

THE GENUS ENDOGONE

GEO. F. ATKINSON

Cornell University

The genus *Endogone* was founded by Link in 1809, and for more than a century its life history and taxonomic relationship have remained very obscure. Notwithstanding this obscurity in relationship and development, the structure of the mature plants is so simple and characteristic, that comparatively few species have been accredited to the genus which do not belong here. The fruit bodies are pulvinate, rounded to reniform or irregular. In size they vary from 2–4 mm. up to 2–3 cm. In life relation they are saprophytes. In habitat they are hypogeous, epigeous or epixylous; and occur under or on the ground, among or underneath fallen leaves, among the rhizoids of mosses or roots of ferns, on dead wood, on sphagnum or other mosses. In color they are whitish to yellow, brown or blackish. Approximately seventeen species are known. The genus is cosmopolitan in distribution. Species are known from Europe (including European Russia), Ceylon, Tasmania, North America, Central America, South America and the Fiji Islands.

General structure of the fruit body.—There is a peridium of slender, interwoven hyphae formed by the terminal branchlets of the hyphae which spring from the basal region, branch profusely and radiate to the periphery. The interior constitutes the “gleba,” the base or central portion of the “gleba” is sometimes hollow or of less density than the broad peripheral zone. The “gleba” is usually packed with numerous, large thick walled “resting spores,” oval, elliptical, or spherical in form, and yellowish, grayish or dark brown in color according to the species. These “resting spores” are 40–100 μ in diameter, are packed among the hyphae, and terminate certain branches. They have been termed spores, sporangia, ampullae, or asci, the latter term apparently having the preference, since it is employed by a majority of writers. Several large elliptical spores in an “ascus” have been described in one species (*Endogone pisiformis*), a single large spore¹ in an ascus in another species (*E. reniformis*), and numerous minute spores in an ascus in several species. It is

¹ The spores in this species are probably the ordinary “resting spores,” the “asci” of authors, for Bresadola (1896, p. 297) says that neither the asci nor their mode of dehiscence was seen.

doubtful, however, if true sporulation has ever been observed. In dead resting spores the contents often segregate into a number of large, rounded or elliptical bodies. In *E. reniformis* the single spore in an "ascus" is probably the "resting spore" itself, while in the species described as having numerous minute sporidia in an ascus (often with an interrogation), the supposed sporidia are probably the numerous fat bodies conspicuous in some species.

ORIGIN AND DEVELOPMENT OF THE "RESTING SPORES" IN
ENDOGONE LACTIFLUA BERK.

Character of the mycelium.—The only important contribution to development in the genus *Endogone*, thus far, was made by Bucholtz in 1912, in his study of *Endogone lactiflua*. This species is subterranean and occurs in various parts of Europe. The fruit bodies range in size from 4 mm. to 2 cm. The material studied by Bucholtz was found in a plantation of *Abies sibirica* in Livland, Russia. The mycelium is coenocytic, profusely branched, the hyphae following a very sinuous course, but the general direction is radial and toward the periphery. It is non-septate, true cross walls being formed only in connection with the reproductive organs, though false cross walls are occasionally found in the vegetative hyphae. The hyphae vary greatly in diameter, in general becoming more slender toward the periphery of the fruit body, but irregularities in the form of swellings occur. Terminal branches on the interior are often clavate. Sack-like enlargements occur from which numerous branches often diverge. The walls of the hyphae are thick. The nuclei are minute, very numerous, and lie in a parietal layer of cytoplasm.

The progametes and conjugation.—The progametes are clavate and of unequal size. They lie nearly parallel and their walls fuse at the lateral point of contact a short distance from the free ends. The nuclei in the progametes, lying near the periphery become larger, more distinct, and undergo one division. The nuclei now retreat from the terminal portion of each progamete and all except one are excluded from each gametangium by a cross wall. A few sterile nuclei sometimes remain in the gametangium but soon degenerate. The origin of the selected gamete nucleus in each gametange is not known, but it is probably derived from one of the peripheral nuclei in the progamete, or one of the daughter nuclei after mitosis. These gamete nuclei are much larger than the progamete nuclei, thus maintaining the nucleo-cytoplasmic relation. Each one occupies the center of its gametange. The walls at the point of contact are now resorbed. The nucleus from the smaller gametange (antherid) migrates into the larger one (oogone).

Formation of the "resting spore" and simple zygo carp.—The "resting spore" in *Endogone lactiflua* is not formed in the immediate zygote resulting from the fusion of the two gametangia nor in the oogone, but in an outgrowth from the latter. During and immediately after fusion of the two gametangia their walls become thickened and firm, so that they can not yield to the pressure from the young growing zygote. As a result there arises a sack-like outgrowth from the end of the oogone into which the cytoplasm from the two gametangia flows accompanied by the two gamete nuclei, the antheridial nucleus following the oogonial nucleus. The sac-like outgrowth enlarges into an oval or broadly elliptical resting zygote. A thick, stratified, hyaline, cartilaginous wall is formed next to the primary zygote membrane, which entirely encloses the cytoplasm and other contents, thus separating them from the empty oogone. The two gamete nuclei lie side by side in the center of the zygote but do not fuse until after the resting period, except in a small variety from Germany in which the gamete nuclei fuse at once according to Bucholtz. During the growth and ripening of the zygote it becomes enveloped by slender branches which coil in a more or less spiral manner around it forming a thick cover of small cells, 2–3 cell layers deep, the walls of these cells become greatly thickened and fuse next the zygote, grading out to the thin walls of the surface. Each resting spore, or zygote, with its individual cellular envelope forms a simple fruit or simple zygo carp (zygosporocarp, as Bucholtz terms it). The fruit body of *Endogone lactiflua* is filled with these simple zygo carps intermingled with the mycelium, and is therefore a compound zygo carp. Germination of the "resting spores" has not been observed. *Endogone lactiflua* is the only species of the genus in which such simple zygo carps are known, *i. e.*, a fruit body with a single zygote enclosed in its individual envelope.

