QUARTERLY CHRONICLE OF MICROSCOPICAL SCIENCE.

BOTANY.

Sexual Reproduction of Thallophytes.

I.

The theory of descent has given—as it has done to every other branch of Biology—an entirely new interest to the study of the lower Cryptogams. They represent forms which if not actually identical with those possessed by the remote ancestors of the more complex plants have probably not been very distantly removed from these ancestral forms by subsequent modification.

It is natural, therefore, to seek amongst the non-vascular cryptogams for indications of phylogenetic relationship. But any examination for such a purpose must of course be unsatisfactory which is not based on a sufficient knowledge of the life-histories of the different types. Without this it is impossible to compare them one with another at stages when such a comparison is really significant.

Unfortunately from the necessity which is constantly imposed upon the systematist of classifying organisms of all kinds without being able to fulfil such a condition, the most erroneous juxtapositions are constantly made, and although an immense body of accurate observations has been accumulated about different types of the lower cryptogams, it is only lately that anything like a real cohesion has been visible amongst the accumulated facts. In the fourth edition of his 'Lehrbuch der Botanik,' published towards the end of last year, Sachs has proposed and adopted a classification of the non-vascular cryptogams which, while widely differing from any which had been previously suggested, for the first time affords something like an intelligible view of their morphological evolution.

II.

The division of the vegetable kingdom into the two regions of Thallophyta and Cormophyta was proposed by Endlicher in 1836. The groups are still valid, though it is by no means easy to frame characters which will satisfactorily limit them. Except perhaps the absence or presence of the "opposition of stem and root," none of the distinctions which Endlicher pointed out are available now; least tenable of all is the absence of sexuality in the *Thallophyta.*

The classification of the vegetable kingdom by A. P. De Candolle into VASCULARES and CELLULARES (1813) is far inferior to Endlicher's, though still in use. The two terms do not properly contrast, and the inclusion of the *Muscineæ* among the *Cellulares* is entirely unnatural in the light of our present knowledge.

For the last half century the *Thallophyta* have been held to fall into the three district groups of *Algæ, Fungi,* and *Lichens;* these were first limited as they now stand by Bishop Agardh ('Aphorismi Botanici,' 1821).

The autonomy of the *Fungi* had been recognised by the oldest systematists, and as early as 1583 Cæsalpinus included under that head at any rate the larger forms which are so designated now. But *Algæ* down to the time of Linnæus were mixed up with Hydrozoa, Actinozoa, and sponges. The group, since so-called, was established by him in 1735; but while he purged it of *Lithophyta* he retained in it *Hepaticæ,* Lichens, and *Rhizocarpeæ.* Jussieu (1789) separated the *Hepaticæ,* and his Algæ consisted of the plants at present recognised as such together with Lichens.

Considered as mere convenient assemblages or depositaries to which plants might be referred, the division of *Thallophyta* into *Algæ, Fungi,* and *Lichenes,* has worked tolerably well. And although it was found impossible to characterize the groups morphologically in the vast proportion of cases, little difficulty was found in referring any particular Thallophyte to some one of them. Berkeley and Lindley (1845) found themselves obliged to limit them by physiological characters: *Algæ,* generally speaking, they regarded as aquatic; *Fungi* and *Lichenes* as aërial. The former, however, drew their nutriment from their substratum, while the latter obtained it from the air.

This classification was adopted without question until 1868, when Prof. Schwendener, of Basle, propounded his now famous theory, that Lichens are not autonomous but composite organisms, consisting partly of an alga, partly of a fungus which forms a filamentous network in which the cells of the alga ("gonidia") are imprisoned. While the latter is probably identical with forms met with in a free state the fungoid part of the lichen is only known as a parasite. In the volumes of this Journal for the last two years[1] notices will be found of all the more important papers in which

[1] 'Quart. Journ. Micros. Science,' 1873, pp. 217, 235; 1874, p. 151.

Schwendener's view has been discussed. The general result has certainly been to confirm it. Lichens must, therefore, be degraded from their position as a principal division of Thallophytes and be referred to ascomycetous Fungi as a characteristic group of parasitic forms.

In 1872 Cohn[1] went a step further in abolishing the division of Thallophytes into Algæ and Fungi—the two groups which survive after the reduction of Lichens. But, as Sachs points out, the characters which Cohn employs in establishing new groups are of quite unequal value, being sometimes morphological, sometimes physiological. There can be no real comparison of such groups as *Zygosporeæ, Tetrasporeæ,* and *Zoosporeæ.*

The classification which Sachs himself has proposed is not open to this objection, being based upon the progressive differentiation of the reproductive organs. It is obviously, therefore, a classification which, on the one hand, has only been rendered possible by modern investigation, and, on the other, is subject to continual correction. He has followed Cohn in attaching little value to the separation of *Algæ* from *Fungi.* He points out that each of these assemblages of organisms may be arranged as a morphological series which runs parallel with the other. The essential distinction between them reduces itself to a difference, which, amongst higher plants, is regarded as an adaptive one. Algæ are Thallophytes in which chlorophyll is present; Fungi are Thallophytes in which it is absent. Cohn and Sachs have attached no more importance to this than is done in the case of Phanerogams. The saprophytes *Corallorhiza innata* and *Epipogium Gmelini* hold their proper systematic position amongst *Orchidaceæ* quite irrespectively of the fact that they are as destitute of chlorophyll as an *Agaricus.* The parasitic Phanerogams are also distributed amongst the forms with which they possess morphological relationship, and are not placed apart in any special group solely on account of their physiological peculiarities.

III.

The fundamental difference between plants and animals resolves itself into a difference of nutrition. Animals are capable, plants are incapable of the ingestion of solid food. A process of *digestion,* by which nutritious material may be reduced from the solid to the liquid form, is therefore necessary to animals, unnecessary to plants. The morphological

[1] Hedwigia, 1872, p. 18; 'Journ. of Bot.,' 1872, p. 114.

adaptations which nutrition requires are in the highest degree complicated in the one kingdom, while they always remain tolerably simple in the other. Of the two functions, therefore, which divide between them vegetable life, reproduction —by which of course sexual reproduction is meant—becomes in the case of plants of far greater morphological importance than nutrition.

The following brief sketch of the rise and progress of our knowledge of the sexual reproduction, more especially of Thallophytes, is instructive as showing how much more influence on the whole a deductive method of investigation has had than an inductive. It is true that we can see now that but little real progress could in any case have been made without modern microscopes. But an equally essential condition was that investigation should be carried on without preconceived ideas, and it is impossible to look through the literature without seeing that generally it was felt to be much more important to make structural arrangements agree with theory than to try to ascertain their real nature.

The phenomena of sexual reproduction in plants was more or less familiar to even classical writers on natural history. Pliny was aware that the female flowers of the Date could not produce fruit unless the "pulvis maris" had been scattered upon them from neighbouring trees. But in modern times the first distinct recognition of the sexuality of plants is generally attributed to Sir Thomas Millington, Savilian Professor at Oxford, who in 1676 communicated his ideas as far as flowering plants are concerned in conversation to Grew.[1] Sprengel considers that to Bobart, "overseer of the physick gardens at Oxford," belongs the credit of having, in 1681, first actually demonstrated experimentally (on *Lychnis dioica*) the function of pollen. The account is given in Blair's 'Botanick Essays' (1720), p. 243, but it must be confessed it is not very conclusive. The experiments of Camerarius (1694), a professor at Tubingen, upon hemp and some other plants, were much more to the point. The sexuality of flowering plants was further developed in England by Samuel Morland (1705), and in France by Geoffroy (1711), and Vaillant (1718). The discovery was very soon over-generalised; from this time till the end of the eighteenth century most of the writers on structural botany deserve the censure passed by Sprengel[2] on Micheli (1729): "quod ubique partes duplicis sexus invenisse fingeret."

[1] 'Anatomy of Plants,' p. 171.
[2] 'Historia rei herbariæ,' vol. ii, p. 232.

Micheli described the apothecia of Lichens as flowers, and the asci as stamens. Hedwig (1783) laid the foundation of an accurate knowledge of the sexual reproduction of mosses, but thought that the function of anthers was performed in Ferns by the hairs on the back of the midrib of the fronds, while in Fungi it was accomplished by the velum.

