

PRINCIPLES OF PLANT TAXONOMY. III.*

JOHN H. SCHAFFNER

Important evidences of relationships are obtained from a study of the life cycles of plants. A knowledge of life cycles is of special importance in delimiting classes and the higher subkingdoms. In fact, the whole phyletic scheme of relationships depends to a very decided extent on the theoretical views that are held as to the origin and evolution of the numerous types of life cycles present in the plant kingdom. In general, all types of life cycles fall into two divisions, the non-sexual and the sexual.

NONSEXUAL LIFE CYCLES.

In the lowest forms of unicellular plants the cycle is simply: 1. Increase in size of cell; 2. division of cell; 3. separation of daughter cells. These three primary processes are a part of all normal life cycles, whether sexual or nonsexual, from the lowest to the highest.

The first modification of this primitive cycle is a delay in the separation of the cells after division, giving rise to all sorts of colonial forms—linear, superficial, and solid aggregates of similar or undifferentiated cells. The cycle is then: 1. Increase in size; 2. division; 3. delayed separation (an intimate association of cells for a greater or less length of time); 4. separation.

The third type of nonsexual cycle is present in nonsexual, differentiated plants in which during the period of association after division, the cells are differentiated from each other, giving rise to differentiated, multicellular individuals. Among the blue-green algae, *Rivularia* represents such a plant with a considerable diversity of cells. The life cycle then becomes: 1. Increase in size of cells; 2. division; 3. indefinite association or hanging together of cells; 4. differentiation of cells; 5. separation of reproductive cells. These three types of cycles are also parts of the cycles of sexual plants which add two very profound stages—the fusion of gametes and the reduction division.

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In the slime bacteria (Myxobacteriales) the life cycle is characterized by the association of the cell units for a long time in a pseudoplasmodium. The cells are, however, not intimately connected as in a colony or multicellular individual and at the end of the life cycle the entire mass of bacteria in the pseudoplasmodium usually builds up a complicated elevated structure or cyst which externally resembles the fructifications of slime molds and of the higher fungi.

LIFE CYCLES OF SEXUAL PLANTS.

THE NEMATOPHYTA.

The development of sex in the organic kingdom represents one of the most remarkable or perhaps it might properly be said the most remarkable event in the whole history of evolution. At a certain stage or period, cells develop primary sexual states and react toward each other in such a way that they are attracted and fuse. We say the one is in the female state or (+) and the other in the male state or (—). This union of cells is just as remarkable, and so far an unexplainable process, as that other more primitive process, cell division. The lowest gametes are isogamous and these lead up to the higher, heterogamous condition. The union of the gametes and their nuclei, however, does not involve the union of the chromosomes, which remain as distinct individualities and are thus doubled in the zygote. Fertilization which properly means conjugation, therefore, requires an "undoing" process or segregation process to separate the chromosomes into two complements with the original numbers. The reduction division is a necessary complement of fertilization. At reduction, the individual pairs of chromosomes or synaptic mates are sexualized and conjugate in the nucleus and are then segregated by the law of chance into the two resulting daughter nuclei. Conjugation or fertilization takes place between the sex cells which are normally haploid and have the primary sexual states. The reduction division normally takes place, in the various groups of plants, at three definite points giving rise to three general types of life cycles, the simple haploid sexual cycle, the simple diploid sexual cycle, and the alternation of generations cycle. In the diagram below, the main types of life cycles and some of their modifications are represented.

The life cycle of the unicellular sexual plants, to whatever group they may belong, is a modification of the unicellular nonsexual cycle thru the development of sexual states at certain periods. Sphaerella is a typical example: Single haploid cell; increase in size; division; isogametes; discharge of gametes; conjugation; resting diploid zygote; germination of zygote with a reduction division giving rise to four reduction spores; development of the spore to a normal unicellular individual