ENDOGONE SPHAGNOPHILA

In July, 1916, a day or two before the close of a fungus foray organized by Mr. F. C. Stewart at his camp on Seventh Lake, in the Adirondacks, Mr. W. H. Sawyer, Jr., a member of the party, brought in some sphagnum on which were rounded, pulvinate, orange-yellow bodies resembling the plasmodiocarps of certain slime molds. A preliminary examination of the internal structure revealed the fact that it was not a slime mold, but apparently a phycomycete with large resting spores having a thick, hyaline, stratified, cartilaginous wall, and orange-yellow content. A pair of stalks, or suspensors, attached to one end of the resting spores in different stages of development, indicated that they had their origin in an interesting type of conjugation. In the afternoon of the same day (July 31, 1916) Mr. Sawyer

and I crossed the lake and visited the same spot in order to collect more material. The dry weather during the latter part of July had lowered the water in the ravines so that this particular sphagnum moor was water-free although the ground was very soft and wet. The fruit bodies of the fungus were not very abundant, but here and there a single one was found on a sphagnum plant, rarely two or more. In nearly all cases the fruit body was attached on the upper side of the central part of the terminal rosette, or one of its radiating branches. Rarely was a fruit body found attached to one of the lower branches. Altogether some 30 or 40 fruit bodies were collected. A number were fixed in Flemming's solution, some in Biondi's solution and some in chrom-acetic solution. Other material was carried to Ithaca on the living sphagnum, where a few more fruit bodies were fixed. Some were kept during the winter in moist situations out of doors, and others in doors in a dried state. Finally, during the winter of 1916-17, it was revealed to me in a semi-vision, that this fungus was a member of the interesting genus *Endogone*.

Structure of the fruit bodies, or complex zygoearps.—The plants are 2-4 mm. in diameter, pulvinate, concave below and convex above, so that a section through the center parallel with the morphological axis is reniform. The larger plants are slightly convoluted or mildly lobed, the upper portion showing two to three broad, low convolutions. As the resting spores mature the plants are orange-yellow in color, but the pigment resides entirely in the spore content, the mycelium and spore walls being hyaline.

The *peridium* is thin, white, and composed entirely of a dense, pliant web of the terminal, slender branches of the radiating mycelium. The terminal branchlets are 3-5 μ in diameter at the base and taper out to a very slender point 1 μ or less in diameter. The walls are much thickened, so that the lumen of these narrow branchlets is nearly closed, quite so toward the apex. Many of these slender branchlets are free above the surface and give to the peridium a minutely tomentose, felt-like surface. Many of these branchlets arise very close together, and then are more or less dichotomously branched at a distance, a peculiarity often quite characteristic of the stouter internal mycelium.

Internal mycelium and hold-fast.—The internal mycelium has a general radial direction from the basal depression, diverging in all directions toward the peridium. The main hyphae are 12-15 μ in diameter. The branching is di- or trichotomous, or 4 to 5 or more branches arise close together, their point of origin often suggesting a ganglion-like enlargement of the parent hyphae from which the branches radiate. The course of the hyphae is more or less sinuous.

No cross walls have been observed, except in the progametes after copulation. The nuclei are minute, very numerous and lie in the peripheral granular cytoplasm. There is a nuclear membrane and a large nucleolus (? karyosome). The fruit bodies are quite firmly attached to the living sphagnum leaves, but the mycelium does not appear to be parasitic, although short haustoria have been seen penetrating the cell. The hold-fast is a rather compact lattice-like layer of mycelium forming a kind of "sole," very closely applied to the surface of the leaves, from which here and there the short haustoria arise. The fungus is probably nourished by organic and mineral solutions carried by the sphagnum from the water of the humus substrate in the capillary stream so well provided for in the peat mosses.

Conjugation of the progametes.—While there is a great resemblance in the process of conjugation and in the formation of the resting zygote of *Endogone sphagnophila* to the situation in *E. lactiflua*, the details of the process are quite different in the two species. The progamete branches lie nearly or quite parallel. In a few cases where they have been observed just prior to conjugation they do not appear to be differentiated from ordinary stout vegetative branches, except that the cytoplasm is more dense and abundant. They do not appear to be enlarged or clavate. In fact many of the vegetative branches are clavate and sometimes they are in pairs lying closely side by side, but in no case have I been able to determine with certainty that such branches are progametes. The progametes also appear to be undifferentiated before conjugation. They conjugate by lateral contact of their walls at the tip. Immediately after contact the progametes begin to swell into a clavate or fusoid form, and the wall at the point of contact is resorbed for some distance, thus forming a broad communicating area where the cytoplasm of the two merges. During the enlargement one of the gametes frequently becomes larger than the other. The cytoplasm is very dense and fills the distal portion of the progametes, while in the proximal direction the cytoplasm is less abundant and lies chiefly in a peripheral zone next the wall. A cross wall is now laid down in each progamete a short distance behind the broad communicating pore, separating the gametangia from the stalks or suspensors.