Such views, as Decaisne and Thuret pointed out in writing on the reproduction of *Fucus,* being based only upon hypothesis or imperfect observations, fell later on into deserved neglect. A reaction began against the application of the doctrine of sexuality to the lower plants. Gmelin (1760) thought that in descending through the vegetable series the diversity of the sexes gradually diminished, till in Fuci a point was reached where fructification took place without fertilization at all. Gaertner (1788) held that the spores of the greater part of the algæ (including the Florideæ) were not true seeds, but "gemmæ." In *Fucus* he believed that the "uterus" (conceptacle) accomplished the fertilisation of the enclosed spores.[1]

At the beginning of the present century the reaction against the belief in the sexuality of the lower plants reached its climax. Endlicher made the absence of sexes, as has already been noticed, one of the distinguishing marks of Thallophytes; Schleiden, in his 'Grundzuge' (1845), ignores, as far as possible, any facts which seem to point to the existence of sexuality amongst them. But even Schleiden could not have shut his eyes to actual demonstration, and his attitude shows that the sexuality of the Thallophytes up to his time had, in reality, been rather inferred than actually proved. The whole of our present knowledge, in fact, rests on the researches of the last thirty years.

Linnæus first made use of reproductive organs as a basis of classification in his 'Systema à Sexu' published in 1735. Sprengel[2] remarks that, a little while before this, when only twenty-three years old, "lectione Vaillantii et Blairii incensus sexualis systematis fundamenta ponere cœpit."

In its essential features sexual reproduction implies the fusion of two individualised particles of protoplasm. De Bary (1858) was the first to point out in his memoir on the *Conjugatæ* that this process exists in its most generalised form in "conjugation." This phenomenon had long been known in the

[1] "Palam est . . . . quod in *Fucis* genuinis . . . . ipse uterus sua fœcundet ovula, et quod ille ipse, officia genitalium utriusque sexûs, præstet solus" ('De Fructibus,' p. xxxiii).

[2] 'Historia,' vol. ii, p. 323.

fresh-water algæ, but even in the eyes of Schleiden it was quite void of significance—an "inessential" process. Yet it is obvious that it may be regarded as identical with fertilisation if we suppose that the two elements which are necessary to take part in it are still *undifferentiated;* the two conjugating elements are indistinguishable, and have not assumed the forms and attributes of oospheres and antherozoids, of germ-cells and sperm-cells.

If we take the processes of reproduction in *Vaucheria* or *Saprolegnia* as representative, those of the *Conjugatæ* and *Zygomycetes* may be compared with them as belonging to a simpler and probably primitive type. In each case a spore is produced as the result of the confluence, in the latter of similar, in the former of dissimilar elements. We may conveniently term this spore a zygospore in the one case, an oospore in the other. The researches of Thuret, Bornet, Tulasne, and Janczewski have further shown, that in all the higher Thallophytes the effects of fertilization are not limited to the production of a single spore, but set in action complicated processes of growth which give rise to structures of great diversity, including a great number of spores, and these may be called carpospores.

From the point of view of the reproductive process we may therefore classify the mass of Thallophytes, as Sachs has done, with more or less certainty, into three large groups—Zygosporeæ, Oosporeæ, Carposporeæ. When this is accomplished it is found that in each group we have a series of Algæ associated with a parallel series of Fungi. It only remains to throw into a fourth group, Protophyta, the organisms in which from their low degree of differentiation it seems probable that sexual reproduction has not made its appearance.

The following pages contain, under the four classes established by Sachs, a brief account of the present state of our knowledge of the sexual reproduction of Thallophytes.

Class I. Protophyta.

In this class—which is to a certain extent no doubt provisional—those organisms are placed in which as far as is at present known spores are only formed by the segmentation of the protoplasm of a single parent cell (asexual reproduction) and not as the result of the fusion of segments of protoplasm derived from two distinct parent cells.

Cyanophyceæ.—This includes the same assemblage of organisms which Rabenhorst has classified as *Phycochromophyceæ.* The protoplasm of their cells is destitute of a nucleus, and besides containing chlorophyll is tinged with the peculiar blue colouring matter, phycocyan. The subordinate families are *Chroococcaceæ*,[1] *Oscillatoriaceæ*, *Scytonemeæ*, *Nostocaceæ* and *Rivulariaceæ*.

PALMELLACEÆ differ principally from *Cyanophyceæ* in the absence of an obvious blue colouring matter masking the chlorophyll. Some genera, as *Glœocystis* and *Tetraspora* develope zoospores. Like *Protococcus* and *Pleurococcus* these will probably have to be removed to the *Zygosporeæ*.

EUGLENEÆ must be placed in this group; they are not known to possess a sexual reproduction, otherwise they might be associated with *Pandorineæ* in the next class.

Fungi contribute to the *Protophyta* the group of *Schizomycetes*[2] (Bacteria), which have some affinity with *Oscillatoriaceæ*[3] and in some respects with *Saccharomyces* (yeast).

Class II. ZYGOSPOREÆ.

We here meet with the simplest mode of sexual reproduction—conjugation. In some cases an incipient differentiation of the two conjugating elements may be noticed as in *Pandorina* and *Zygnemeæ*. Indeed, in all the series there is probably a disposition to progress towards the degree of differentiation which belongs to the *Oosporeæ*.

Two divisions may be conveniently made according as the conjugating cells are motile or non-motile.

A. *Conjugating cells motile.*

Amongst the green algæ the number of forms in which the zygospore has been ascertained to be produced by the conjugation of two zoospores is gradually receiving additions. In all these cases it may be stated more or less generally that the zoospores which are produced by the successive segmentation of the protoplasm of a *vegetative cell* are of two kinds which have been named respectively *macrozoospores* and *microzoospores*. While in some cases it would appear as if the difference between these merely depended on the degree to which the successive segmentation of the contents of similar cells is carried, in others the different kinds of zoospores are produced from different kinds of filaments or perhaps even from different individuals.

The function of the macrozoospores is purely vegetative.

[1] Bornet has figured the spores of *Glœocapsa*, 'Ann. des Sc. Nat.,' 5e sér., tom. xvii, Pl. 16, fig. 3.

[2] On "Bacteria," see 'Quart. Journ. Mic. Sci.,' 1873, p. 156.

[3] On "Saccharomyces," see 'Quart. Journ. of Mic. Sci.,' 1875, p. 142.

They come to rest, "germinate," and so reproduce asexually the parent plant.

The function of the microzoospores, on the other hand is sexual. They conjugate and the zygozoospore (Areschoug), after passing into a resting phase, no doubt, also reproduces the parent plant.

The following are the cases in which up to the present time the conjugation of zoospores has been observed.

PANDORINEÆ (*Dyer*).—*Chlamydomonas* is a microscopic organism which consists of a green protoplasmic mass with a lateral speck of red pigment, varying in form from ovoid to globular and furnished with two or four vibratile cilia, attached at a hyaline apex where the green colouring matter is more or less absent. It is bounded by a delicate closely applied cellulose wall; *Chlamydococcus* only differs in the wall being separated from the green contents by an interspace. By division into two or four each individual *Chlamydomonas* gives rise to macrozoospores which eventually attain the same size and appearance as the parent. Occasionally, however, the division proceeds further, and eight daughter cells are produced — the microzoospores. Rostafinski[1] first observed that these microzoospores conjugated. Two of them touch by their colourless extremities and then gradually fuse together, eventually producing a cell with a rounded contour, but with eight cilia and two lateral pigment spots. The colourless apex of this zygozoospore soon disappears; the eight cilia follow and the zygozoospore passes into the resting condition. After having been allowed to dry up and then again moistened it gave rise—not to new zoospores, but to vegetative forms arising from repeated cell division and referable to the genus *Pleurococcus*.[2]

[1] "Beobachtungen über Paarung von Schwärmsporen," von J. T. Rostafinski, 'Botanische Zeitung,' 1871, p. 785.

[2] If we follow the example of Bornet ('Ann. des Sc. Nat.,' 3e sér., tom. xvii) and unite *Pleurococcus* with *Protococcus*, we shall then have an intelligible view of the complete life-history of a type the name of which is at any rate a very familiar one.

Rabenhorst ('Flora Alg. Aq. Dulc.') maintains *Pleurococcus vulgaris*, Menegh., and *Protoccus viridis*, Ag., not merely as distinct species, but as belonging to separate families—the former to the *Palmellaceæ*, the latter to the *Protococcaceæ*. At the same time he remarks with regard to *Protococcus viridis*, "fieri potest ut *Pleurococci vulgaris* status pro ratione loci natalis siccioris sit." *Pleurococcus vulgaris* may probably, therefore, be regarded as a more actively vegetative condition of *Protococcus viridis*, the only real difference between the two being, that one undergoes cell-division, while the other does not. As *Chlamydomonas Pulvisculus*, after the conjugation of its zoospores, develops into a *Pleurococcus*, it also may

A supposed conjugation has been described by Velten[1] in *Chlamydococcus.* But according to his observations the macrozoospores and not the microzoospores took part in it. Rostafinski[2] accordingly concludes from this and other abnormalities which occur in Velten's account that he had mistaken for conjugation the destruction of a cell of *Chlamydococcus* by a parasitic monad.