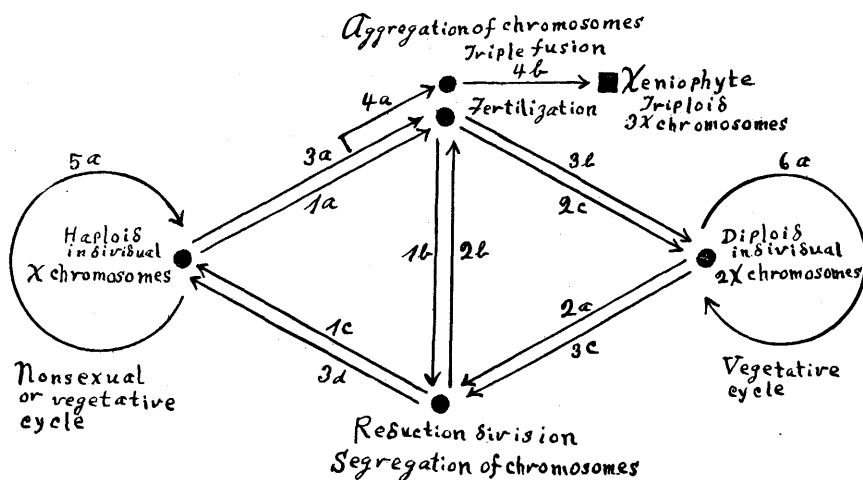


Fig. 1. Life cycles of organisms, generalized diagram. From the winter's "Laboratory Outlines for General Botany." Fifth Edition.

1. Simple sexual cycle, the individual being haploid. Haploid gametophyte—fertilization—reduction (1a-1b-1c).
2. Simple sexual cycle, the individual being diploid. Diploid gametophyte—reduction—fertilization (2a-2b-2c).
3. Life cycle with antithetic alternation of generations. Haploid gametophyte—fertilization—diploid sporophyte—reduction (3a-3b-3c-3d).
4. Life cycle with antithetic alternation of generations and xenophyte. Haploid gametophyte—fertilization and triple fusion—diploid sporophyte and triploid xenophyte—reduction (3a and 4a—3b and 4b—3c—3d).
5. Haploid vegetative and non-sexual spore propagation (5a). This cycle also represents the primitive nonsexual cycle.
6. Diploid vegetative and nonsexual spore propagation (6a).

which may divide vegetatively for some time. (See Fig. 1. 1a - 1b - 1c.) In the colonial forms and those with differentiated multicellular body, the life cycle is the same except that in the vegetative period the cells hold together.

All three types of general life cycles found in the Nematophyta probably originated directly from the unicellular condi-

tion and consisted of a two-phased condition represented by a haploid and a diploid cell as in *Sphaerella*. In the higher development of the simple, haploid sexual cycle, the main evolution was in the multicellular development of the vegetative, neutral phase. In *Coleochaete* there was an addition of vegetative divisions before spore-formation following the reduction division in the zygote. This multiplication of divisions after reduction is known in other plants and in certain animals. It does not represent a true alternation of generations. In *Coleochaete* the individual is haploid, in *Fucus* it is diploid. In both cases the multiplication of cells after the meiotic phase is to be regarded as a vegetative intercalation.

If a vegetative multicellular phase is developed between fertilization and reduction, a simple, diploid, sexual cycle becomes established as in animals, Charophyta, and Fucaceae.

If the original haploid unicellular plant evolves a multicellular haploid body and at the same time intercalates a vegetative phase between fertilization and reduction thru a delay in the time of sexualization of the synaptic mates and if this intercalated phase results in a diploid multicellular body, the result will be an antithetic alternation of generations. This life cycle is present in some of the red and brown algae and especially in the typical antithetic cycle of all the meta-thallophyta. The term alternation of generations is often used in a very loose way to designate life cycles of very diverse types. Animals, Rockweeds, and Spirogyras, for example, do not have an alternation of generations. With the evolution of the sexual state the life cycle established depends then on the stage at which sexualization of cells (gametes) takes place, the time at which sexualization of the synaptic chromosomes (reduction) takes place, and the point or points of the life cycle at which vegetative growth and differentiation take place. As stated above, there are three primary types each with its particular stage at which reduction takes place. The three sexual cycles can then be modified in various ways by changes or modifications of the time of sex determination, loss or partial loss of primary sexual states at given points in the cycle and intercallations of vegetative divisions at various points.

MYXOMYCETAE. The Myxomycetes must be regarded as plants which were highly differentiated in certain functional processes while still in a rather primitive morphological condition. Their nuclei are well organized. They are not to be

regarded, as has commonly been the case, as primitive plants. They are on a much higher level than the Schizophyta. The life cycle in the typical forms seems to be as follows: Vegetative haploid plasmodium; beginning of sporangium stage with conjugation of pairs of nuclei; later stage of sporangium with diploid nuclei; reduction division resulting in the production of the nonsexual haploid resting spores; liberation of zoospores from the resting spores; amoeboid protoplasts; coalescence of amoeboid protoplasts to form the plasmodium.