Formation of the resting spore or resting zygote.—At the time of conjugation and resorption of the contact wall the conjugating gametangia resembles the same stage of conjugation in *Eremascus fertilis*. The zygote is not formed by the enlargement of the copulating gametangia as in the majority of the Mucorales, but the young zygote begins to grow at once in an apical direction. Sometimes the origin

of the young zygote is symmetrical in relation to the two gametangia, that is, the tip of each gametange shares equally in the growth. In other cases the new growth arises more from one than the other, usually from the larger one where they are unequal in size. More rarely does the new growth arise entirely from the larger gametange, but the communication is so broad that both gametangia remain in direct communication with the contents of the new growth. This new growth, or progressive zygote, enlarges to a broadly elliptical structure, 35-60 x 30-45 μ . It stands on the two supporting gametangia, and the protoplasm of the gametangia and new zygote is continuous. When the new zygote has reached its full size the protoplasm in the gametangia withdraws and merges with that in the zygote. A new wall is now laid down inside of the primary zygote membrane. At first thin, it increases in thickness, forming a white, stratified, cartilaginous layer around the protoplasm, thus cutting off communication with the empty gametangia. The two stalks which support the mature resting zygote are not simply the suspensors, but the empty gametangia plus the suspensors. The resting zygote is nearly filled with very minute rounded or slightly irregular hyaline bodies, which appear to be fat bodies, since they stain red with Sudan III. There is a rounded clear space in the center, *i. e.*, in the middle of the long axis, but in some zygotes it lies on one side next the wall. In fixed and stained material the center of this vacuole (?) appears to be occupied with a coarsely granular body or mass of minute bodies.

Cytology of conjugation and zygote formation.—The number of nuclei in the gametangia is variable, probably from five to ten or more in each. No evidence of nuclear division in the progametes or gametangia has been observed, and no evidence has been seen of a selection of gamete nuclei. Nor does it appear that there is any nuclear degeneration in the progametes before the formation in the cross wall which differentiates the gametangia. Following this stage nuclei in the suspensors may degenerate. The cytoplasm in the gametangia is so dense and stains so deeply that it is sometimes difficult to differentiate the nuclei. When the stain is not too deep the nuclei are clearly seen. They are considerably larger than the vegetative nuclei, the increase being due to growth. There is a nuclear membrane, a clear court in which are sometimes visible a few delicate threads, perhaps portions of the linen or chromatin. There is a prominent central, spherical, nucleolus or karyosome, which stains red with Flemming's triple stain, dark with iron haematoxylin. The nuclei are disposed in the cytoplasm of the gametangia without order. They gradually migrate into the new zygote, as it is formed, along with the cytoplasm.

In the young zygote the cytoplasm is at first dense and rather

homogeneous as in the gametangia. But as the new zygote enlarges the cytoplasm becomes coarsely reticulate. The strands are coarse and with an irregular outline. They radiate irregularly from the center to the periphery and anastomose by irregular branches, forming a large meshed network the strands of which are coarser in the central region, thinner toward the periphery. During the early stages of development of the young zygote the nuclei appear to have a general distribution, but have not been observed near the periphery. As the zygote approaches its full size the nuclei occupy the more central region, being distributed from the center to a zone half way, or a little more, to the periphery. Sometimes the centralization is more marked. At this stage there appears to be a differentiation of the cytoplasm, or rather, the appearance of a clear homogeneous plasma occupying the nuclear region and in which the nuclei die. When the nuclei are strongly centralized, the homogeneous plasma appears to form a single large central area. When they are more widely distributed, the homogeneous plasma is separated into several areas, each area containing several nuclei. During all this period the coarsely reticulate cytoplasm occupies the entire zygote.

A provisional suggestion as to the function of this homogeneous plasma is that it serves as a medium for the freer movement of the nuclei than can take place in the coarsely reticulated cytoplasm; or the homogeneous plasma may actually serve to move the nuclei to a certain extent, possibly bringing them into closer proximity in the center and later carrying them into the peripheral zone. In this central region the nuclei are generally in pairs and the two nuclei of a pair appear to fuse. This fusion of paired nuclei in the zygote corresponds with the fusion of paired nuclei in certain of the Mucorales as described by Gruber (1901) in *Sporodinia grandis*, Dangeard (1906) in *Rhizopus nigricans*, and Moreau (1911-1913) in *Rhizopus nigricans* and species of *Zygorhyncus*. The fusion of the nuclei of a pair is suggested by the fact that they are found close together, sometimes the nuclear membranes in contact, again an elongated nucleus (? fusion) with one membrane and this constricted between the two nucleoli, and further two nucleoli surrounded by one membrane which is not constricted. Of course these relations might be the result of nuclear division, but no figures appear at this stage which suggest a division of the nuclei.

In a later stage of development the coarse reticulum of the cytoplasm disappears. The cytoplasm becomes more homogeneous. The nuclei appear to occupy a zone about half way between the center and periphery. Figures are present which suggest a division of the nuclei at this stage, for the nuclei are often two to three times

longer than broad, presenting the appearance of rods, deeply stained, lying in a peripheral zone of the cytoplasm.