Pandorina was the plant in which the conjugation of zoospores was first described by Pringsheim.[3] He distinguishes it from *Eudorina* with which English writers have generally identified it. According to him it consists of a colony of sixteen zoospores, each of which may give rise to new colonies by division. This is the asexual mode of reproduction. The first stages of the sexual condition are very similar. But in the final result the new colonies resolve themselves into their constituent zoospores which are frequently eight instead of sixteen in number. They vary in size, but though there are zoospores that are comparatively large, and some which are small, there are others which correspond to every intermediate dimension. Pringsheim considers that this difference of size indicates a certain amount of sexual differentiation. For usually a small zoospore (antherozoid) conjugates with a large zoospore (oospore). When the zoospores which conjugate are equal in size they possess the mean dimensions; these might be regarded, therefore, as sexually undifferentiated. The largest sexual zoospores never conjugate with one another.

In *Pandorina* it must be borne in mind that size ceases to be a criterion of difference between the vegetative zoospores (macrozoospores) and the sexual (microzoospores).

The phenomena of conjugation repeat what has already been stated in *Chlamydomonas.* The sexual zoospores, according to Pringsheim, appear to seek out and approach one another in pairs. They touch by their transparent anterior extremities, blend at these points, and eventually form a united body geminate in shape. The double notch, which indicates the original distinctness of the two zoospores, gradually disappears, and the zygozoospore assumes a rounded form which gives no indication of its composite origin, except that its anterior extremity has two lateral

be referred to *Protococcus*, of which it may now be regarded as the motile condition.

[1] 'Bot. Zeit.,' 1871, p. 383.

[2] Ibid., 1871, p. 788.

[3] "Ueber Paarung der Schwärmsporen," Pringsheim, in 'Monatsber. der Berliner Akad.' Oktob., 1869.

red spots and four cilia. Both red spots and cilia subsequently disappear; the zygozoospore passes into the resting condition, and eventually gives rise to a new *Pandorina* colony. The whole process of conjugation occupies at the most five minutes.

With respect to other forms allied to *Pandorina* our knowledge is far from complete. In *Gonium* the formation of microzoospores is unknown. In *Stephanosphæra* they have been described by Cohn and Wichura,[1] but their conjugation has not hitherto been seen. In *Eudorina* and *Volvox*, to which *Volvocinaceæ* is here restricted, the sexual process has attained a higher degree of differentiation and will be referred to further on.

HYDRODICTYEÆ.—The well-known fresh-water alga *Hydrodictyon* is in many respects nearly allied to the *Pandorineæ*. The contents of the individual cells undergo separation into macrozoospores and microzoospores. Of the former from 7000 to 20,000 are produced, of the latter from 30,000 to 100,000. The swarming of the macrozoospores takes place entirely within the mother-cell, and the "net," which is finally set free by its rupture, is the aggregate of these which has reached the resting condition. The microzoospores, on the other hand, are set free, and their ultimate destination is not properly known. According to Pringsheim[2] they are intended to reproduce the plant in a future season. It is highly probable, therefore, that they undergo a process of conjugation (although, as Sachs remarks, this has not yet been observed); and this may be the real meaning of the double spores which Cohn long ago figured,[3] but which he explained as the result of a casual adhesion or gluing together of two microzoospores adjacent to one another in the mother-cell. On this view the "Doppelspore," which Cohn figures, would be the zygozoospore (fig. 1).

FIG. 1.—Microzoospores (one with two cilia) and 'doppelspore' of *Hydrodictyon* × 500 (after Cohn, l. c.).

Cohn[1] also observed double spores in *Cladophora* (fig. 2), and Thuret in *Enteromorpha*, in both of which genera, as

[1] See 'Quart. Journ. Micr. Sci.,' 1858, p. 136, Pl. VI, figs. 26, 27.
[2] See Quart. Journ. Mic. Sci.,' n. s., vol. ii, p. 54.
[3] "Untersuchungen über die Entwickelungsgeschichte der mikroskopichen Algen und Pilze von Dr. F. Cohn." 'Nov. Act. Acad. Nat. Cur.,' vol. xxiv (1854), pp. 225, 226. Tab. 19, fig. 14.

will be seen below, conjugation is now known to take place. Amongst the multicellular green algæ (*Nematophyceæ*,

FIG. 2.—Conjugation of microzoospores of *Cladophora glomerata* × 500 (after Cohn, l. c., tab. xx, fig. 26).

Rabh.) the formation of zygozoospores has recently been determined in a considerable number of species.

ULOTHRICHACEÆ only differ from *Confervaceæ* in their filaments never branching and being composed of very short cells. There seems to be no really valid ground for separating them in these respects.

Hormiscia.—Cramer[1] discovered the conjugation of the microzoospores in 1870 in *H. zonata,* Web. and M. (*Ulothrix zonata*, Kutz.). Some cells of this species produce two to eight macrozoospores, others sixteen to thirty-two microzoospores. The details of conjugation agree in every respect with what Pringsheim has described in *Pandorina.*

Urospora.—Areschoug[2] distinguishes this genus from *Hormiscia* by the presence of only two cilia on the zoospores in place of four. He has described the formation (fig. 3)

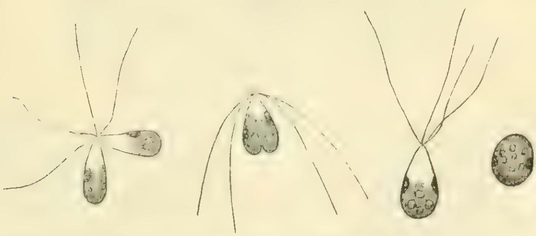

FIG. 3.—Conjugation of microzoospores of *Urospora penicilliformis* × 1000 (after Areschoug, l. c., tab. i, figs. 4-6).

of the zygozoospore (first noticed by him in 1863) in *U. penicilliformis* in the following vivacious language:—

"Microzoosporas celeriter natantes cum intuemur, duas

[1] "Naturf. Gesellsch. in Zürich," Marz, 1870; 'Bot. Zeit.,' 1871, pp. 76, 89. For the development of the zoospores, cf. Braun, "Rejuvenescence in Nature," 'Ray Soc.,' pp. 148, 159.

[2] 'Observationes Phycologicæ,' Act. Reg. Soc. Sc., Ups., 1874.

videmur sæpenumero microzooporas, quarum altera alteram fugientem persequitur. Haec est microzoospora fœminea, quæ illam, seu microzoosporam masculinam, effugere tendit, quæ contentio, quamquam nonnunquam prospera, est tamen plerumque inanis. Tunc microzoospora masculina rostrum suum rostro microzoosporæ femineæ infigit, quo facto utraque rostris cohæret. Corpus huc et illuc jactans, microzoospora fœminea se liberare conatur, spe autem fracta, utraque cursum celerrime iterat. Hoc in cursu lateribus earum adpositis, ab rostris versus extremitates earum sensim adglutinantur, ut denique copulatione absoluta, adsit zoospora, e duabus microzoosporis sexualibus composita, quattuor ciliis ornata et utrinque lateraliter granulo fusco-rubro insignita quam zygozoosporam nominare licet" (p. 3).

In this plant the macrozoospores and the microzoospores are produced by different filaments, those producing the latter being narrower. The formation of macrozoospores also takes place during the summer, while that of the microzoospores occurs during spring.

Confervaceæ. — Areschoug has detected conjugation (fig. 4) in *Cladophora sericea.* His observations lead to the

Fig. 4.—Conjugation of *Cladophora sericea* × 1000 (after Areschoug, tab. ii, fig. 12).

conclusion that the macrozoospores (also first detected by him) and the microzoospores are produced by different plants. The microzoospores are not all of the same size. "Microzoospora feminea et masculina nunc ejusdem magnitudinis, nunc masculina quam feminea minor" (p. 9).

Ulvaceæ.—Thuret first described the macrozoospores and microzoospores in this group. In *Enteromorpha* the former are furnished with four cilia, the latter with two. The formation of the zygozoospore in *E. compressa* has been repeatedly seen by Areschoug and takes place in a manner in no respect differing from that already described.

Myxomycetes.—Amongst fungoid types Sachs associates these with the groups which have been enumerated above.

This at first sight may seem surprising. Zoospores, however, are masses of protoplasm whose conjugation has many important features of resemblance to the formation of plasmodia. The cell-wall of zoospores is feebly developed, or at any rate offers but little valid resistance to the fusion of two individuals. The spores of the *Myxomycetes* set free their protoplasm as uniciliate zoospores which gradually lose their characteristic form and become amœboid. The amœbæ being destitute of any cell-membrane readily run together in a kind of wholesale conjugation and produce a plasmodium—a kind of compound zygospore, which eventually passes into a resting state and by processes more or less complicated developes the spores.