ZYGOPYTA. In the conjugates like Spirogyra there is a simple haploid sexual cycle: Nonsexual or reduction cell; development (germination proper) of the haploid gametophyte; gametes developed with slight modification inside of the cells; fertilization thru conjugation tube; diploid zygospore; resting condition; reduction division in the zygote during germination; survival of one of the four reduction nuclei in the zygospore wall which becomes the initial cell of the new generation. There is no alternation of generations and no evidence that the group ever possessed such a condition.

GONIDIOPHYTA. So far as known all the typical green algæ have haploid individuals, except apparently some of the Siphonæ, the reduction division taking place in the zygote. In *Codium tomentosum*, May M. Williams found that the cenocytic body contained nuclei having the diploid number of chromosomes ($2x$) and that reduction takes place before the formation of the gametes. Hence the life cycle is essentially like that of Chara or Fucus. Whether the Siphonæ have this type of life cycle in general is not known. The question arises whether the time of reduction may be shifted in the life cycle of lower plants from one point to the other as the time of sex determination is shifted in the higher plants.

Since reduction normally requires two divisions resulting in four cells for its completion, the normal condition is the development of four spores or four gametes. These four cells are not to be regarded as a generation of an alternating cycle, if our terms are to mean anything in particular. If further vegetative divisions occur they are to be regarded as vegetative intercalations. If the process is leading up to nonsexual spore formation, the mass of resulting cells may for convenience be called a haploid sporophyte, as in Coleochaete, but is never to be homologized phylogenetically with such diploid sporophytes as Riccia, which has been done quite generally in the past.

Ulothrix may be taken as a normal representative of the *Gonidiophyta*. Its life cycle is: Haploid gametophyte; isogametes; conjugation in the water; zygote; resting stage; reduction (?); reduction zoospores; germination.

The *Oedogoniaceæ* have very suggestive life cycles which may throw light on the origin of some of the obscure life cycles of other *Algæ* and the *Fungi*. In general there are four types of *Oedogonium*. 1. Species with normal hermaphrodites. 2. Species with normal unisexual plants, the male filaments being a little smaller in size than the female. 3. Hermaphroditic species in which the normal plant produces oogonia and androsporangia with androspores, the androspores producing dwarf male filaments with spermatozoids. 4. Species in which the filaments are unisexual, but the imperfect male filament, because of incomplete sexualization, produces only androspores, which germinate to produce the dwarf males with spermatozoids. The dwarf males appear to be an intercalated generation thru the parthenogenetic development of androspores which represent original spermatozoids.

The dwarf males range in the several species from unicellular to multicellular filaments. The androspores have not lost their primary male state entirely for they are usually attracted to the oogonium and settle down on it or in the cell immediately below. The reduction division probably takes place at the germination of the zygote. The life cycle of the third type of species is therefore as follows: Hermaphroditic haploid gametophyte with incomplete male sexualization; oogonium and androsporangium; androspores and immature eggs; dwarf male; antheridium on dwarf male; mature eggs and spermatozoids; fertilization in the oogonium; resting diploid zygote; reduction division in the zygote; four haploid zoospores; germination of zoospores. Had the egg also developed a parthenogenetic female filament, the result would have been a complete but peculiar type of alternation of generations, the parthenogenetic egg and sperm simulating a megaspore and a microspore. The life cycle is evidently a direct modification of the simple sexual cycle. See Fig. 1. 1a-1b-1c.

In *Coleochaete* the normal, simple, haploid, sexual cycle is present except that a vegetative phase is introduced between the reduction division and the nonsexual spores, so that 16-32 cells are produced instead of the usual 4, all of which develop into zoospores. The life cycle therefore is: Haploid herma-

phroditic gametophyte; gametangia; gametes; fertilization in the oogonium; zygote; resting stage; germination of the zygote with reduction; haploid "sporophyte;" nonsexual zoospores; germination of zoospores. This life cycle seems to be directly derived from the simple, haploid, sexual cycle. Another interpretation is possible by assuming that the two or more divisions following meiosis are a vestige of repeated divisions before zoospore production, handed down from a unicellular condition, but more probably they represent a mutative addition to the original cell lineage like the extra division stage which results in a 16-celled female gametophyte in some *Peperomias*.

PHAEOPHYTA. The knowledge of the life histories and cytology of the Brown and Red Algæ is still very incomplete, so it is impossible to delimit the larger groups with any certainty. A number of recent discoveries, however, make necessary a rearrangement of the classes of the Phaeophyta. All arrangements must be regarded at present as tentative.