The material on which this cytological study was made was not as well fixed as it might have been. The peridium of the fruit bodies is very dense and tough, not permitting the rapid penetration of the fixing fluids. Then in the later stages of zygote formation the thick cartilaginous wall of the resting zygote very likely offers great resistance to the penetration of the fluids. An attempt will be made to collect more material during the present season, when the fruit bodies will be cut open before placing them in the fixing solutions, and also it is hoped that younger stages of development may be secured.

Up to the present time no one has succeeded in germinating the resting zygotes of any species of *Endogone*. Link (1809), Fischer (1897, p. 121, 124) and Bucholtz (1912) have described sporulation in the "resting spores" (azygotes) of *Endogone pisiformis*, a parthenogenetic species. In this species the wall of the resting spore is only slightly thickened. According to Fischer and Bucholtz the content of the resting spore is gradually divided into angular areas which round up and form a number of large elliptical spores inside the wall of the resting spore (or ? sporangium). Their study was not made on living material, but on specimens preserved for several years. There was no intersporal substance or epiplasm.

I have made several attempts to germinate the resting zygotes of *Endogone sphagnophila*, but thus far without success. The first attempts were made in December, 1916, with material kept on sphagnum under cover of a bell jar in the shade on the north side of a building. The cultures were made by tearing out mats of mycelium with the resting zygotes in a thin layer of water on glass slides which were kept in moist chambers. The cultures were examined day by day for a period of two weeks. These cultures were then allowed to remain out of doors on a window ledge with a southern exposure until the middle of January, 1917, when they were brought inside and again examined daily for a period of a week. During the latter part of March and early in April, 1917, fresh cultures were started from the same source, *i. e.*, from fruit bodies kept on sphagnum out of doors, where they were subject to freezing and thaw. Thus far (Apr. 17, 1917) there has been no evidence of germination, although the great majority of the zygotes appear to be alive and in good condition. A few of the zygotes, however, appear to be dead. In many of these the content is divided into irregular bodies. Others are filled with elliptical or globose bodies, in some instances with intersporal substance. These bodies, some of them, at least appear to be spores,

but I am strongly inclined to believe that they are spores of some parasite.

RELATIONSHIPS OF ENDOGONE

The coenocytic mycelium with no true cross walls, except those which separate reproductive organs from the mycelium, with the formation of resting zygotes soon after the conjugation of gametangia, are phycomycete characters. The method of conjugation of equal or slightly unequal gametangia indicates a closer relationship with the Zygomycetes than with the Oomycetes, although in *Endogone lactiflua* the content of the small gametange, or antherid, flows into the larger one which is comparable to the oogone. In *Zygorhyncus* the two gametangia are very unequal in size, but the zygote is formed within and includes all of both gametangia, a strictly zygomycete feature. In *Conidiobolus* the gametangia are of very unequal size, and are worthy of being distinguished as antherid and oogone. The content of the antherid passes into the oogone within which the zygote is formed. In *Basidiobolus*² also there is a supplying gametange and a receiving one, but other features of these genera, especially conidial formation, show such a close relation to *Empusa* that they are generally regarded as members of the zygomycetes with a leaning toward the oomycetous type of fructification, but not having reached the characteristic feature of egg differentiation in the oogone. *Endogone* departs from the usual type of zygote formation present in the zygomycetes. The zygote is an outgrowth from the conjugation point of the gametangia (*E. sphagnophila*), or from the larger gametange (*E. lactiflua*, rarely in *E. sphagnophila*). A similar situation, however, is present in *Piptocephalis freseniana* and in *Empusa* (*Entomophthora*) *fresenii*, where the zygote is an outgrowth of the point of conjugation much as in *Endogone sphagnophila*. In *Empusa occidentalis*, *echinospora*, *sepulchralis*, etc., the zygote is an outgrowth of one of the gametangia, a situation similar to that in *Endogone lactiflua*, or sometimes it arises from the point of conjugation in these species of *Empusa*.

In the selection of a single sex nucleus in each gametange, *E. lactiflua* presents a situation similar to that in the Peronosporales, though there is no differentiation of ooplasm and periplasm in the oogone of *Endogone lactiflua*, as there is in the Peronosporales. In *E. sphagnophila* there is no sex selection of nuclei in the gametangia so far as we can determine, for all of the nuclei without manifesting any differentiation pass with the cytoplasm into the new outgrowth where the zygote is formed. The nuclear behavior in the zygote has not yet been made entirely clear. The present evidence suggests that

² *Basidiobolus* by some is placed in a distinct family.

there is first a nuclear fusion in pairs, perhaps some of the nuclei degenerating. If this is confirmed the situation in *E. sphagnophila* agrees in this respect with that in the Mucorales. It appears also that later, when the nuclei lie in a peripheral zone, they undergo at least one division. At the present stage of the investigation the possibility is not excluded that fusion of nuclear pairs does not occur. It is also possible that after the division of the nuclei in the peripheral zone of the zygote all but two may degenerate, the two selected ones later uniting to form the fusion nucleus. This would bring *E. sphagnophila* more nearly in line with the process in *E. lactiflua* as described by Bucholtz, the selection of the sex nuclei being postponed to a late period in *E. sphagnophila*. I do not think, however, that this is the case, but am inclined rather to believe that there is multinuclear fusion in pairs,³ similar to that which takes place in the Mucorales as described by Gruber (1901) in *Sporodinia*, by Dangeard (1906) in *Sporodinia*, and by Moreau (1911-1913) in *Rhizopus*, *Zygorhynchus* and *Sporodinia*. That in certain species of *Endogone* there is fusion of but one pair of sex nuclei in the zygote, while in other species there may be fusion of several pairs of sex nuclei, is not incomprehensible in view of the nuclear process in fertilization in *Cystopus* (See Stevens 1899, 1901), where in *C. bliti* and *portulacae* there are fusions of many pairs of sex nuclei in the egg, while in other species there is fusion of a single pair of sex nuclei.