CHYTRIDIEÆ.—In the 4th edition of his 'Lehrbuch,' p. 256, Sachs suggests the propriety of placing this group in juxtaposition with the *Myxomycetes*, as it would be probably found that the zoospores conjugate. This has been actually found to be the case by Sorokin[1] in a form described by him as *Tetrachytrium*. *Chytridieæ* may occupy an intermediate position between *Myxomycetes* and *Saprolegnieæ*.[2]

PROTOMYCES is a parasitic fungus of obscure affinity. It produces sporangia which discharge with considerable force their contained spores. These conjugate in pairs to form a zygospore.[3]

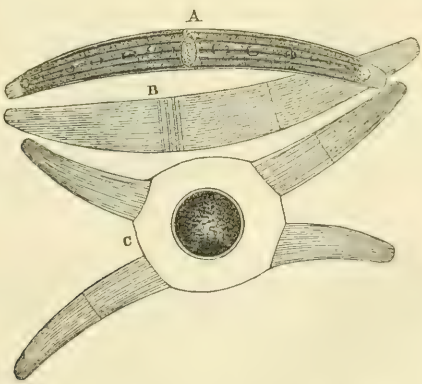

FIG. 5.—*Closterium striolatum*. A, before; B, after; C, in conjugation (after Ralfs).

[1] See 'Quart. Journ. Mic. Sci.,' 1874, p. 298.
[2] See Sachs, 'Traité de Bot.,' traduit par Van Tieghem, p. 382.
[3] See De Bary, 'Beitr. z. Morph. d. Pilze,' Hft. i.

B. *Conjugating-cells non-motile.*

DESMIDIEÆ.—In 1836 Morren[1] published his account of the conjugation of *Closterium* (fig. 5), and was therefore the first discoverer of this process amongst the *Desmidieæ* as now constituted. This important observation had as Morren himself remarks for its not least important result the final separation of the species of *Closterium* from the animal kingdom to which they had been supposed to belong. They were seen to agree in essential points notwithstanding their curious motility with the filamentous *Conjugatæ*, which no one ever doubted to be true plants.

DIATOMACEÆ.—It was not till 1847 that Thwaites discovered conjugation (fig. 6) in this group which in many respects runs parallel with *Desmidieæ*.

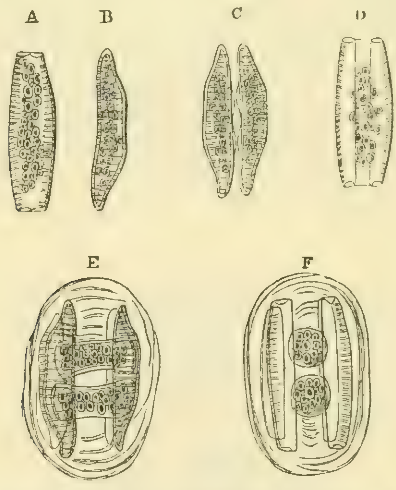

FIG. 6.—Conjugation of *Eunotia turgida* with formation of two zygospores. A, front view of frustule; B, side view; C, side view of frustules, conjugation commencing; D, front view; E and F, side and front views after formation of zygospores (after Thwaites).

ZYGNEMACEÆ.—Conjugation was discovered much earlier in the filamentous forms. It was first observed by O. F. Muller in 1782, and he figured in the Flora Danica (tab. 883), under the name of *Conferva jugalis*, examples of a *Spirogyra* in a state of conjugation. Twenty years later the whole process was studied by a Swiss botanist, Vaucher, and described in his *Histoire des Conferves d'eaux douces* (1803),

[1] 'Ann. des Sc. Nat.,' 2me sér., tom. v.

a book which has been justly called classical, and which gives us the same pleasure in reading it that is to be found in the first account of the exploration of some entirely new country. It is worth while quoting a few sentences from Vaucher, because they illustrate very admirably the advantage of patience and persistence in this kind of study.

"I had one day," he says, "collected a considerable quantity of these plants, and, as was my practice, I was examining them rather as a matter of habit and rule than from the hope of finding anything new. I witnessed, however, a phenomenon as novel as it was unexpected. On all the segments of the cylindrical tube small swellings or papillæ, irregular in form and mostly obtuse, made their appearance. Each gradually elongated itself till it met a papilla of the other conjugating filament" (p. 43). Since this time conjugation has been observed to take place with differences in detail in other genera.

The conjugation is either effected transversely between the cells of different filaments (fig. 7 B), or longitudinally between adjacent cells of the same filament as in *Rhynchonema* and *Pleurocarpus*. In such genera as *Mesocarpus* and *Pleurocarpus* the zygospore is formed *between* the conjugating cells, while in *Zygnema*, *Spirogyra* and *Rhynchonema* the zygospore is formed *in* one of the conjugating cells (fig. 7 C). This may be regarded as the commencement of a differentiation which leads eventually to the type of reproduction characteristic of the *Oosporeæ*.

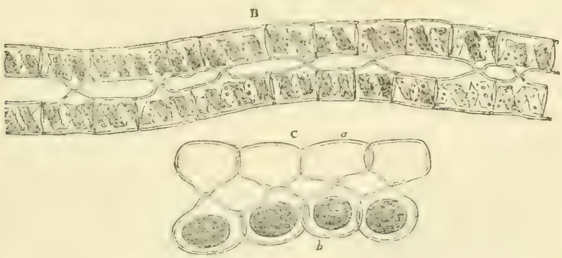

FIG. 7.—Conjugation of *Spirogyra quinina* (after Kutzing).

Amongst Fungi a similar mode of conjugation has been observed to that in *Mesocarpus*. The first instance in which it was observed was by Ehrenberg (1829), in *Sporodinia* (*Syzygites*); the other instances in which it is known are *Rhizopus* (De Bary, 1866), *Mucor fusiger* (Tulasne, 1866), *M. Mucedo* and *Phycomyces* (Van Tieghem and Le Monnier, 1872), *Chœtocladium* and *Piptocephalis* (Brefeld, 1872).

In *Phycomyces*, after the partitioning of the cells to form the zygospore, a number of dichotomously branched processes are developed from the conjugating filaments.[1] Van Tieghem and Le Monnier point out that these processes are not developed simultaneously on both conjugating filaments and they trace in this a first step in sexual differentiation. It may be suggested also that the formation of the branched processes which form a kind of investment of the zygospore is a kind of anticipation of the more elaborate developments of the same kind met with amongst the *Carposporeæ*.

Sorokin has also discovered a Chytridineous plant *Zygochytrium* which produces zygospores by the union of filaments instead of zoospores.[2] This proves that there is no absolute distinction between the two processes.

Class III.—Oosporeæ.

If, as already pointed out, the two similar elements which take part in a conjugation become differentiated, we pass without difficulty from the formation of a zygospore to that of an oospore. For aught we can see to the contrary, the quantitative and qualitative factors are equally balanced in the one case, but it is evident that they are unequally so in the other. The oosphere is generally enormously larger than the antherozoid, which consequently can do little more than give the oosphere some kind of impulse. Amongst the *Zygosporeæ* either the entire protoplasmic contents of two cells of equal size take part in the conjugation, or at any rate fractions of their contents of equal value do so. It is part of the essential difference of the *Oosporeæ* that while the oosphere represents the entire contents (or in *Fucaceæ* a very large fragment) of a single cell—the oogonium, the antherozoid is only a very minute fragment of the contents of the unicellular antheridium.

Volvocineæ.—If we compare the whole series of forms usually included in this group (but which is here restricted to *Eudorina* and *Volvox*) it appears to offer a complete transition from the zygospore to the oospore. Sachs preserves a complete silence with regard to these genera, yet both are furnished with distinct antherozoids discharged from an antheridial cell.

According to Carter in *Eudorina*, the contents of the four cells adjacent to one pole of the colony undergo conversion into antherozoids, make their escape from the parent cell, and "freely come into contact with the capsules of the twenty-

[1] See 'Quart. Journ. Mic. Sci.,' 1874, pp. 63, 65.

[2] 'Quart. Journ. Mic. Sci.,' 1874, p. 298.

eight remaining or female cells (oogonia)...... to the capsules of which they apply themselves most vigorously and pertinaceously, flattening, elongating and changing themselves into various forms as they glide over their surfaces, until they find a point of ingress, when they appear to slip in, and, coming in contact with the female cell, to sink into her substance as by amalgamation."[1]

In *Volvox* antheridia and oogonia are, as in *Eudorina*, found in the same colony, which is then monœcious, or they are found exclusively in different colonies, which are therefore diœcious. The sexual cells exhibit a further degree of specialization, inasmuch as only a small proportion of the cells of a colony are developed into them. The oospheres are conspicuous by their large size, and are surrounded by a gelatinous cell-wall (oogonium). This is penetrated by the antherozoids when they escape from the antheridia (fig. 8).