In the Ectocarpales and probably all of the Phaeosporæ proper, an alternation of generations seems to be lacking. Of the two types of sporangia produced, the unilocular sporangia are nonsexual and develop the nonsexual zoospores. The plurilocular sporangia are the sexual organs or gametangia. In some species at least, as in *Ectocarpus siliculosus* both unilocular sporangia and plurilocular gametangia may be present on the same individual at the same time. The gametes range from isogamous free-swimming gametes to heterogamous motile micro-and mega-gametes. In some species the female isogametes settle down first and the male gametes move to them, when conjugation takes place. Is the frond of *Ectocarpus* and related forms haploid or diploid? and where does reduction take place? Until these questions are answered for a considerable number of genera, no final classification of the Brown Algæ is possible. The life cycle so far as known is: Gametophyte; unilocular sporangium with nonsexual zoospores repeating the gametophyte; plurilocular gametangium; gametes; fertilization; zygote.

The life cycle of *Fucus* is well known and is as follows: Diploid gametophyte; gametangia (unilocular); oocyte and spermatocyte; reduction divisions (meiosis); vegetative multiplication of incipient sexual cells; heterogametes; fertilization in the water; zygote; germination. This is not to be regarded

as a reduced alternation of generations as has sometimes been done, but as a simple diploid sexual cycle, with intercalation of cell divisions between meiosis and gamete maturation (development of primary sexual state.) See Fig. 1 2a-2b-2c.

The greatest discoveries have been made by Sauvageau and others in the Laminariales or giant kelps, where a peculiar alternation of generations has been established for several genera. But the real knowledge required for making proper deductions are again lacking. The large frond is apparently a diploid organism and in Chorda, according to Kylin, the first division of the primary nucleus of the sporangium is a reduction division. The sporangia are of the unilocular type and agree in this respect with the unilocular gametangia of the Cyclosporæ. The spores produced in the unilocular sporangia of Lammaria and Postelsia develop into small male and female gametophytes. The life cycle would then be: Large, diploid frond (sporophyte); unilocular sporangium; reduction division; nonsexual zoospores; germination; small haploid female and male gametophytes; gametangia; gametes; zygote; germination.

There appears to be a much closer relationship between the Lammariales and the Cyclosporæ, than between the former and the Phaeosporæ. If we regard the Fucales and Lammariales as having a common primitive origin with a simple diploid sexual life cycle, then the Fucales have evolved by simply intercalating vegetative divisions between reduction and gametogenesis while the Lammariales have developed a small intercalated or secondary gametophyte thru the development of parthenogenesis in the originally isogamous gametes produced on the diploid plant. The change took place in both male and female gametes and not in the male gamete alone as in Oedogonium. The decided change in life cycle will warrant placing the giant kelps in a distinct class as has recently been done by some, otherwise they should be associated with the Cyclosporæ.

DICTYOTEAE. The life cycle of these Brown Algæ indicates only a remote relationship to the other groups. Dictyotas were probably segregated directly from the primitive phaeophyte stock and developed their alternation of generations cycle immediately after passing the unicellular condition. The life cycle of *Dictyota dichotoma* is: Haploid male and female gametophytes; gametangia; gametes; fertilization in

the water; zygote; germination; diploid nonsexual plant or sporophyte; sporangium; sporocyte; reduction; haploid tetraspores; germination. The gametophyte and sporophyte are both prominent plants.

RHODOPHYTA. There are various life cycles in the red algae but apparently all have been derived from one common type. Not enough is known as yet to make conclusive deductions. The life cycle of *Polysiphonia* is a typical alternation of generations cycle with some complications and is well known: Haploid gametophyte; gametangia; gametes; fertilization by non-ciliated sperms in the oogonium; zygote; germination of diploid zygote in the oogonium; diploid carpospores; germination of carpospores; diploid sporophyte; tetrasporangium; sporocyte; reduction division; reduction spores (tetraspores); germination. Compare with Fig. 1. 3a-3b-3c-3d.

The life cycles of *Bangia*, *Batrachospermum*, and other genera seem to be somewhat different and *Bangia* and its relatives probably constitute a distinct class.

CHAROPHYTA. The stoneworts, according to the investigations of Tuttle on *Nitella*, have apparently a simple, diploid sexual cycle, the plant being diploid with the 2X number of chromosomes and the reduction taking place in the gametangia. Diploid gametophyte; gametangia; reduction; gametes; fertilization in the oogonium; resting zygote; germination. The stoneworts are, therefore, quite distinct in life cycle from most of the other green algae.