There is another feature in *E. lactiflua* which is paralleled in certain of the Zygomycetes. This is the hyphal envelope which encloses each zygote. Crude tendencies to such an envelope are present in *Phycomyces* and *Absidia* of the Mucorales and in *Empusa rhizospora* of the Entomophthorales (Thaxter, 1888), while in *Mortierella* there is a well-developed envelope. In no other species of *Endogone*, however, is such an envelope around each zygote known, not even a rudimentary one. In this respect *E. lactiflua* represents a more advanced stage of evolution, which is manifested also in the origin of the resting zygote as a distinct outgrowth of the larger gametange. This species may possibly represent the type of a distinct genus, so widely does it depart in these two respects from all the other known species.

There is another feature, however, in which *Endogone* departs widely from any other known phycomycete. The mycelium and numerous zygotes ("resting" spores or "sporangia" in the parthenogenetic species) are united into a compact and distinct fruit body, or

³ According to Leger (1896) in *Sporodinia grandis*, and according to Miss McCormick (1912) in *Rhizopus nigricans*, all nuclei but two degenerate in the zygote, but this has not been confirmed.

zygocarp with a definite and well-developed peridium. This represents a distinct progression in development over all other phycomycetes, a cephalization of zygotes into a complex fruit body.

The heterogamous character of the gametangia of *Endogone lactiflua* and the selection of a single gamete nucleus in each are oomycete features. But the lack of differentiation in the cytoplasm in the oogone, or gametangia, is a zygomycete feature. For these reasons Bucholtz⁴ interprets *Endogone* as occupying an intermediate position between the zygomycetes and Oomycetes, but constituting a distinct group, the Endogoneae.⁵ He probably regards this intermediate position as simply taxonomic, not phylogenetic.

RELATION OF ENDOGONE TO THE ASCOMYCETES

Endogone has been shifted in all the three great divisions of the fungi. It was first placed in the Basidiomycetes near *Rhizopogon* by Link (1809) who was followed by Fries (Syst. Myc. 2, 295, 1822). For a long time it has remained in the Ascomycetes, being placed in the Tuberaceae by Vittadini (1831), by Tulasne (1857), by Saccardo (Syll. Fung. 8, 905, 1889). Schroeter (1889) placed *Endogone* with some uncertainty in the Order Protomycetes, the highest order of the Phycomycetes. He was followed by Saccardo (Syll. Fung. 14, 829, 1899), and it is significant that the genus *Protomyces* has by many students been placed in the Phycomycetes. In 1897 Schroeter, while still retaining *Endogone* in the Protomycetaceae, transferred the group to the Hemiascineae.

Until we know the morphological and cytological phenomena in connection with the germination of the resting zygotes of *Endogone* we cannot say with any degree of precision what relation it bears to the Ascomycetes, nor how near that relation is. It appears quite probable that *Endogone* does bear an interesting relation to the Protoascomycetes. If the resting zygotes germinate fructificatively with free cell sporulation, somewhat as occurs in *Dipodascus* or *Protomyces*, its relation to the Protoascomycetes would be very clear. The question would then arise whether with its coenocytic mycelium it should be placed on a level with *Dipodascus* or just below it, representing the highest level of the Phycomycetes. Even if the germination phenomena should prove to be of the phycomycete type, *Endo-*

⁴ He describes two large nuclei in the zygote of *E. ludwigii*, a sexual species.

⁵ The genus has been considered for a long time by a number of students to represent a distinct family. Fries (Summa Veg. Scand. 1849) proposed the family Endogonaceae and in view of Bucholtz's studies it is interesting to note that Schroeter in 1889 placed it along with *Protomyces* as the highest member of the Phycomycetes.

gone would still represent the nearest approach of the phycomycete type to the ascomycete type. The method of conjugation of the gametangia, and the growth of the zygote, in *Endogone sphagnophila*, is surprisingly like that in *Eremascus fertilis* and in *Dipodascus*. Even without the knowledge of germination of the resting zygotes in *Endogone*, the genus seems to offer more of the characteristics of a prototype of the Protoascomycetes (and perhaps also of the Uredinales) than any other known phycomycete.⁶ *Endogone* presents additional strong evidence of the phycomycete ancestry of the Ascomycetes.

All of the evidence considered, it appears to point more strongly to the zygomycete alliance as the source of the primitive ascomycete stock, rather than to the oomycete alliance. In the oomycetes the sexual organs and the processes of fertilization have become very highly specialized. The sexual organs are highly differentiated; one or more distinct eggs are differentiated in the oogone, in many cases the protoplasm being differentiated into ooplasm and periplasm; while a special fertilization tube from the antherid penetrates the oogone, or in a rare and specialized case a motile sperm enters the oogone through a pore (*Monoblepharis*).

In the zygomycetes the sexual organs have retained a simple and generalized condition. Copulation is by pore formation with merging of the content of the gametangia. In most cases the gametangia are equal and the zygotes mature *in situ*, within and comprising all of both gametangia. Progression in the zygomycetes, however, is manifested in five directions.

