Observations on the Conjugatae.

BY

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With Plates IV and V.
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DURING a prolonged study of Freshwater Algae from all parts of the world, many more or less interesting observations concerning the Conjugatae have accumulated: in this paper we propose to set forth some of them, together with certain conclusions derived therefrom. This group of Algae has been extensively studied by many previous botanists, amongst whom particular mention may be made of De Bary, Wittrock, Nordstedt, Lagerheim, Klebs, Bennett, and others; and we have here attempted to correlate with each other and with our own observations, a few of the facts described by these several observers, and from this to ascertain, as nearly as possible, the relationship existing between the various members of the group.

We classify the Conjugatae into the three following families: ZYGNEMACEAE, TEMNOGAMETACEAE, and DESMIDIACEAE, and in this paper we think it advisable to deal with them separately.

Many authors regard the Mesocarpeae as a separate family, owing to the peculiar formation of the spores; but we think

it is better regarded as a sub-family of the Zygnemaceae, as *Pyxispora* has the same method of formation of its spores, although the chromatophores are similar to those of *Zygnema*.

These plants may occur as solitary cells, or they may be filaments which at some or all periods of their existence more or less easily dissociate into the separate cells of which they are composed. The genus *Gonatozygon* may be taken as an illustration; it is sometimes found in long filaments of about thirty or more cells; but on being subjected to the least disturbing influences these filaments break up, and in some species of the genus the filamentous condition is rarely attained. There is a tendency in many of the small species of *Cosmarium*, very noticeable in *C. moniliforme* and *C. Regnellii*, to assume a filamentous condition, and this may have induced Rabenhorst¹ to place *C. pygmaeum* under *Sphaerosozoma*. We have also noticed this tendency in *Euastrum binale* (cf. Fig. 38). In *Micrasterias foliacea*, a representative of a genus the species of which normally occur as solitary plants, this filamentous condition has been attained by a remarkable degree of specialization of the polar lobes of the semi-cells, which possess an arrangement of apical teeth which interlock so firmly with those of the adjoining cell, that the connexion is too rigid to allow of hardly any flexibility in the filaments. A filamentous condition of the genus *Mesotaenium* (which is generally unicellular) is found in the Arctic plant named by Berggren *Ancylonema Nordenskioldii*. The filaments of *Hyalotheca* dissociate into separate cells just prior to conjugation, and the dissociated cells remain imbedded in a mucus derived from that which surrounded the original filaments. Conjugation is very soon general throughout the mass, as can readily be seen in a conjugating example of *H. dissiliens*. The fragmenting of the old filaments into individual cells is well known as a method of reproduction in some genera of Zygnemaceae. It can therefore be considered that a strictly filamentous condition is of no essential importance to the life of the Conjugatae.

¹ Flor. Europ. Algar. III, p. 150.

All Conjugates are surrounded by a definite mucilaginous envelope. In the great majority this covering is very thin, but in others it is profusely developed, e.g. *Zygnema anomalum*, *Hyalotheca mucosa*, *Staurastrum tumidum*, *S. longispinum*, &c.; and even in those species in which it is normally almost absent it is occasionally developed to a large extent. We have seen very extensive mucilaginous envelopes round *Closterium Lunula*, *Penium Libellula*, and *Cosmarium ovale*, species which are normally destitute of such extensive investments. No doubt this mucus serves in many cases as a means of attachment, as we have seen as many as a dozen specimens of *Staurastrum tumidum* attached to one leaf of *Utricularia minor*, and in the case of many of the species which occur on dripping rocks, this mucus is absolutely necessary for the purpose of attachment; but an equally important use is probably that of protection from epiphytes and parasites (Chytridiaceae, &c.). With regard to the nature of this gelatinous investment, it must be considered either as a secretion or a mucous condition of the outer layers of the cell-membranes. Klebs regards it as quite independent of the substance of the cell-wall; and as the cell-membrane of most Desmids is perforated by a large number of minute pores—excessively minute in some and not visible although perhaps present in others—one would be inclined to regard this mucous envelope as a secretion. But in some species of *Zygnema* it seems to us to be partly if not entirely due to the diffuent outer layers of the cell-wall, and this may be also true for some Desmids. In an almost pure gelatinous gathering of *Cosmarium cymatopleurum*, var. *tyrolicum*, many of the specimens were seen casting the outer coats of the cell-membrane, and in some cases many such successive coats could be seen round each individual gradually fading into the mass of jelly in which the plants were imbedded. This gathering was from the vertical face of a dripping rock. We have also noticed *Cosmarium pyramidatum*, when imbedded in a gelatinous mass of Desmids, casting its outer cell-membrane in a similar manner.