FUNGI.

Unfortunately, in the case of the fungi, as in various other groups of *Thallophyta*, the taxonomist meets with difficulty in attempting to compare the life histories of one group with another for the purpose of discovering phyletic relationships. There is much work for the cytologist. If, for example, the life history of various species of *Mucor* (*Rhizopus*) were definitely known and especially their nuclear activities during conjugation and reduction, one might be able to deduce some very important conclusions in relation to numerous experimental facts known about them as well as to their probable origin.

It is probable that in *Rhizopus* the reduction division takes place in the sporangium developed on the germ-tube. If this is the case and if we assume a relationship to the green

algæ with a simple haploid cycle, as for example the more primitive Siphonæ, then the germ-tube represents either an intercalated diploid or a conjugate generation, resulting from the cenocytic development of the zygospore. Whether the conjugation of the male and female nuclei takes place in the zygospore or in the sporangium of the germ-tube is not known. It seems reasonable, however, to consider the nuclei of the two conjugating branches as having originally been incipient isogamous gametes.

In *Saprolegnia monoica* the haploid mycelium is cenocytic. The oogonial and antheridial branches are decidedly dimorphic. Several female nuclei are left functional in the female gametangium and several male nuclei in the male gametangium. The male nuclei are discharged thru a penetrating tube into the oogonium. A single male nucleus unites with each egg, thus forming uninucleate zygotes. Reduction takes place at the germination of the zygote giving rise to the vegetative haploid mycelium. This is, therefore, a simple haploid sexual cycle.

In *Albugo* a single male or female nucleus functions in each gametangium. The resting zygote in some species produces zoospores on germination which is probably accompanied by a reduction division.

There has been much dispute about the origin and relationships of the ascomycetous and basidiomycetous fungi. Their life histories indicate that they originated from organisms with a simple haploid sexual cycle. In the meantime, a binucleated phase has been intercalated thru the partial desexualization of the sex nuclei before nuclear fusion has taken place, the complete primary sexual state with fusion being attained again at a later stage. The conjugate nuclei have not lost their primary sexual state entirely, however, since they must exert an influence on each other, otherwise it does not seem possible that conjugate division, thru which the binucleate mycelium is developed, could be accomplished.

A number of life cycles of the Ascomycetæ are fairly well known. *Pyronema confluens* according to the work of Harper and of Claussen, has a uninucleated haploid mycelium. The essential part of the life history is as follows: The male and female sexual branches become multinucleate, fuse, and the nuclei from the antheridium pass over into the oogonium. The nuclei partially lose their primary sexual state at this

time, if it is really fully developed, and simply pair off without fusing.

Several hyphæ are produced from the oogonium and the pairs of conjugate nuclei pass into them and undergo several conjugate divisions. Thus each ascogenous hypha has binucleated cells, the pair of nuclei representing descendants of the original male and female nuclei produced. Following a complex process of division, a penultimate cell with a male and female nucleus, each with a complete primary sexual state, is finally produced and conjugation takes place, the delayed zygote. From this cell an ascus is developed in which reduction takes place giving rise to four free haploid nuclei, which with a further division give rise to the eight ascospores.

The binucleate stage arises thru the incomplete sexualization of the sex nuclei, preventing conjugation, vegetative divisions are intercalated and the binucleated condition is the result. The simulated "sporophyte" is a secondary development from an original simple, haploid sexual cycle. The binucleate phase in this case and in the basidiomycetous fungi can be called a conjugate generation. There is no evidence that the Ascomycetæ had an alternation of generations with a true sporophyte originally. In a normal sporophyte generation the nuclei are diploid, in a conjugate generation the cells contain conjugate, haploid nuclei. The generation ends by the sexualization of the conjugate nuclei and their fusion into a zygote nucleus rather than in the sexualization of synaptic chromosomes in a reduction division. Sexualization of the chromosomes with synapsis occurs at the germination of the zygote as in plants with a typical simple haploid sexual cycle. This conjugate phase seems to be developed only in the higher fungi and represents a new type of intercalated vegetative development between the fertilization and reduction stages. The fact that it is much less developed in the Ascomycetæ than in the more highly evolved Teliosporæ and Basidiomycetæ indicates that it has not degenerated from a true diploid sporophytic phase. It seems to become more prominent in the progressive evolution of the higher fungi.