1. In a tendency to differentiation in size of the gametes.
2. A tendency to differentiation of the gametangia in function, the larger one becoming the receiving gametange, the oogone, but without differentiation of content into egg and periplasm; the other serving as the supplying gametange, antherid (*Conidiobolus utriculosus*, *Basidiobolus ranarum*, *Dispira americana* Thaxter, 1895, *Endogone lactiflua*, etc.).
3. The progressive tendency shown in the germination, or outgrowth, of the young zygote immediately after fusion from the copulation point, or from one of the gametangia, the ripe zygote being formed outside the gametangia, not within them according to the typical process. The tendencies in this direction appear at different levels in the zygomycete alliance. Examples are *Piptocephalis freseniana*,

⁶ The following forms among the phycomycetes have been suggested as prototypes of the ascomycetes. The Peronosporales by de Bary (1881) for the usual ascomycete type, *Piptocephalis* for the *Eremascus* type; *Myzocyttium* and *Protascus* by Dangeard (1903-06, 1910), *Cystopus* by Lotsy (1907) and *Monoblepharis* by Nienburg (1914).

Empusa (*Entomophthora*) *fresenii*, *Empusa rhizospora*, *sepulchralis*, etc., *Endogone sphagnophila* and *lactiflua*.

4. Progression in the direction of selection of sex nuclei. In *Endogone lactiflua* one sex nucleus is selected from among all the potential ones in each gamete. This illustrates how the situation in *Dipodascus*, *Eremascus fertilis* and in *Endomyces* has arisen. This situation is presaged in some of the lower zygomycetes in the degeneration of some of the gamete nuclei in *Rhizopus*, *Sporodinia* and *Zygorhynchus*, if we may accept the account by Moreau (1911, 1913). In *Endogone sphagnophila* there are many potential and many functional nuclei in the gametangia and these are carried on into the young germinating, or progressive zygote. This type illustrates a situation which has been retained in those ascomycetes with multi-nucleate gametangia as in *Monascus*, the Gymnoascaceae, *Ascodesmis*, *Pyronema*, etc.

5. The postponement or moving forward of the moment of nuclear fusion from the gametangia to the new outgrowth, or progressive zygote. The examples are the same as those given in paragraph 3. In the zygomycete alliance *Endogone lactiflua* represents the most progressive stage in these directions of any known species, unless *Dipodascus* should be regarded as a phycomycete. The sex pair of nuclei is organized by the migration of the antheridial nucleus into the oogone. The pair then migrates into the new outgrowth where the sex nuclei lie side by side in the resting zygote, or fuse, in one variety. As Bucholtz (1912) points out there is wanting here only the conjugate division of the nuclear pair to parallel the situation in the ascogenous hyphae of the true ascomycetes.

From the situation reached by progression in these directions, by members of the zygomycete alliance, there is but a small gap over which to bridge in reaching the protoascomycetes. The principal steps may be indicated as follows:

1. Free cell sporulation of the progressive zygote of *Endogone*. This alone would place this zygote in the category of a generalized ascus, and *Endogone* would become a fit member of the protoascomycetes. Intersporal substance present in the sporangium of some phycomycetes during sporulation may possibly presage typical free cell sporulation. Other steps toward the true ascomycetes are indicated in the following.

2. The omission of a period of rest by the progressive zygote and the immediate free cell sporulation of the same. This step alone would reach the level of *Dipodascus*, *Eremascus*, *Endomyces magnusii*, etc.

3. Vegetative growth of the zygote and postponement of free cell

sporulation until the second or third cell of the new growth, would carry the zygote to the level of that in *Sphaerotheca*, in the true ascomycetes.

4. Vegetative growth of the zygote with splitting of the same by branching, thus multiplying the terminal branches of the zygote in which free cell sporulation takes place, carries the zygote to the level of *Pyronema*, *Monascus*, etc., in the true ascomycetes.

5. Organization of a fruit body by formation of a peridium of the interwoven terminal branches of the mycelium. This is already realized in the complex zygo carp of *Endogone*, the peridium being on a level with that in the Gymnoascaceae.

6. Organization of a peridium by enveloping hyphal branches of the type in *Monascus*, the *Erysiphaceae*, *Aspergillus*, etc. This feature is already realized in the simple zygo carp of *Endogone lactiflua*.

RELATION OF THE ZYGOTES AND AZYGOTES IN ENDOGONE

Several species of *Endogone* are parthenogenetic (*E. macrocarpa*, *microcarpa*, *pisiformis*, etc.), yet the "resting spores" are similar to the resting zygotes of *E. sphagnophila*, *ludwigii*, etc., in all other respects so far as known at present, with the exception of the number of nuclei in the resting stage. According to Bucholtz the zygotes of the sexual species, *E. lactiflua* and *E. ludwigii*, are binucleate in the resting stage, while the azygotes of *E. pisiformis*, *macrocarpa*, *microcarpa*, etc., are multinucleate. However, the zygotes of the sexual species *E. sphagnophila*, are probably multinucleate in the resting stage. It is very probable that at the time of germination the zygotes of *E. lactiflua* and *E. ludwigii* become multinucleate by successive divisions of the fusion nucleus. It is, therefore, very likely that the phenomena of germination, whatever the type of germination is for *Endogone*, is the same in the sexual and parthenogenetic species. It is quite evident that the branch in which the azygote is formed is the morphological equivalent of a gametange, just as the sporangia and gametangia of *Monoblepharis*, *Saprolegnia*, etc., are morphological equivalents. If there were sex differentiation among the nuclei of the zygotes followed by fusion, then the azygotes would be strictly homologous with the zygotes, in fact they would be zygotes. Bucholtz (1912) regards the simple zygo carp of *Endogone lactiflua* as homologous with the germ sporangium (carposporangium) of the Mucorales and Peronosporales. In a certain degree this is true, but it is also homologous with the zygote of the Mucorales and Peronosporales. In the Mucorales the germ sporangium is external to the zygote while in the Peronosporales it is internal. The germ sporangium of *Endogone* is not known, it may be internal or external to the zygote. The zygote