That this mucus is often of a tough nature is proved by a consideration of the genus *Spondylosium*, in which the individuals are united into long filaments by a layer of mucus between the apposed ends of the cells; and that the connexion is by no means a weak one is shown when the filament is fractured, the cells more often breaking across the isthmus than coming apart at the apical attachment.

Organs for attachment are occasionally developed in young plants of *Spirogyra*¹ (Fig. 20) and *Mougeotia* (Fig. 16), but have not been noticed in any other genus of Conjugatae; they are special outgrowths (simple or branched) at the base of the shoot, and are homologous to those organs of attachments found amongst other Algae and usually termed *rhizoids*, but more recently known as *haptera*. We have also noticed them to be developed in *Spirogyra*, as a result of the modification of a conjugating-tube protruded by a cell some distance removed from those cells of the filament engaged in conjugation (Fig. 21).

Branching amongst members of the Conjugatae is abnormal and of somewhat rare occurrence. When present in the Zygnemaceae it is generally limited to lateral outgrowths consisting of a few cells; we have only noticed it in the genera *Zygnema*² and *Mougeotia* (Figs. 17–19). In the Desmidiaceae one semi-cell occasionally undergoes a partial lateral³ or dichotomous⁴ branching (Fig. 40).

The apical cells of filamentous Zygnemaceae are generally rounded at the free end, but they often become elongate and irregular.

The filamentous forms consist of but one series of cells, longitudinal septa rarely making their appearance; they have

¹ Borge, Ueber die Rhizoidenbildung einiger fadenförm. Chloroph., Upsala, Nya Tidnings Aktieb., Tr. 1894. Wille, Freshw. Alg. U. S., Pl. CXLII, f. 7, 8.

² Cf. *Zygnema pachydermum*, West, Alg. from W. Indies, Journ. Linn. Soc. Bot., Vol. xxx, Pl. XIII, Figs. 12–15.

³ Reinsch, Contrib. Alg. et Fung., T. xviii, f. 12 and 15.

⁴ Jacobsen in Journ. de Botanique, Copenhagen, 1874, t. viii, f. 31.

been noticed in an incomplete form in *Zygnema pachydermum*, var. *confervoides*¹.

With regard to the effect of temperature on the Conjugatae, a paper by Alfred J. Ewart, entitled 'On Assimilatory Inhibition in Plants,' has recently appeared², in which the author states (p. 395) that 'freshwater Algae . . . are not very resistant to cold, all those examined being killed by being frozen. This statement we cannot agree with, as we have found them to be very resistant to cold, and as a large number of the plants belonging to the Alpine Algal flora are Conjugates we illustrate the matter by a few examples.

We have melted out of the ice from Mitcham Common, Surrey, excellent examples of *Spirogyra cataeniformis* in a state of conjugation, the vitality of which was in no way impaired. From Frizinghall, W. Yorks., we have also melted out of the ice hundreds of specimens of *Closterium Leibleinii*, which subsequently remained in a perfectly healthy and normally active condition (moving to that side of a vessel exposed to most light, just as we find all other species of Desmids to act), and in each of these cases the specimens examined had been frozen for over fourteen days. These facts alone disprove the generality of Mr. Ewart's statement; but let us now consider some still more convincing ones. Many of the upland tarns of Yorkshire, the Lake District, the Scotch Highlands, and other places, are situated at altitudes of over 2,000 feet, some of them being much higher, and the water in them is of a relatively low temperature even in summer. For many months in the winter these tarns are frozen, and the small ones often buried in deep snow drifts, although by the middle of summer they are fairly crowded with filamentous Algae, of which the most abundant forms are small species of *Mougeotia*. We have never yet seen these species of *Mougeotia* in conjugation from these altitudes³,

¹ Cf. West, l. c., Pl. XIV, Fig. 5.