The highest fungi show many of the peculiarities of the Ascomycetæ and even of the Phycomycetæ in relation to their sexual processes, indicating a close relationship as to origin. The same general method of fusion of the gametangia, the loss for a time of the primary sexual states of the conjugate nuclei,

and development to a greater or less degree of a binucleate cell condition strongly indicate a common origin, probably from uninucleate, haploid sexual green algæ with isogamous gametes which, either in the algal stage, or after passing into the fungus condition, segregated into a cenocytic subphylum and a subphylum with uninucleated cells.

In the rusts, *Caeoma nitens* may be a representative of the more primitive condition. On the other hand it is possible that it represents an abbreviated life history. At present the evidence does not seem to be sufficient to establish either proposition. *Caeoma* has a uninucleated, haploid mycelium. In the aecium stage the tips of branches representing male and female gametangia conjugate and the contents of the one pass over into the other. The nuclei lose their primary sexual state and become conjugate nuclei. A chain of binucleate aeciospores is produced. These spores on germination become zygotes when the conjugate nuclei develop complete primary sexual states and fuse into one. In some cases at least a reduction division follows with a promycelium or basidium and four haploid basidiospores. If this is the primitive condition, it shows but a slight development of the binucleate phase. But if characteristic teliospores do develop in some unknown stage of the life cycle it would have to be regarded as a derived condition, the conjugate generation being lost thru a change in the time of the complete sexualization of the conjugate nuclei. The pycnidia may represent vestigial conidial sori.

The life cycle is then: Haploid uninucleate sexual plant; uninucleate gametangia; conjugation of cells and cytoplasmic union; partial loss of primary sexual state of the conjugate nuclei; a number of vegetative conjugate divisions resulting in the formation of aeciospores; complete sexualization of the conjugate nuclei; nuclear fusion resulting in a diploid nucleus or zygote; development of a basidium or promycelium with reduction division; four haploid basidiospores.

In some of the rusts, as in *Puccinia graminis*, the binucleated phase or conjugate generation has been extensively developed. The life cycle is: Haploid uninucleate mycelium on the barberry; uninucleate gametangia; conjugation and cytoplasmic union; pairing of the sexual nuclei without fusion; a number of conjugate divisions to produce aeciospores; germination of binucleate aeciospores on wheat; binucleate mycelium; vegetative propagation by binucleate uredospores; production

of teliospores; complete sexualization of the conjugate nuclei in the teliospore; fusion of sexual nuclei to form the diploid uninucleate condition or zygote proper; germination of zygote (teliospore) with reduction division; promycelium or basidium with four haploid uninucleate basidiospores; germination of basidiospore on the barberry again. This cycle can readily be derived from the simple, haploid sexual cycle.

The basidiomycetæ appear to present the same fundamental conditions as the other fungi, namely, a modification of the simple, haploid sexual cycle at the isogamous stage of sexual evolution. The vegetative body appears to begin as a haploid mycelium with uninucleate cells. Later cells may become cenocytic by fragmentation of the nuclei or cenocytic divisions. At the beginning of the development of the fruiting body and earlier, a conjugation of gametangia normally takes place, resulting in binucleate cells and a conjugate mycelium. A peculiar method of division of the binucleate cells gives rise to the "clamp connections" and is carried on in such a way that each cell receives a pair of the conjugate nuclei. Finally basidia are formed at the tips of hyphal branches in the fruiting body, the conjugate nuclei become sexualized in the incipient basidia, unite, and form the diploid zygotic nucleus. Reduction follows, typically with four reduction nuclei which develop the four uninucleate, haploid basidiospores.

A careful study of some of the known life cycle of the Ascomycetæ, Teliosporæ and true Basidiomycetæ shows that these groups are much more closely related than was formerly supposed. The relationship between the rusts and typical basidiomycetous fungi has been recognized for some time, but many still hold to a special origin of the Ascomycetæ. But the character of the vegetative body together with the remarkable similarity of the fundamental stages in the life cycle and the very similar sexual modifications far outweigh the slight resemblance and the duplication of superficial characters which the ascocarp may have to the sporocarps of the red algæ. The writer is convinced of the primary monophyletic origin of all the Mycomycetæ.

LIFE CYCLES OF THE META-THALLOPHYTA.