of *Endogone* presages the beginning of a new structure, not more so than does the zygote of *Piptocephalis* and of certain species of *Empusa*, etc., but it is still homologous with the zygote of the other phycomycetes.

In the Mucorales, aside from the meiotic divisions of the fusion nuclei, the process of sporulation in the germ sporangium (sporangium formed on germination of the zygote) is the same as that in the "asexual" sporangium. The germ sporangium and the asexual sporangium are morphological equivalents. The germ sporangium is not a new morphological structure, though the zygote and early stages of its germination presage the origin of a new morphological structure. Historical experience turns it quickly back into the well-worn trail. The very simple primordium of the new structure does not mark out a new path until the accumulation of new experiences, together with environment, provide the threshold for progress to the new structure.

If nuclear fusion does not occur in the azygotes of *Endogone* then the chromosome history, so far as we know, would run from generation to generation without change. The two situations may be represented thus:

Sexual species of <i>Endogone</i> .	{	IX → IX → IX → IX	↗ ^{2x} ↘	IX → IX etc.
	{	Mycelium and gametangia	zygote	spores, mycelium.
Parthenogenetic species of <i>Endogone</i> .	{	IX → IX → IX → IX	→ IX →	IX → IX etc.
	{	Mycelium and gametangium	azygote	spores, mycelium.

As sporulating organs the zygote and azygote (or germ sporangium of the same) of *Endogone* are homologous structures. The true asexual sporangium has been eliminated. Likewise, in the protoascomycetes, where the threshold from the phycomycetes has been crossed, the zygote ("germ sporangium," a generalized ascus) of *Dipodascus*, and the azygote ("germ sporangium," "generalized ascus") of *Ascoidea*, as sporulating organs are homologous structures. *Ascoidea* is probably parthenogenetic, the "generalized ascus" being a transformed gametangium. Free cell sporulation occurs in both genera. This interpretation of the relation of the free cell sporulating organs of *Dipodascus* and *Ascoidea* is supported by the situation in *Eremascus fertilis* and *Endomyces magnusii* where the ascus is in some cases of sexual origin, in others of parthenogenetic origin, a single gametange becoming the ascus. *Endogone*, with several sexual species having sexually produced sporulating organs (zygotes), and other species with parthenogenetically produced sporulating organs (azygotes), is interesting in that it illustrates the homology of these structures, and suggests how the parthenogenetic sporulating organs (generalized asci) of *Ascoidea*, *Protomyces*, etc., may have arisen. It is interesting

to note that the forms with parthenogenetic asci, generalized or not, were not endowed with potentialities of progress, nor with the evolution of any important lines. They have made practically little progress and are few in number. On the other hand, those forms with sexually produced asci, even though the sexuality be of a very greatly reduced type, were endowed with great potentialities as evidenced by the large group of Euscomycetes with high specialization, and great divergence of character in several different series.

TECHNICAL DESCRIPTION

*Endogone sphagnophila*⁷ n. sp. *Plants* (zygocarps), 2–4 mm. in diameter, pulvinate, reniform, plain or subcerebriform with two to three low lobes or convolutions, orange yellow when mature, *Peridium* white, submembranous, tough, of interwoven coenocytic, profusely branched hyphae, minutely tomentose or downy from free, terminal, very slender branchlets, 4–5 μ at base, 1 μ or less at the tips. *Mycelium* of the zygocarp 10–15 μ in diameter, coenocytic, stout, non-septate, branched in a dichotomous, or trichotomous manner, or several branches springing from enlargements, radial, the terminal branches interlacing to form the peridium. *Progametes* equal. *Gametangia* separated from mycelium by a cross wall, equal or usually slightly unequal, multinucleate. “*Resting spores*” (zygotes) formed as an outgrowth from the conjugation point of the gametangia, or more rarely from the larger one, one resting spore formed in the primary zygote membrane from each pair of gametangia, elliptical to oval, rarely irregular, with orange yellow content and a thick, white, stratified cartilaginous wall, 35–60 x 30–45 μ , germination unknown.

On sphagnum in a ravine in region of Seventh Lake, Fulton Chain, Adirondack Mts., New York, July 1916, Aug. 1917; and in Cranesville moor, Western Maryland, Sept. 1917 (rarely on other mosses or on dead twigs). Thaxter (Bot. Gaz. 24: 12, 1897) reports it on sphagnum in Maine.

Latin diagnosis. Pulvinatis, reniformibus, subcerebriformibus, aureis, 2–4 mm.; peridiis albidis submembraneis, lentis, floccosis intertextis, tomentosulis; myceliis glebae 12–15 μ , radiatis, dichotomis vel trichotonis vel plurichotomis, ramulis terminalibus peridium formantibus; sporis orientibus ab gametangiis copulantibus, ellipsoideis vel ovalibus, maximis, 35–60 x 30–45 μ , plasmate aureo. Hab. on sphagnum, Adirondack Mts., New York, and in Maine and Maryland.