² Journ. Linn. Soc. Bot., Vol. xxxi, 1896, No. 217.

³ We have examined sterile species of this genus, obtained at 3,000 feet in the Scotch Highlands and 6,500 feet in Switzerland.

and in ordinary seasons in all probability they never do conjugate. How, then, are they preserved throughout the winter? It must be by means of the survival of some of the plants (without the formation of spores) through the prolonged freezing they have to undergo, which is followed by their active division in the spring. We can also mention instances of this in the Desmidiaceae. There is a small peaty ditch in Eldwick, on the edge of Rombald's Moor, W. Yorks., in which countless numbers of *Micrasterias denticulata* have occurred in a perfectly pure state for very many years. We have examined this ditch carefully at all times of the year, and always find some specimens of this Desmid, even when it is frozen; but never once have we come across a single zygospore from this locality, although constant search for them has been made. Here, then, the perpetuation of the species must be dependent upon the survival of some of the ordinary vegetative plants through the winter; and we may mention that the locality is a bleak one, its altitude being near 1,000 feet, and the water is generally frozen for some weeks during the winter.

It is also worthy of note that in all the contributions to the Algal Flora of the Arctic regions yet published, the occurrence of the zygospores of Desmids has seldom been mentioned, though many species are recorded from places noted for their intense cold in winter, for instance, Greenland, Spitzbergen, Nova Zembla, and northern Siberia. We have a species of *Oscillatoria* from a valley in the Davos Platz district in Switzerland, collected by Mr. A. Howard in August, 1897, from a stream at 8,000 ft. elevation with the temperature of the water at 5°C. This is the summer condition, and the winter one may be easily imagined; we must therefore reject Mr. Ewart's statement that 'owing to their slight powers of resistance to cold, the temperatures to which they can be exposed without being permanently injured are necessarily relatively high.' Stationary masses of water, such as pools and small lakes, even at this altitude, attain during summer a comparatively warmer temperature than the streams; a lake

close to the above-mentioned locality, and at the same altitude, had a water-temperature of 20°C. In this lake fine examples of *Staurostrum Meriani* occurred, and it is evident that they must be capable of withstanding frost for a few months during the winter. We have found specimens of *Closterium striolatum* and *Cylindrocystis Brebissonii*¹ in material collected on the top of Green Hill, Clova Mts., at 2,700 ft., from water which was derived from melting snow close by, and which could not be more than 1° or 2°C. These specimens were collected by Mr. J. H. Burkill in May, 1897. We also point out the four following papers dealing entirely with snow-floras:—

- S. Berggren: Alger från Grönlands inlandis (Öfvers. K. Vet.-Akad. Förh. 1871, No. 2).
V. B. Wittrock: Om snöns och isens flora, särskildt i de arktiska trakterna (A. E. Nordenskiöld, Studier och forskningar föranleda af mina resor i höga norden), Stockholm, 1883.
G. Lagerheim: Bidrag till kännedomen om snöfloran i Luleå Lappmark (Botanisk Notiser, 1883, Heft 6), Lund, 1883.
G. Lagerheim: Die Schneeflora des Pichineha, ein Beitrag zur Kenntniss der Nivalen Algen und Pilze (Bericht. d. Deutsch. Botan. Gesellsch., Jahrg. 1892, Bd. x, Heft 8), Berlin, 1892.

In the same paper by Mr. Ewart we also find (p. 439) the following statement: 'It is well known that prolonged exposure to direct sunlight is fatal to . . . many Algae.' From our own experience we should at once say that nothing could be more beneficial to Freshwater Algae than prolonged exposure to direct sunlight, provided they remain under natural conditions.