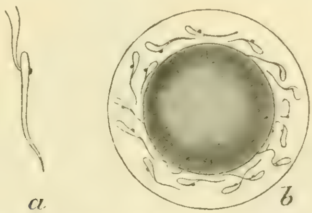

FIG. 8.—Fertilization of *Volvox*. *a*, antherozoid × 800; *b*, oogonium with antherozoids penetrating the gelatinous cell-wall × 400 (after Cohn).

SPHÆROPLEA.—If we are compelled to divorce *Eudorina* and *Volvox* from the *Pandorineæ* we are equally obliged to separate on the same grounds *Sphæroplea* from its confervaceous allies. The contents of the cells of this filamentous alga, instead of forming microzoospores, develope into oospheres and antherozoids. These are formed in different filaments, and the antherozoids being set free find their way through apertures in the walls of the oogonial cells and fertilize the oospheres.

FUCACEÆ.—As early as 1711, what we now know to be the organs of reproduction of *Fucus* were discovered by Réaumur. He observed the orange-red exudation from the openings of the conceptacles which Decaisne and Thuret (1845) showed to consist of a mass of antheridia containing antherozoids. Linnæus with tolerable accuracy described as the "feminei flores" of *Fucus* the club-shaped ends of the branches of the frond or vesiculæ, as he termed them, "adspersæ punctis perforatis semine fœtis." The male

[1] 'Ann. Nat. Hist.,' 3rd ser., ii, 1858, pp. 239, 240.

organs he identified with the hairs which line the bladders found on the fronds, but which, as Mirbel pointed out are nothing more than the *débris* of cellular tissue.

Fucus will always have a special interest in the history of these researches. It was the first alga in which the actual phenomenon of the fertilization of the oosphere, by the incorporation with it of the antherozoids, was ever witnessed. Thuret's observations on the subject were communicated to the *Académie des Sciences* in 1853. The peculiarity of the *Fucaceæ* is that both oospheres and antherozoids are set free, which is to a certain extent a return to the form of conjugation met with in *Pandorina*. The contents of the oogonium form from one to eight oospheres, which are naked masses of protoplasm destitute of motile organs. The antherozoids collect about them in such numbers as to impart to them a movement of rotation (fig. 9).

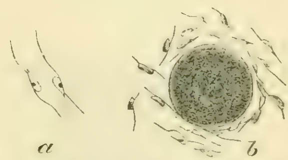

FIG. 9.—Fertilization of *Fucus*. *a*, antherozoids × 330; *b*, oosphere surrounded by antherozoids × 160 (after Thuret).

In a memoir on *Volvox* which Cohn has lately privately published as a Festschrift in honour of Prof. Göppert, he has remarked that the agreement of all the sexual relations of *Volvox* and *Eudorina* with *Sphæroplea* on the one hand, and with *Fucus* on the other, is so clear that the distribution of these algæ in two different classes must appear unnatural, and the position of all the genera named amongst the *Oosporeæ* cannot be doubted.

It will, no doubt, seem a grave objection to a classification that it requires the breaking up of a group apparently so natural as *Volvocineæ* as generally limited. The progressive morphological differentiation of the members of that group cannot fail to be apparent and to suggest their close genetic connection.

But it must now be clear that Sachs's classes have no strict genetic signification, and only mark and measure grades of development. We must still, therefore, attempt to arrange our groups in genetic linear series independently of it. These will be vertical, and will be intersected by the horizontal boundaries of Sachs's classes.

PHÆOSPOREÆ.—Sachs suggests as a provisional arrangement placing near the *Fucaceæ* the Algæ resembling them in habit, such as *Macrocystis, Laminaria, Sargassum,* &c.; of these the zoospores and antherozoids are known, but the female organs have not been discovered.

CŒLOBLASTÆ.—This group includes algæ and fungi in which the protoplasm is continuous throughout the vegetative organs of the plants, and is not divided into cells. Approximately it may be said to include the *Siphophyceæ* on the one end, and Sorokin's *Siphomycetes* (excluding the *Mucorini,* and possibly the *Chytridineæ*) on the other.

Amongst the *Siphophyceæ* we know little of the reproduction of any genus except *Vaucheria.*

The antheridia and oogonia of this genus were discovered, and their functions correctly apprehended, by Vaucher (1803)[1]. But Pringsheim first put their meaning entirely beyond doubt in 1855 by observing the actual process of fertilization (fig. 10).[2] In *Bryopsis* Pringsheim[3] believes he

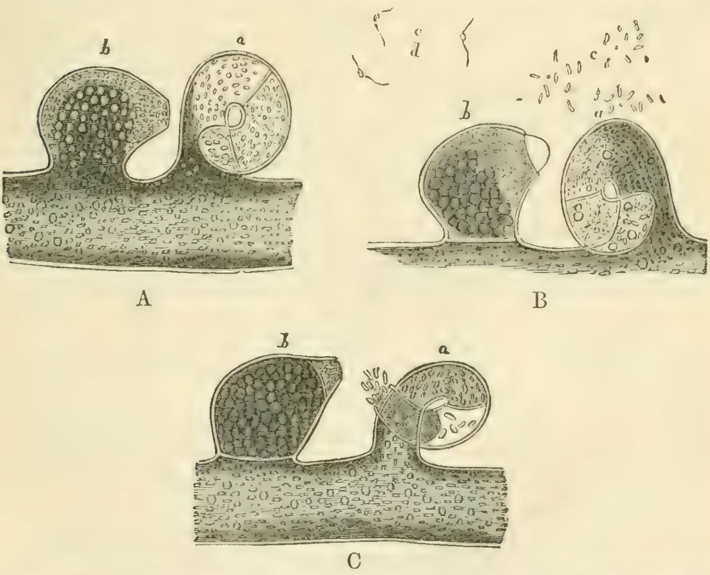

FIG. 10.—Fertilization of *Vaucheria sessilis.* A, antheridium (*a*) and oogonium (*b*) before fertilization; B, antheridium (*a*) emitting antherozoids (*c*), the cilia of which are visible (*d*) when they come to rest; C, oogonium (*b*) containing fertilized oosphere (oospore) surrounded with a cell-wall (after Pringsheim).

[1] 'Hist. des Conf. d'eaux douces,' p. 17.
[2] 'Berlin. Monatsb.,' 1855, pp. 133-165.
[3] Ibid., 1871, pp. 240-255.

has found the antherozoids, but the female organs have not as yet been seen.

SAPROLEGNIEÆ.—In these plants the antheridia effect the fertilization of the oogonia by a species of conjugation. If we may contrast *Saprolegnia* with *Vaucheria* amongst *Oosporeæ,* we have a parallel contrast ready to our hand amongst *Zygosporeæ* in *Zygochytrium* and *Tetrachytrium* already alluded to. And there is the same relation between fertilization by means of a so-called pollinodium and the conjugation of filamentous processes that there is between fertilization by means of antherozoids and the conjugation of zoospores.

Braun (1851) first noticed [1] the "pollinodia" (antheridia) of *Saprolegnia,* and compared them to the antheridia of *Vaucheria.* The oogonia were described by Schleiden, who simply regarded them as asexual "spherical sporangia" [2] But Pringsheim [3] in 1857 first ascertained, with any certainty, the real sexuality of the *Saprolegnieæ.* He made out the kind of conjugation which takes place between the antheridia and the oogonia in the monœcious species, and by which, instead of by the access of motile antherozoids, the oospheres are fertilized. Pringsheim thought that, notwithstanding the conjugation, antherozoids were formed, and that in the diœcious forms, where no conjugation was possible, these antherozoids were really motile. Max Cornu (1872)[4] believes that in the forms in which conjugation is the rule motile antherozoids are not formed in the antheridium, but that this empties itself by an influx of its protoplasmic contents into the oogonium. The motile antherozoids which Pringsheim had described in the cases where conjugation did not occur, Max Cornu believes really to belong to a Chytridineous endophyte. He thinks that the antherozoids in the diœcious species closely resemble the zoospores in appearance, and have been overlooked in consequence. In *Monoblepharis* the spermatozoids are half the size of the zoospores, but of the same form; they creep with amœboid movements over the wall of the oogonium, and fertilize the oosphere by blending with it.