LITERATURE CITED

Atkinson, Geo. F. Phylogeny and Relationships in the Ascomycetes. Ann. Mo. Bot. Garden 2: 315–376. Figs. 1–9. 1914.

⁷ Closely related to *E. ludwigii* Bucholtz, but this species is subterranean with a prominent germ pore in the thick wall of the zygote and the nuclei are reduced to two which fuse at maturity.

- de Bary, A. Untersuchungen über die Peronosporeen und Saprolegnieen und die Grundlagen eines natürlichen Systems der Pilze. In de Bary und Woronin, Beitr. z. Morph. u. Physiol. d. Pilze 4: 1-145. Pls. 1-6. 1881.
- Brefeld, O. Die Hemiasci und die Ascomyceten. Untersuch. Gesammtg. Myk. 9: 1-156. Pls. 1-3B. 1891.
- Ascomyceten II. Ibid. 10: 157-378. Pls. 4-13. 1891.
- Bucholtz, F. Beiträge zur Kenntnis der Gattung Endogone Link. Beihefte Bot. Centr. 29: 147-225. Pls. 3-10. 1912.
- Dangeard, P. A. Recherches sur le développement du périthèce chez les Ascomycetes. Première partie. Les ancêtres des champignon supérieurs. Le Botaniste 9: 157-303. Pls. 1-18. 1903-1906.
- La fécondation nucléaire chez les Mucorinées. C. R. Acad. Sci. Paris. 1906.
- Recherches sur le développement du périthèce chez les Ascomycetes. Le Botaniste 10: 1-385. Pls. 1-91. 1907.
- Fischer, E. Tuberaceen und Hemiasceen, in Rab. Krypt. Fl. 2nd Auf. Die Pilze 5th Abt. 1-151. 1897.
- Pilze in Handwörterbuch der Naturw. 7: 880-929. 1912.
- Gruber, E. Ueber das Verhalten der Zellkerne in den Zygosporien von Sporodinia grandis. Ber. deuts. bot. Ges. 19: 51-55. Pl. 2. 1901.
- Léger, M. Recherches sur la structure des Mucorinées. Paris, Poitiers. 1896.
- Link. O. B. S. Pl. nat. 3: 33. 1809.
- Lotsy, J. P. Vorträge über botanische Stammesgeschichte 1: I-IV and 1-828. F. 1-430. 1907.
- McCormick, F. L. A. Development of the Zygosporium of Rhizopus nigricans. Bot. Gaz. 53: 67-68. 1912.
- Moreau, F. Deuxième note sur les Mucorinées. Fusions de noyaux et dégénérescence nucléaire dans la zygosporie. Soc. Myc. France Bull. 27: 334-341. 1911.
- Moreau, F. Sur la reproduction sexuée de Zygorhynchus moelleri Vuill. C. R. Soc. Biol. 73: 452-455. 1911.
- Les phénomènes intimes de la reproduction sexuelle chez quelques Mucorinées hétérogames. Soc. Bot. France Bull. 58: 618-623. 1911.
- Une nouvelle Mucorinée hétérogame Zygorhynchus dangeardi sp. nov. Soc. Bot. France Bull. 59: LXVII-LXX. 1912.
- Recherches sur la reproduction des Mucorinées et quelques autres thallophytes. Thèses présentées à la Fac. Sci. Univ. Paris 1-136. Pls. 1-14. 1913.
- Les karyogamies multiples de la zygosporie de Rhizopus nigricans. Soc. Bot. France Bull. 60: 121-123. 1913.
- Schroeter, J. Cohn's Krypt. Fl. Schlesien. 3¹: Pilze. Protomycetes. 257-260. 1886.
- Hemiascineae in Engler & Prantl. Pflanzf. 1¹: 143-149. 1894.
- Stevens, F. L. The compound oosphere of Albugo bliti. Bot. Gaz. 28: 149-176, 225-245. Pls. 11-15. 1899.
- Gametogenesis and fertilization in Albugo. Bot. Gaz. 32: 77-98, 157-169, 238-261. Pls. 1-4. F. 1. 1901.
- Thaxter, R. New or peculiar American Zygomycetes. I. Dispora. Bot. Gaz. 20: 513-518. Pls. 34. 1895.
- Tulasne, L. R. et Ch. Fungi Hypogaei. Pp. I-XIX, 1-222. Pls. 1-21. 1851.
- Vittadini. Monographie Tuberacées. 1831.



Atkinson, George Francis. 1917. "The Genus *Endogone*." *Memoirs* 1, 1–17.

View This Item Online: <https://www.biodiversitylibrary.org/item/49841>

Permalink: <https://www.biodiversitylibrary.org/partpdf/326237>

Holding Institution

New York Botanical Garden, LuEsther T. Mertz Library

Sponsored by

The LuEsther T Mertz Library, the New York Botanical Garden

Copyright & Reuse

Copyright Status: Public domain. The BHL considers that this work is no longer under copyright protection.

Rights: <https://www.biodiversitylibrary.org/permissions/>

This document was created from content at the **Biodiversity Heritage Library**, the world's largest open access digital library for biodiversity literature and archives. Visit BHL at <https://www.biodiversitylibrary.org>.