Round the margins of the two ponds on Frensham Common, Surrey, there is a belt of very shallow water, which is the home of large numbers of Algae, and these plants on bright

¹ This species occurs in pure gelatinous masses (during early spring before Easter) on the peat at the extreme summit (2,346 feet) of Great Shunnor Fell in N. Yorks.

days are not unfrequently exposed to direct sunlight from almost the rising to the setting of the sun. We have noticed this shallow water become quite warm. What is the effect of this prolonged exposure to sunlight and the increase in the temperature of the water? It is certainly not a detrimental one, because there is an acceleration in the growth of the lower green and blue-green Algae¹, and the Conjugatae form zygospores much more abundantly than they otherwise would do: we could multiply instances indefinitely, but the following one will suffice.

From Vehar Lake, Parel, Bombay, we have examined the finest specimens of *Clathrocystis aeruginosa* we have yet seen, and these are exposed to direct sunlight every day for weeks; moreover the atmospheric (shade) temperature was 96° Fahr., and that of the water 87° Fahr. The material was collected for us in 1895 by Mr. S. Tomlinson, C.E., the Government Engineer to the Waterworks.

Yet Mr. Ewart would inform us that prolonged exposure to direct sunlight is fatal! It is so (as we well know) in the small vessels of the laboratory, but not in nature².

There are four methods of reproduction in the Conjugatae: by fragmentation of the filaments (asexual); rarely in some genera by resting-cells or cysts (asexual); by conjugation with formation of zygospores or carpospores; and by aplano-spores (asexual). Temperature and climatic conditions affect reproduction only so far as to promote or prevent it; they have little effect on the method, although an increase of temperature considerably helps conjugation, and so far as we have observed, a higher altitude (which is usually accompanied by a lower temperature) favours the formation of 'cysts.'

During conjugation the activity of the filament is increased; even those cells which take no part in it show greater vigour.

¹ Specially noticeable were *Clathrocystis aeruginosa* and *Crucigenia rectangularis*, the latter with single families of 128 cells, the normal number being 16 or 32.

² The reader should consult the excellent work by Klebs entitled 'Bedingungen der Fortpflanzung bei einigen Algen und Pilzen,' chapter on Conjugatae, in which he shows (among other things) that they bear intense light very well, and that bright light is necessary for conjugation.

We have often noticed these cells begin to divide actively and ultimately produce new filaments (Figs. 62 and 65). That their activity is increased is also proved by the extraordinary development from these cells of swellings and processes, which so often occurs as an accompaniment to conjugation (cf. Fig. 58). Moreover, as previously mentioned, some cells by reason of this activity are induced to put out conjugating-tubes, which, not meeting with others, and not being able to fulfil their proper function, ultimately become rhizoids or organs of attachment.

FAM. I.—ZYGNEMACEAE.

Sub-fam. I.—*Mesocarpeae.*

This sub-family includes two genera, *Gonatonema*, comprising but four species, and *Mougeotia*, comprising upwards of thirty species.

I. *Mougeotia*. This genus now includes, and we think quite correctly, the genera *Mesocarpus*, *Craterospermum*, *Plagiospermum* and *Staurospermum*, all those characters regarded in the past as generic distinctions having been found by Wittrock¹ to be present in one species (*M. calcarea*). Many other observations also tend to prove the identity of these so-called genera. The conformation of the young zygospores of *M. uberosperma* (not taking into consideration the four outer processes) is decidedly that of a *Staurospermum*, whereas the adult zygospores are almost globose (cf. Figs. 42 and 43).

In this genus an axile plate-like chromatophore is present in each cell; and so far as our observations go, there is but one exception to this, *M. capucina* having an axile sub-irregular rod of chlorophyll connected to the lining primordial utricle by fine colourless threads of protoplasm. The rest of the cell-cavity between these meshes of protoplasm is filled with purple-coloured cell-sap²; the nucleus also stands out

¹ V. B. Wittrock, Om Gott. och Ol. Sotv. Alg., Bih. till K. Sv. Vet.-Akad. Handl., Bd. i, No. 1, Stockholm, 1872.

² Cf. remarks on this species by Lagerheim, Ueber das Phycoporphyrin, Vidensk.-Selsk. Skrift., I. Mathem.-natur. Kl., Kristiania, 1895, No. 5, p. 6 (Sep.).

very plainly, being opposed to the axile rod of chlorophyll towards the centre of the cell.

