the origin of the *Ascomycetes* from the *Phycomycetes* through some such form as *Monoblepharis.* He would find the evidence for this in the homology of the archicarp of *Polystigma rubrum* with such forms of *Monoblepharis* in which the stalk cell of the oögonium is an antheridium, and where the oögonium is terminated by one or more sterile cells. The archicarp of *Polystigma* he interprets as having two fertile cells at the base and prolonged into a long sterile septate portion (so-called trichogyne) which forks, sending a branch to either surface of the leaf. The basal multinucleate cell is the antheridium. After pore formation one nucleus migrates into the unicellular egg. Interesting as this suggestion is, forms of *Pythium* (see de Bary, '81, '84; Atkinson, '95) with intercalary oögonia and stalk antheridia present a closer analogy to the archicarp of *Polystigma* as described by Nienburg, but it is extremely doubtful if the point of contact is to be sought through such structures.

*Brief comparative summary of the above views on the phylogeny of the Ascomycetes.*—The adherents to the doctrine of the red algal origin of the *Ascomycetes* interpret the point of contact in three different ways: *first,* sac fungi with highly developed "trichogyne" (sterilized archicarp) of the *Collema* type with red algae like certain of the existing forms, *Nemalion,* or some of the higher forms in the vicinity of *Harveyella,* etc.; *second,* sac fungi with highly developed "trichogyne" (= sterilized archicarp) of the *Polystigma* type with hypothetical trichogyne algae representing the common stock for the origin of both groups; *third,* sac fungi with simple generalized copulating gametes of the *Gymnoascus* type with hypothetical algae having a simple procarp representing the stock from which both groups originated.

According to the two first interpretations the sac fungi have been derived through highly developed and specialized forms from either quite highly developed and specialized red algae, or both groups from a common trichogyne algal stock, and then by degeneration have slid backward from complex and specialized structures to simple, generalized and primitive ones. The third view which recognizes a simple procarp, without regard to a trichogyne, as the important character of the hypothetical stock, is far more comprehensible.

But if we must go back to some hypothetical ancestor, which cannot be represented by any known red alga, for the source of the sac fungi it is far more reasonable to search for one in another fungus line, where, in the light of present-day knowledge, there are known forms with sexual organs very much like the sexual organs of simple, known forms of the *Ascomycetes.* But we are not yet in a position to name any known phycomycete[1] as a probable ancestor of the *Ascomycetes,* though it appears very likely that the ancestral stock possessed phycomycetous characters.

[1] Lotsy ('07) suggests *Cystopus;* Miss Dale ('03) in her study of *Gymnoascus* suggests *Basidiobolus;* Nienburg ('14), *Monoblepharis;* while Dangeard ('07) suggests *Myzocytium vermicolum* as the prototype of the higher fungi.

## PROVISIONAL ARRANGEMENT OF MAIN LINES OF DEVELOPMENT IN ASCOMYCETES

For those who are interested in the suggestions as to the phylogeny and relationships of the *Ascomycetes* presented in this paper, a diagrammatic arrangement of the principal series or lines which will illustrate the relationships tentatively held by the writer may be acceptable. It is with considerable hesitation that this arrangement is presented. The writer trusts that it will be accepted as provisional and in the nature of a working hypothesis which he hopes will further stimulate investigation, suggestions and criticisms on the ideas embodied in this paper, all of which, for or against, will be gladly welcomed.

*Dipodascus,* a primitive form, cells of mycelium polyenergid, gametogenous branches large, unequal, polyenergid. Ascus is elongated, broadened zygospore, zygote germinating immediately forming a broad germ tube in which spores are formed. Since the process does not go on to the formation of a sporangium, a different mode of internal free cell-formation then arose in connection with the precocious formation of spores in the zygote and retention of epiplasm which assists in discharge of spores. *Dipodascus* retains tendency of gamogenic branches to copulate early before they become strongly differentiated as gametangia, just as in *Mucorales.*

I.   PROTOASCOMYCETES are derived by descent and degeneration from some such primitive ascomycete form as *Dipodascus.* The ascus when of sexual origin is the zygote, except in *Nadsonia.*

*Endomyces Magnusii* is the nearest known form to the generalized condition seen in *Dipodascus.* Cells of mycelium usually polyenergid, those of stout mycelium are polyenergid. Formation of ascus in *Endomyces Magnusii* repeats formation of zygospore in *Zygorhynchus.* Gamete branches in both are multinucleate, but when cell wall is laid down delimiting the gametangia all but one nucleus in each gametangium of *E. Magnusii* are excluded. After contact of the two sexual branches the male gametangium is formed by enlargement of its tip, into which protoplasm and the one nucleus migrates,

exactly as male gamete of *Zygorhynchus* is formed, except the latter is multinucleate. By disappearance of the separating wall, ascus is formed of the two gametes.

*Endomyces series,* then, derived from *Dipodascus*-like ancestors, with *Endomyces Magnusii* the lowest and most generalized.

*Developmental tendencies* from here in four, five, or six different directions:

1. *Eremascus,* both gamogenic branches uninucleate, ascus more definite and specialized in shape. Loss of conidial formation. *Endomyces fibuliger* indicates step toward *Eremascus* (*E. fertilis*) in small size of gametes.