The latest contribution to the history of this group is that of Pringsheim in the ninth volume of his 'Jahrbucher.' He has modified his views, and proposes a very remarkable explanation of the sexual phenomena. Fertilization is always effected by antheridia; when these are absent the oogonia develop without fertilization, and are therefore partheno-

[1] See 'Rejuvenescence in Nature' (Ray. Soc.), p. 298.
[2] 'Principles of Scientific Bot.,' p. 100.
[3] 'Jahrbucher,' Pringsheim, pp. 289-305.
[4] Max Cornu, 'Ann. des Sc. Nat.,' 5e sér., tom. xv.

genetic; the spores in this case only differ from those which have been fertilized in germinating more rapidly.

ANCYLISTEÆ.—This is a new group of aquatic parasites described by Pfitzer. *See* 'Q. J. M. S.,' 1874, p. 296.

PERONOSPOREÆ.—This group of which the white rust of cabbages and other cultivated *Cruciferæ* (*Cystopus candidus*) and the potato-disease (*Peronospora infestans*) are well-known representatives, was thoroughly investigated by De Bary[1] in 1863. The phenomena of fertilization closely resemble those which take place in the *Saprolegniaceæ*. From the oospore of *Cystopus* antherozoids are produced which give rise to the sexual plant.

ŒDOGONIEÆ are a group of filamentous algæ which in many respects are typical *Oosporeæ*. The oosphere is fertilised as in *Vaucheria* by antherozoids. Zoospores, oospheres, and antherozoids are formed from the cells of the filament, an arrangement which is clearly not far removed from that which obtains in *Confervaceæ* the microzoospores of which are repre-

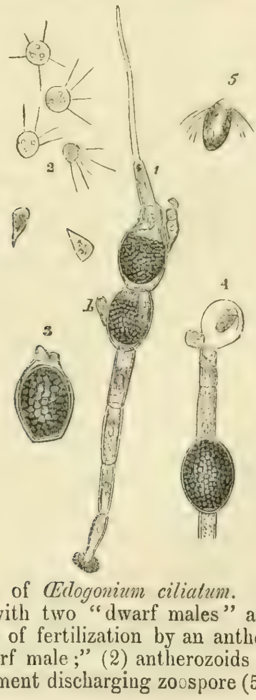

FIG. 11.—Fertilization of *Œdogonium ciliatum*. (1) Filament with two oogonia, the lower with two "dwarf males" attached, the upper with oosphere in process of fertilization by an antherozoid set free from its accompanying "dwarf male;" (2) antherozoids; (3) oogonium containing oospore; (4) filament discharging zoospore (5); (after Pringsheim.)

sented here by non-motile oospheres and antherozoids. In

[1] 'Ann. des Sc. Nat.,' 4e sér., tom. xx.

some species a diœcious condition exists, which reaches back to the formation of the zoospores. Some of these, instead of producing the normal plant, produce a form of a very modified character ('dwarf-males'), which attach themselves to the filaments containing oospheres, and merely serves the purpose of developing antherozoids (fig. 11). The oospore produces a succession of asexual generations. The zoospores germinate and form a filament which eventually becomes septate. Sometimes, however, while still in the unicellular condition, it discharges its contents as a zoospore by a terminal opening in a manner which suggests a comparison with *Vaucheria.* That, however, is more probably related to *Saprolegnieæ* than a reduced form of *Œdogonium.*

Alternation of generations.—The comparison of the different groups of Thallophytes requires that the relationship of the sexual and asexual generations of an organism should be taken into account. In *Nostoc* the asexual generations succeed one another uniformly; in *Spirogyra* there is equal uniformity in the succesion of generations which are sexual. But generally the two kinds are intermixed in varying proportions. In the simplest alternation a sexual and an asexual generation follow each other with perfect regularity. In others the sexual generations are intercalated at more or less remote intervals in a series the other terms of which are asexual. This is what happens in *Œdogonium.* It may easily happen that if the sexual generation makes its appearance at very distant periods it may for a long time remain unobserved. This may be the reason that it has not yet been detected in any of the *Siphophyceæ,* except *Vaucheria.*

An important feature in the life-history of any organism consists in the similarity or dissimilarity of the two kinds of generations which arise from sexual and asexual reproduction. In *Vaucheria,* for example, there is no difference between the character of the sexual and asexual plants. But such a case as a moss is a conspicuous example of the loss of all vegetative characters by the asexual generation which is reduced to a mere mass of spores. These, collectively, are due to a sexual process of which each, therefore, is only a partial product. The sporocarp of mosses represents a type of alternation of generations where an asexual one is so reduced as to have lost all individualization, and has become merely a means of extending as widely as possible the effects of the sexual act in the other generation. Good examples of this arrangement are afforded by *Cystopus,* where the oospore developes from its contents a number of zoospores; *Sphæroplea* does the same; in *Œdogonium* the oospore produces four zoospores.

In other groups this is also the case in a less marked degree. In *Mucor* the zygospore develops a filament, which, without branching, terminates in a sporangium filled with spores; here the vegetative development (represented by the filament) is not entirely suppressed. Amongst *Pandorineæ* we get an interesting condition in *Pandorina*, where the zygozoospore sets free a single zoospore, or rarely two or three, after the resting phase. According to Cohn,[1] Cienkowski, in 1856, found that the oospore of *Volvox* finally produces eight zoospores.

The anomalous sexual processes of *Myxomycetes* give rise to a many-spored fruit, which Sachs[2] suggests may be considered comparable with the sporocarp of mosses. In the organisms which belong to the next class the part played by the sporocarp, which amongst the *Oosporeæ* is only indicated in such instances as those above mentioned, rises into great prominence.

Class IV.—Carposporeæ.

The most interesting part of the taxonomic scheme which Sachs has propounded for the Thallophytes is that which relates to his fourth and highest class—the *Carposporeæ*. The following summary is in the main taken from the fourth edition of his 'Lehrbuch,' pp. 240—243.

The *Carposporeæ* agree with the *Oosporeæ*, in so far that the two sexual organs contribute in very different proportions to the formation of the sexual product. While the male only stimulates its development, the female supplies the material for the whole subsequent growth.

The female organ, or carpogonium, may consist of one or more cells. The male organ varies very considerably in the different subordinate groups. Fertilization may—as in the *Oosporeæ*—be effected by antherozoids (which may be actively motile or passively locomotive), or by a kind of conjugation, or even by a mere apposition and subsequent diffusion of the fertilizing medium.

The product of the act of fertilization is sometimes a single cell developing directly into a new individual (*Chara*). In other cases the fertilized female organ produces zoospores (*Coleochæte*), and still more usually a multicellular mass is produced in which spores are finally developed. This involves

[1] 'Festschrift,' p. 22.
[2] 'Lehrbuch,' 4th ed., p. 267.

an alternation of generations of the type of that met with in the sporocarp of *Muscineæ*. And we may have every grade of development, from the simplest case, in which the sporocarp appears as a mere appendage of the parent plant, of inconsiderable dimensions, to the most extreme condition in the other direction, in which the sporocarp is capable of independent growth, and therefore represents a second generation which is entirely distinct.

The sporocarp also differs essentially from the oospore, in the fact that cells contribute to its formation which have not been *directly* influenced by fertilisation, and that in consequence the part of the fruit which produces the spores is surrounded by what—for want of a more convenient term—we may call the *pericarp*, in which no spores are developed, and which serves as a mere protective investment, or is subsequently draw upon for purposes of nutrition.

In *Phycomyces*, which belong to the *Zygosporeæ*, it is noteworthy that there is a kind of anticipation of the development of a protective investment to the zygospore.