The Meta-thallophytes present no such difficulties or complexities in their life cycles as the Thallophytes. All the life cycles belong to a single type with clear modifications, the

typical antithetic alternation of generations cycle. The cycle simply becomes more complex with the upward progress of evolution, the fundamental stages and conditions remaining unchanged. In Fig. 2 are represented the twelve fundamental, antithetic stages, which show that there is no exactly similar life cycle in any of the Thallophytes.

The life cycles of the main groups of higher plants are given below without special discussion, since they are well known and involve no diversity of views as to their nature.

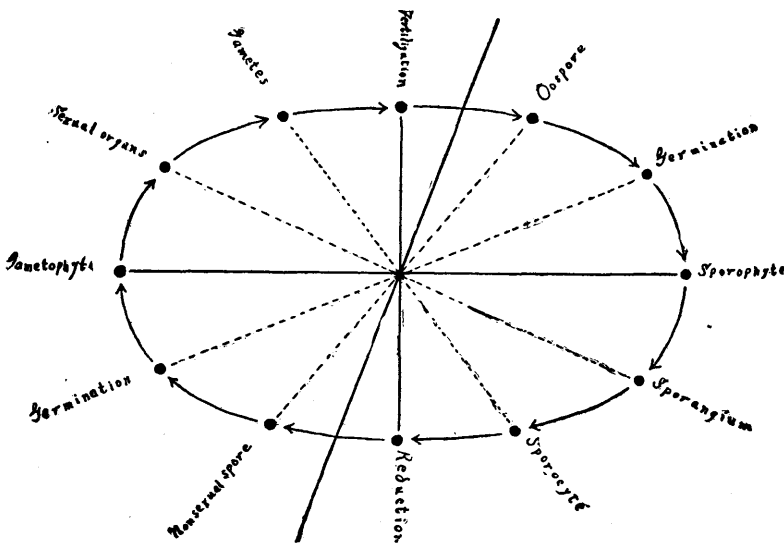


Fig. 2. Diagram showing the principal stages in the life cycle of the higher plants. From the author's Laboratory Outlines for General Botany. Fifth edition.

Whatever one may think about the origin of the antithetic cycle it is now completely established on a single type as stated above.

MARCHANTIA. Haploid male and female gametophytes; archegonium (ovary) and antheridium (spermary); female and male gametes (oosphere and spermatozoid); fertilization; zygote (oospore); germination in venter; diploid parasitic sporophyte; sporangium; sporocyte; reduction division (with primary sexual states in the synaptic chromosomes); non-sexual spores (reduction spores or tetraspores); germination on the ground. See Fig. 2 and Fig. 1. 3a-3b-3c-3d.

TYPICAL MOSS. Haploid hermaphroditic gametophyte with protonema and gametophore phases; archegonium and antheridium; oosphere and spermatozoid; fertilization; oospore; germination in venter; diploid parasitic sporophyte; sporangium; sporocyte; reduction; nonsexual spores; germination on the ground.

TYPICAL FERN. Haploid hermaphroditic gametophyte; archegonium and antheridium; oosphere and spermatozoid; fertilization; oospore; germination in venter; diploid sporophyte with parasitic embryonic and independent mature phases and with indeterminate growth; sporophyll; sporangium; sporocyte; reduction; nonsexual spores; germination on the ground.

EQUISETUM ARVENSE. Haploid male and female gametophytes which show much sex reversal; archegonium and antheridium, oosphere and spermatozoid; fertilization; oospore; germination in venter; diploid sporophyte with parasitic embryonic and independent mature phases and with indeterminate and determinate shoots; reproductive determinate shoot or flower (strobilus); sporophyll; sporangium; sporocyte; reduction; nonsexual spores; germination on the ground.

MARSILEA QUADRIFOLIA. Reduced haploid male and female gametophytes (connected with the spore wall); archegonium and antheridium; oosphere and spermatozoid; fertilization; oospore; germination in venter; diploid heterosporous bisporangiate sporophyte with dependent and independent phases and with indeterminate axes; sporophyll with enclosed sporocarps; sex-determination in the sorus; megasporangium and microsporangium; megasporocyte and microsporocyte; reduction divisions; megaspore and microspore; germination in the water.

SELAGINELLA. Reduced haploid male and female gametophytes connected with the spore walls; archegonium and antheridium; oosphere and spermatozoid; fertilization; oospore; germination in venter; diploid heterosporous bisporangiate sporophyte with dependent embryonic and independent mature phases and with determinate and indeterminate axes; bisporangiate strobilus with sex-determination in the incipient sporophylls; megasporophyll and microsporophyll; megasporangium and microsporangium; megasporocyte and microsporocyte; reduction divisions; megaspore and microspore; beginning of germination in the sporangia; completion of development of gametophytes on the ground.