2. *Endomyces* diverging into the two series, one chiefly with sprout conidia, the other chiefly with oidia; the latter preserves the *E. Magnusii* character, the former takes on sprout conidia in addition to oidia (*E. fibuliger* and *E. capsularis* form both oidia and sprout conidia); oidia formation the more primitive and generalized condition in *Ascomycetes.*

3. *Saccharomycetes.* Still more specialized and reduced than in *Endomyces fibuliger* and in this same line. *Schizosaccharomyces* may have come from same line with dropping of sprout conidia, or may be descended from form near *Endomyces Magnusii.*

4. *Exoascaceae.* From *Endomyces*-like ancestors. Nuclear phenomena not well known. Diploid young ascus may have arisen in connection with cell wall formation, two nuclei being retained in ascogone instead of one as in *E. Magnusii,* where all but one are excluded at time of wall formation, i. e., ascus fundament may have retained the polyenergid character of the most primitive forms like *E. Magnusii.* Tendency to form hymenia may be controlled by host since asci in all, except *Taphrina laurencia,* come to surface to mature.

5. *Ascocorticium,* saprophytic on wood where food is not so rich, tendency to drop conidial formation (?), association of asci in hymenium, highest development of the *Endomyces* series, or of the *Protoascomycetes.* Series is terminated early, tendency in *Endomyces* line to specialization of zygote into one ascus with reduced number of spores, and line soon terminated.

6. *Ascoidea, Protomyces, Taphridium,* etc., probably represent forms derived by reduction and loss of distinct sexual organs but preserving primitive feature of many divisions of nucleus in the generalized ascus.

II. EUASCOMYCETES. Lowest forms with generalized archicarp. Similar to *Monascus, Gymnoascus,* etc.

1. *Tendency* to late copulation of gamogenic branches, so that archicarp becomes large and many-nucleate, or tendency to elongate, or both.

2. As it elongates *tendency* to septation, first a single terminal cell ("trichogyne"), and later longer and multiseptate "trichogyne," or rather sterilization of terminal portion of archicarp. One of the early tendencies in connection with elongation of the archicarp may have been the origin of a receptive terminal portion under chemotactic or similar stimulation; such a condition suggested in *Cystopus.*

3. This made the passage of antheridial nuclei increasingly difficult, and resulted in early *tendency* to sterilization of antheridium or failure to function because of functionless condition of "trichogyne." Led in many cases to modified sexuality by differentiation of sex among nuclei in ascogonium, vegetative cells, or ascogenous threads.

4. *Progressive tendency* to multiplication of spores by postponement of nuclear fusion and spore formation; conjugate division of sex nuclei, and multiplication of the specialized structures (asci) in which spores are formed, so that spore formation and distribution is extended over greater period of time. This most advantageously attained by sprouting of zygote (ascogone), branching of threads, and terminal formation of specialized asci.

Diverging lines from *Gymnoascus* and *Monascus*-like ancestors or related prototypes in which asci are irregularly arranged but associated in groups with imperfect envelope.

1. A line with interwoven asci, *Plectascales* as a highly specialized lateral group, with *Gymnoascaceae* at base. *Aspergillaceae* a progressive line, with *Perisporiales* an offshoot, or *Perisporiales* direct from *Monascus*-like ancestors.

2. *Elaphomycetaceae,* asci interwoven in groups but separated by sterile walls.

3. *Pezizales,* asci remaining in groups not interwoven in mycelium, but spaced by sterile threads (paraphyses). *Pyronema* represents one of the generalized, lower forms. The *Helvellales, etc.,* are probably derived from the *Pezizales.*

4. The *Microthyriales*[1] have usually been placed among the *Perisporiales* with which they have little in common. I believe they

[1] Recent studies by several authors, particularly by von Höhnel ('10) and by Theissen ('12, '13, '14) have greatly increased our knowledge of these interesting fungi, partly by the discovery of new forms but especially by uncovering many forms from the clouded situation in which they have been placed for lack of an adequate study of their structure.

represent reduced forms derived on the one hand from the *Phacidiales* and perhaps on the other from the *Sphaeriales* and possibly some from the *Perisporiales*. The formation of the characteristic shield has rendered superfluous the perithecial wall as a protective structure. The genus *Diplocarpon,* the structure and development of which was investigated by one of my former students (see Wolf, '12), I believe is an excellent illustration of a form on the way (by reduction of the perithecial wall in conjunction with the formation of the shield) from the *Phacidiales* to the condition presented by many members of the *Microthyriales.*

The above provisionally suggested relationships may be represented by the following five or six series, or lines of development, with the accompanying diagram (fig. 10):

1. Apocarp line     from *Dipodascus*-like forms and by reduction.

2. Plectocarp line     from *Dipodascus*-like forms, perhaps similar to *Monascus.*

3. Perispore line     arising from *Monascus*-like prototype, before splitting of archicarp, or from *Aspergillaceae.*

4. Pyrenocarp line     arising near *Monascus*-like prototype. *Laboulbeniales* side line near base, and some of the *Mycrothyriales* as reduced from *Sphaeriales.*

5. Discocarp line     from *Dipodascus*-like forms near *Monascus,* but lower (it is not improbable that some of the members of the stock of primitive *Euascomycetes* showed considerable variation in the strength of the ascocarp envelope, also in its presence or absence in forms where it is more or less rudimentary[1]); and some of the *Microthyriales* as reduced forms from *Phacidiales.*

Or a 6th line also, *Laboulbeniales* from *Monascus*-like ancestor.

[1] This variation sometimes occurs in existing forms. Zukal ('89) describes an abnormal case in *Eurotium* (*Aspergillus*) *herbariorum* where the antheridial branch and envelope are wanting, the mass of asci being exposed. In this connection it is worthy of note that Fraser and Chambers ('07) regard *Aspergillus* "as representing a primitive ascomycetous type from which most others can be derived." This suggestion was based on the assumption that the red algae were the ancestors of the sac fungi. On the basis of the counter theory (phycomycetous origin) *Gymnoascus* and *Monascus*-like forms are more comprehensible as primitive *Euascomycetes.*

Fig. 10.  Chart showing suggested phylogeny of the *Ascomycetes*.

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