Coleochæteæ.—In *Coleochæte* the carpogonium (hitherto considered an oogonium) consists of a single cell tapering into a long slender canal open at the apex (fig. 12, *a*). Fertilization is effected by motile antherozoids (fig. 12, *m*), as the result of which the protoplasm contained in the basal portion surrounds itself with a firm cell-wall. Except in the presence of the long canal, there is nothing here which differs essentially from the mode of formation of the oospore in *Vaucheria* and *Œdogonium*. The essential difference consists in the fact that the apparent oospore grows after fertilization very considerably, and the cells adjacent to the female organs are stimulated into growth, and surround the fertilised female cell with a pericarp (Fig. 12, *b*). A sporocarp is thus formed, the central cell of which develops a mass of tissue, the whole of the cells of which produce zoospores, each of which is capable of giving rise to a plant similar to the original parent. Here we have the essential features of the oospore combined with the essential features of the sporocarp. The zoospores developed from the central cell must be regarded as members of a second generation, homologous with the spores of a moss.[1]

Florideæ.—In *Nemalion* the carpogonium consists of a single cell, which is thick below and elongated above into a

[1] Braun (1851) regarded the formation of the "pericarp" in *Coleochæte* as a species of conjugation analogous to what takes place in *Saprolegnieæ;* 'Rejuv.' (Ray Soc., p. 298). Pringsheim (1860) made out the true nature of its development ('Jahrb.,' vol. ii).

closed hair-like body—the Trichogyne. The antherozoids attach themselves to this. A further development of the basal

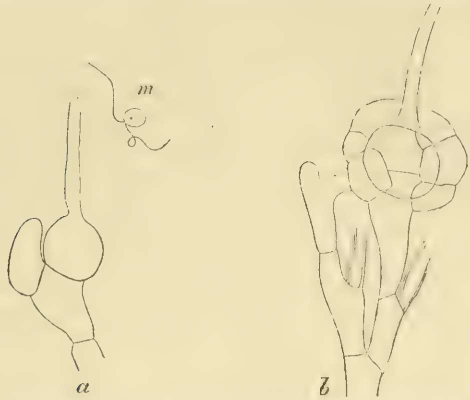

FIG. 12.—Diagrammatic representation of the development of the sporocarp in *Coleochæte; a*, carpogonium with antherozoid (*m*); *b*, fertilized carpogonium invested with its pericarp (after Pringsheim).

cell of the carpogonium results; it increases in circumference, divides into numerous cells, which grow out into closely crowded shoots; at the end of each a spore developes. The aggregate of the spores, with their short pedicles, constitute the sporocarp, which is in *Nemalion* destitute of a pericarp.

Nemalion is the simplest type of the *Florideæ.* In others (*Ceramieæ*) the carpogonium, even before fertilization, consists of numerous cells (fig. 13, *b*), a lateral row of which—the Trichophore—bears the trichogyne. Fertilization takes place as in *Nemalion*, but neither trichogyne nor trichophore take any part in the subsequent development. The sporocarp results from the growth and division of other cells of the carpogonium. The pericarp is produced by a process of budding from cells beneath the carpogonium.[1]

In the genus *Dudresnaya* the process of fertilization becomes very complicated, and, in fact, involves a double process, of which the first stage consists in the application of antherozoids to a trichogyne, and the second in the development, from below the trichophore, of a "conducting filament," which conveys the fertilizing influence to the terminal cells of a number of small branches, with which it successively

[1] The trichophore and trichogyne were discovered (1861) by Nageli; the sexual meaning of these structures was made out by Bornet and Thuret (1866); see 'Ann. d. Sc. Nat.,' 1867, tom. vii, p. 137. The antheridia of the *Florideæ* were discovered by Ellis in 1757.

conjugates. At each point of conjugation a sporocarp is developed.

Amongst the *Ceramieæ* it may be observed that there is something comparable to this double process.

The fertilizing influence which is conveyed by antherozoids to the trichogyne have afterwards to be communicated by a process of diffusion from the trichophore to the cell from which the spores are developed.

CHARACEÆ.—Certainly, however, the most ingenious interpretation which Sachs has proposed is that by which *Chara* is assigned a position amongst the *Carposporeæ*. Translating his words ('Lehrbuch,' 4th ed., p. 242):—"The sporocarp of *Chara*, which has hitherto stood in an entirely isolated position, becomes intelligible when we compare it on the one side with *Coleochæteæ*, on the other with the *Florideæ*. The carpo-

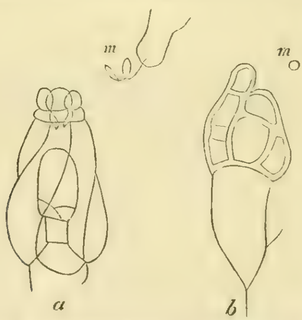

FIG. 13.—Diagrammatic representation of the carpogonium in *Chara* and *Lejolisia*. (*a*) *Chara* (the pericarp developed before fertilization), the basal cells (trichophore) of the carpogonium are shown; (*m*) motile antherozoid (after Sachs); (*b*) *Lejolisia* (pericarp not developed); the trichophore and undeveloped trichogyne shown on left-hand side; (*m*) passively motile antherozoids (after Bornet).

gonium consists of a large cell supported by several smaller basal ones, which take no part in the growth resulting from fertilization. They play, therefore, the part of a trichophore although there is no trichogyne, and fertilization is effected by motile antherozoids which blend directly with the carpogonium." A one-spored sporocarp is the result; the pericarp is formed before fertilization.

Chara is, therefore, in its reproductive aspects a *reduced* type of *Carposporeæ*. The trichophore is rudimentary, and the carpogonium unicellular instead of multicellular. These simplifications of the arrangements, which in other allied *Carposporeæ* precede fertilization, are balanced by the previous instead of subsequent development of the pericarp.

The peculiar mode of development of the "cortex" of the stem of *Chara* is also a matter in which a comparison may be made with some of the *Florideæ*, such as *Ceramium*.[1]

Turning now to the series of fungoid forms we find a considerable number of which the sexual reproduction in its main points agrees with that of the *Florideæ*.

ASCOMYCETES.—*Erysipheæ*.—This group, although not the earliest to be investigated, supplies us with the least complicated case of a sporocarp. In *Podosphæra*, in which its development was described by De Bary in 1870,[2] the carpogonium and antheridium are both unicellular. After fertilization the carpogonium divides into two cells, the upper of which produces spores in its interior, and so may be regarded as an ascus; the pericarp is formed of short filaments which branch out below its pedicle.

Baranetski[3] has described under the name of *Gymnoascus* a fungus found on horse and sheep dung, which is probably a reduced rather than a simpler form of such a type as *Podosphæra*. The carpogonium and antheridium closely resemble one another, but after fertilization the carpogonium divides into a number of cells, which grow out into filaments producing asci at their extremities. There is only an indication of the formation of a pericarp.

Amongst the *Erysipheæ* must also be placed *Aspergillus*, the sporocarp of which has been described as a distinct genus under the name of *Eurotium*.

Discomycetes.—The sexual reproduction of the larger fungi was first observed by De Bary amongst the members of this

[1] The taxonomic migrations of *Chara* have been most remarkable. Linnæus originally placed it in his group of *Algæ*, the contents of which, however, were in many respects heterogeneous. In the twelfth edition of his 'Systema' he transferred it to flowering plants ("ad mentem Scheberi," as Hedwig tells us, 'Theor. Gen.,' p. 125). It has been referred to *Naiadaceæ* by Jussieu and De Candolle, and to *Hydrocharaceæ* by Brown. Richard (1815) established it as a separate order. Agardh referred it to *Confervaceæ*. Endlicher and Lindley associated it with other *Algæ* (see Lindley, 'Veg. Kingd.,' 3rd ed., p. 26). Latterly it has been rather the fashion to regard *Characeæ* as an independent or problematic intermediate group, standing between Thallophytes and Cormophytes. This was the view taken by Schleiden and by Sachs up to the fourth edition of his 'Lehrbuch.'

The contemporaries of Linnæus were acquainted with the reproductive structures of *Chara*. Correa de Serra (1796) thought that the pollen consisted of mucus, and was conveyed to the germen by a kind of circulation. Bischoff (1828) discovered the antherozoids, and Thuret (1840) observed the cilia upon them, this being also their first discovery on the antherozoids of any plant.

[2] 'Beitr. z. Morph. u. Physiol. d. Pilze,' dritte Reihe.

[3] 'Bot. Zeit.,' 1872.

group. His observations in 1863 (on *Peziza confluens*) were further confirmed and extended by himself and Tulasne in 1866, and more recently by Janczewski in *Ascobolus* (fig. 14).[1] The carpogonium is no longer unicellular, but consists of a row of numerous cells, which is fertilized by the ramified antheridium. As a result of this process numerous filaments branch out from the middle cell of the carpogonium, which in their

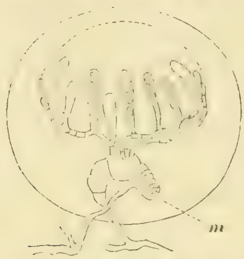

Fig. 14.—Diagrammatic representation of the development of the sporocarp in *Ascobolus*. The ramified antheridium is shown applied to the end of the multicellular carpogonium, from the middle cell of which the asciferous filaments are developed. The external outline indicates the boundary of the subsequently formed "pericarp." (After Janczewski.)

turn develop the asci. The pericarp, which forms a solid pseudo-parenchymatous investment, is formed of consolidated filamentous branches of the mycelium below the carpogonium. The mycelium itself, from which these comparatively large sporocarps are developed, is relatively inconspicuous. The sporocarp constitutes, in point of fact, a second and distinctly marked independent generation.