CYCAS. Parasitic haploid male and female gametophytes; development of pollen-chamber in the young ovule; discharge of male gametophytes (pollen grains) and pollination in pollen-chamber; development of parasitic pollen-tube and second period of development of male gametophyte; archegonium (ovary) and reduced antheridium; oosphere and spermatozoid; discharge of spermatozoids into archegonial chamber; fertilization; oospore with determination of sex; germination in venter inside of the megasporangium (ovule); embryonic diploid parasitic carpellate and staminate sporophytes; resting condition of embryonic sporophytes in the ovule (mature seed); discharge of seed; sprouting of seed in ground; juvenile independent sporophytes developing into the mature carpellate and staminate sporophytes—the former with indeterminate reproductive axis, the latter with a determinate reproductive axis, the staminate strobilus; megasporophyll (carpel) and microsporophyll (stamen); megasporangium (ovule) and microsporangium (pollen sack); megasporocyte and microsporocyte; reduction with sexualization of the synaptic chromosomes; megaspore and microspores; germination of the two kinds of spores in the sporangia.

PINUS. Parasitic haploid male and female gametophytes in the microsporangium and megasporangium; discharge of the male gametophyte (pollen) with pollination on the micropyle of the ovule; development of pollen-tube and second parasitic phase of the male gametophyte; archegonium (ovary) and reduced antheridium; oosphere and nonmotile sperms; primary sexualization of the gametes; discharge of the sperms into the archegonium venter; fertilization; germination of oospore; development of diploid parasitic sporophytic embryos (polyembryony); survival of one embryo with resting condition of the surviving embryo sporophyte in the seed; discharge of the seed; sprouting of embryo in seed; juvenile independent sporophyte; mature neutral sporophyte; determination of male and female sexual states in certain buds (monecious condition); staminate and carpellate strobili or cones (flowers); megasporophyll (carpel) and microsporophyll (stamen); megasporangium (ovule) and microsporangium (pollen sack); megasporocyte and microsporocyte; reduction divisions with primary sexualization of the synaptic chromosomes; megaspore and microspore; germination of the two kinds of spores in the sporangia to produce the gametophytes again.

ALISMA SUBCORDATUM. Greatly reduced parasitic haploid female and male gametophytes in the megasporangium and microsporangium (ovule and pollen sack); discharge of the male gametophytes (pollen); pollination on stigma, the carpel being closed and forming an ovulary; development of pollen-tube with second parasitic phase of the male gametophyte; egg apparatus (greatly reduced ovary or archegonium) and greatly reduced antheridium (two spermatogenous cells); oosphere and two polar nuclei and two nonmotile sperms; development of primary sexual states in the five cells; discharge of the sperms into the female gametophyte; fertilization and triple fusion; diploid oosphere and triploid definitive or primary endosperm nucleus; germination of oospore and division of definitive nucleus; parasitic diploid embryonic sporophyte and parasitic triploid xeniophyte (endosperm) in the seed; resting stage of sporophyte embryo; discharge of fruit containing seed; sprouting of embryo sporophyte; juvenile stage of independent sporophyte; mature neutral diploid sporophyte; development of flower; determination of sex, originally the male state with later reversal to female state (bisporangiate flower); megasporophyll (carpel) and microsporophyll (stamen); megasporangium (ovule) in the ovulary and microsporangium (pollen sack); megasporocyte and microsporocyte; reduction divisions with primary sexualization of the synaptic chromosomes; megaspores and microspores; germination of the two spores in the sporangia to produce the parasitic gametophytes again. See Fig. 1, 3a and 4a, 3b and 4b, 3c, 3d.

Note. The differentiation of normal megaspores has been eliminated by abbreviation of the cell lineage. In many Angiosperms four megaspores are developed following reduction, one of which is functional.

CANNABIS SATIVA. The life cycle is essentially the same as in *Alisma* except that sexualization in the sporophyte takes place in the oospore, giving rise to the diecious condition with carpellate and staminate, highly dimorphic sporophytes. Under certain conditions sex reversal takes place abundantly in the growing sporophyte.

By comparing the life cycles from the Bryophytes to the Angiosperms it will be noted, as stated before, that they are all of one fundamental type with a gradual development of complexity in the evolution toward the highest condition.