The method of conjugation and the formation of the rudimentary sporocarp are very well known, but we wish to point out a few irregularities which are occasionally met with. It is no uncommon thing for conjugation to take place through the end of one of the cells, the latter cell forming no conjugating-tube; we have observed this in *M. parvula* (Fig. 44) and *M. nummuloides*. We have also seen a hybrid example (Fig. 55), corresponding to *Spirogyra maxima*, var. *inaequalis* and others (Figs. 70 and 71), in which conjugation has taken place between two species of different thickness. Fig. 45 is an example of *M. recurva* in which three cells were conjugating to form one spore (analogous to other cases in *Spirogyra* and *Zygnema*; cf. Fig. 66).

There is a most noticeable disparity in size between the carpospores of different species in relation to the size of the sterile cells of the sporocarp (cf. Figs. 47 and 46 of *M. nummuloides* and *M. angolensis*, also similar remarks relating to the aplanospores of *Gonatonema*). An example of *M. capucina* from the New Forest is figured, in which there are two carpospores present in the same sporocarp (Fig. 48). This is analogous to the double zygospores of *Closterium lineatum* and certain abnormal cases of *Spirogyra* (Figs. 75 and 76). The carpospores of *M. irregularis* are worthy of note for the extreme irregularity of their spore-membrane (Figs. 56 and 57).

Spores resembling aplanospores are occasionally found in *Mougeotia*, but we have not been so fortunate as to meet with any. They are spores produced by the division of the original cell¹, and not by a rounding off of the contents as in *Gonatonema*; they may be regarded as carpospores formed from sporocarps (consisting of two or three cells) produced without conjugation, but possibly in consequence of the

¹ Wittrock, l. c., t. ii, f. 7 s, s (pseudospora tripartitione (more Staurospermi) sine copulatione formata), et 8 m, m (pseudospora bipartitione (more Mesocarpi) sine copulatione formata).

stimulus which has already caused conjugation to take place in a distant part of the filament.

Indications of sexuality are to be found in the Mesocarpeae, but they are much less marked than in the Zygnemeae. The spores are often seen to be nearer one filament, and the conjugating-tubes of that filament to be thicker and shorter than those of the other (cf. Fig. 47); hence the former may be looked upon as a female and the latter as a male filament. As these scarcely appreciable indications of sexuality are often absent, we may regard the Mesocarpeae as having lost almost all traces of differentiation into male and female gametes.

2. **Gonatonema.** The sterile specimens of this genus are undistinguishable from those of *Mougeotia*, although the chromatophore is more an axile rod (as in *Mougeotia capucina*) than an axile plate; the species of this genus are also of very much rarer occurrence than those of *Mougeotia*. The spores are asexual and parthenogenetic, and the whole contents of the cell are utilized in their formation.

During the formation of the spore and just before the appearance of the thin membrane round the cell-contents, we have noticed, both in *G. Boodlei* and *G. tropicum*, that in a few of the cells a more or less indistinct division of the cell-contents into two portions takes place. As to the precise import of this we cannot at present offer an opinion. Is it merely a chance arrangement of the cell-contents, or may it not be some slight retention of the last traces of ancestral sexual characters? Much is yet to be observed from the study of living *Gonatonema* during the active formation of spores.

It is also noticeable that the great difference in size between the spores of *G. Boodlei* and *G. tropicum* is more than can be accounted for by the difference in cubical capacity of the vegetative cells and contained cell-contents, the latter being almost the same in each case.

Figs. 1-15 illustrate the spore-formation in two species of *Gonatonema* which as yet have not been figured.

Sub-fam. 2.—*Pyxisporeae*.

This family is represented solely by the genus *Pyxispora* obtained from West Central Africa¹. The vegetative cells, which are about 12–13.5 μ in thickness, contain two chromatophores very similar to those present in *Zygnema*, and in the sterile condition the plant could not be distinguished from the vegetative filaments of a species of the latter genus; each of these chromatophores has a small central pyrenoid. The conjugation is scalariform and similar to that present in the Mesocarpeae, resulting in an immediate tripartition into a sporocarp consisting of two sterile cells and an intervening carpospore.