Tuberaceæ.—This group is characterized by the sporocarp not being aerial, as in the former groups, but subterranean. The well-known *Penicillium glaucum*, of which the conidiferous form is so common, has been found by the beautiful investigations of Brefeld,[2] to produce a sporocarp which is analogous to *Tuber* in its structure. Such a relationship is probably the very last that could have been, *à priori*, suggested for it.

Pyrenomycetes.—In this group the asci are contained in a bottle-shaped perithecium. The perithecia may either occur singly as in *Sphæria*, or aggregated as in *Claviceps*, in a so-called stroma. In the former case the researches of Woronin prove that each perithecium is the result of a process of fertilization.[3] In the latter case it is as yet doubtful what

[1] 'Bot. Zeit.,' 1871.

[2] 'Bot. Untersuch. u. Schimmelpilze,' heft ii, 1874.

[3] De Bary and Woronin, 'Beitr. z. Morph. u. Phys. der Pilze,' Erst. Bd., dritte Reihe, 1870.

happens, but it seems probable that *one* act of fertilization may give rise to *numerous* perithecia, and the sporocarp must therefore be regarded as compound instead of simple.

Lichens must now be placed, as indicated above, amongst the *Ascomycetes*. Their fructification may be referred partly to the type of *Discomycetes,* such as we find in *Peziza,* partly to that of the *Pyrenomycetes,* such as we find it in *Sphæria*. But in no case at present has the sexual act which doubtless underlies the development of their apo- and peri-thecia been detected. This would, indeed, if observed, conclusively clinch the case in favour of the Schwendenerian theory of Lichens.

Æcidiomycetes.—No observations of any sexual organs have been made in this group.

Basidiomycetes.—In the last edition of his 'Lehrbuch,' Sachs remarks that though no sexual process had been detected in the case of any form belonging to these fungi, analogy would lead to the supposition that the mycelium developed sexual organs, and that the spore-bearing body must be regarded as a sporocarp. Amongst the *Erysipheæ* and even the *Discomycetes* the degree of differentiation exhibited by the constituent tissues of the pseudo-parenchymatous mass of which the sporocarp is, at first at any rate, principally composed, is not very striking. But amongst the *Basidiomycetes* the gradual evolution of the final spore-bearing structures is in such genera as *Phallus* and *Crucibulum* most elaborate.

Attempts which have fallen out of notice have been made by Karsten as well as by Œrsted[1] to establish the fact of a sexual process amongst the *Basidiomycetes*. The most recent observations are those of Van Tieghem[2] on *Coprinus*. Van Tieghem found by sowing the spores in a solution of horse-dung that they are diœcious. They produce a mycelium which, in the case of a male spore, developes from the ends of lateral branches tufts of minute rod-like bodies (antherozoids), which fall off and are renewed like the conidia of a *Penicillium*. The mycelium developed from the female spores produces upon its branches, only more slowly, club-shaped bodies (carpogonia), three or four times as long as broad, and terminated at the apex by a small papilla, which Van Tieghem describes as playing the part of a trichogyne, the rod-like non-motile antherozoids becoming affixed to it. The contents of one of these pass into the carpogonium, leaving the empty cell-wall attached to the papilla. Van

[1] See 'Quart. Journ. Mic. Sci.,' 1868, p. 18.
[2] 'Comptes rendus,' Feb. 8, 1875, p. 373.

Tieghem even succeeded in cross-fertilizing the carpogonia of *Coprinus ephemeroides* with the antherozoids of *C. radiatus*.

Rees,[1] working about the same time on *Coprinus stercorarius*, has observed the development of the "antherozoids," and has also seen the fertilized carpogonia, but he had not observed their unfertilized condition, or the process of fertilization.

IV.

From the preceding sketch of the present state of our knowledge, it will be seen that Sachs's classification, though in some respects it does violence to a perfectly natural arrangement, on the whole succeeds in marshalling the Thallophytes according to their morphological complexity. That being the case, it must, to a certain extent, have also a phylogenetic significance. Sachs's four classes are, in fact, as already suggested, horizons which intersect the branches of the yet imperfectly understood phylogeny. And it is probable that the groups included between these horizons are rightly placed there, but that what we have still to learn is their vertical relations to one another. So far, then, the classification is an improvement on most artificial classifications, which usually, on grounds of expediency, abandon all attempt to preserve anything of a natural, *i.e.* of a phylogenetic, arrangement. Even Linnæus, who is generally regarded as the great supporter of utilitarian taxonomy, was by no means satisfied with an artificial classification. At the commencement of his 'Fragmenta Methodi Naturalis' (1738) he declares, "Diu et ego circa methodum naturalem inveniendam laboravi, bene multa quæ adderem obtinui, perficere non potui, continuaturus dum vixero."

In the third edition of his 'Lehrbuch,' Sachs suggested that the Algæ were the original stock of the vegetable kingdom, and that the Fungi branched off from the *Siphophyceæ*, which produced the *Phycomycetes* and these in turn the other types. The agreement between these two groups of unicellular *Oosporeæ* is undoubtedly very great, and it is sufficiently explained if we suppose that the *Phycomycetes* are simply *Siphophyceæ* modified for a parasitic life. There is no reason to suppose that the agreement has more significance than this, and Sachs has therefore abandoned the *Siphophyceæ* as the starting-point of the fungoid series.

Without attempting actually to construct a phylogeny of

[1] 'Ueber den Befruchtungsvorgang bei den Basidiomyceten; Sitzungsb. d. Physik. Med. Soc. in Erlangen,' Hft. vii, 1875.

the *Thallophytes*, a few remarks may be made as to the indications which might be made use of for such a purpose.

The *Schizomycetes* would appear to afford a starting-point. Those who advocate spontaneous generation will probably seize upon this as an important admission. Nevertheless there are good grounds for believing the doctrine which may be formulated as '*omne protoplasma e protoplasmate*.' Mr. Herbert Spencer is probably right in his conjecture that conditions once existed in which the interval between the chemical combinations which obtain in the organic and the inorganic world might easily be passed, while now apparently they cannot be, or only with extreme difficulty. Under such conditions, matter doubtless existed in such states of spontaneous aggregation as fitted it to subserve the nutrition of Bacteria. Now, we know that it only does so when derived from some organic source.

The interesting observations of Professor Lankester, on *Bacterium rubescens*[1] seem to show that we may pass without much difficulty from the *Schizomycetes* to forms belonging to to *Chroococcaceæ*, and other writers have also indicated their relationship to *Oscillatorieæ*. From *Chroococcaceæ* we pass apparently through *Palmellaceæ* (*Palmella cruenta*), *Pleurococcus*, *Confervaceæ* (proper), *Œdogonieæ*, *Coleocheteæ*, *Nemalion*, *Florideæ* to *Chara*. This has been probably the course of the main line from which branches would be given off, which readily suggest themselves. The earliest plants, supposing them to have been allied to *Schizomycetes*, were therefore probably more like the Fungi than the Algæ. And the food which is now furnished to Fungi from the organic world must then have been obtained from inorganic sources. Chlorophyll we may imagine to have made its appearance when these pseudo-organic sources of nutriment ran short, and to have been seized upon by a kind of natural selection as soon as its power of promoting deoxidation in substances fitted for plant nutrition made itself manifest.

Turning now to the forms from which chlorophyll is absent (Fungi), it must be remarked that notwithstanding the remarkable morphological parallelism which, as has been shown, they present at every step to the forms in which chlorophyll is present, it is still much more easy to connect them in a series with one another than to suggest, at present, the transverse links. It is interesting, however, to note the tendency of truly algoid types to assume a parasitic and consequently fungoid life. Reinsch finds that almost every large

[1] 'Quart. Journ. Mic. Sc.,' 1873, p. 408.

red seaweed is attached by species of *Entonema*. Other red seaweeds support a parasitic form (*Choreocolax*) which is itself a Rhodosperm.[1]

Except in the case of the *Siphophyceæ* already mentioned, it is difficult to imagine any passage from, for example, *Zygnemeæ* to *Mucorini*, or *Florideæ* to *Ascomycetes*. We can see indications of a linear series from *Zygomycetes*, *Saprolegnieæ*, *Ascomycetes*, perhaps to *Basidiomycetes*. And possibly *Zygomycetes* may have been not very remotely derived from *Schizomycetes*.

If the lines of *Algæ* and *Fungi* really were as this would seem to indicate, after all, distinct, the undoubted fact of their morphological parallelism is one of the most remarkable and yet suggestive facts in the whole field of Biology.

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[1] Reinsch, 'Contributiones ad Algologiam et Fungologiam,' 1874. See also, for other instances, 'Quart. Journ. Mic. Sc.,' 1873, p. 366, and 1874, p. 295.