The characters of this carpospore are unique, and sharply demarcate this genus from any other in the Zygnemaceae. It is broadly elliptical with rounded poles: it is disposed transversely to the longitudinal axes of the conjugating filaments, and around its edge, in the plane of its shorter diameter, is a small annular ridge marked by a circumscissile crack.

Some further figures of this interesting genus are given (Figs. 53 and 54).

Sub-fam. 3.—*Zygnemeae*.

This is the largest family of filamentous Conjugatae, and includes the five genera, *Zygnema*, *Pleurodiscus*, *Spirogyra*, *Sirogonium*, and *Debarya*.

The chromatophores of the genus *Spirogyra*, according to some botanical text-books, 'take the form of green spiral bands with toothed edges'; this is often true, but throughout the genus they exhibit much variation, there being every gradation between the slender, perfectly smooth spirals of *S. neglecta* with their axile uniform series of pyrenoids, and the broad serrated spirals of *S. nitida* and *S. porticalis*, containing scattered pyrenoids of various sizes. In fact, the

¹ West and G. S. West, Welw. Afric. Algae, Journ. Bot. 1897, p. 39.

characters of the chromatophores are not only remarkably constant but also widely different in many of the common species of the genus; those species with toothed edges to the chromatophores are however the most frequent.

The presence of straight chromatophores in the genus *Sirogonium* is in itself of no generic value, as those of *Spirogyra majuscula* are quite as straight, if not straighter, but the method of conjugation seems to us quite distinctive.

Owing to the somewhat irregular thickening of the walls of some species of *Zygnema*, such as *Z. ericetorum* and *Z. pachydermum*, and the more or less non-stellate condition of their chromatophores, they can be readily mistaken in the sterile condition for species of *Rhizoclonium* (a genus of Confervaceae Isogamae), and the short, few-celled branches of *Z. pachydermum*¹ render it still more liable to an error of this nature.

There are two modes of conjugation, *scalariform* and *lateral*, the details of which have been minutely followed out. In the former the cells of two or more filaments take part in the formation of the zygospores, but in the latter, conjugation takes place between the adjoining cells² of one filament only.

If conjugation is affecting only a portion of a filament, the increased activity along its whole length (as previously mentioned) often causes the cells of its free portions to develop conjugating-tubes, which, after making futile attempts to meet with a fellow, become more or less irregularly branched³; such is also the case in many examples in which conjugation has been interrupted.

On examining a large number of conjugated examples of *Spirogyra* or *Zygnema*, there is one prominent feature which at once strikes the observer, and on this point we cannot

¹ West, Algae from the West Indies, Journ. Linn. Soc. Bot. Vol. xxx, Pl. XIII, Figs. 12-15.

² In Cooke's Brit. Freshw. Alg., Pl. XXXI, f. 3 c, an example of lateral conjugation is shown between two non-adjacent cells.

³ Cf. West, Sulla Conj. delle Zygn., Notarisia, 1891, Vol. vi, t. 12, Figs. 3, 5-7, and 9.

do better than quote Bennett and Murray¹. 'As De Bary has pointed out—and his statement is confirmed by nearly all more recent observers—the direction of conjugation is clearly governed by some physiological law, the movement of the protoplasm between the two filaments almost invariably taking place in one direction only, so that one of the two conjugating filaments is entirely emptied, while the other is filled with zygospores.' In this paper we shall refer to the filament filled with zygospores as the female, and the emptied one as the male filament.

As a rule a zygospore is formed by the fusion of the contents of two conjugating cells, but very rarely it is seen that three cells (two male and one female) have participated in its formation² (vide Fig. 66); in this way even three filaments may be concerned in the production of one zygospore. That this manner of conjugation is abnormal is proved by the larger number of failures than of completed attempts (vide Figs. 67 and 69). In those species belonging to the sub-genus *Zygogonium*, in which the zygospore is formed in the conjugating-tube, conjugation between three cells entails the production of two somewhat smaller zygospores, as in the example figured (Fig. 63).

Two filaments are generally concerned in an example of scalariform conjugation, but three, four, five, and even six are not uncommonly seen³. In such cases we have to deal with either polygamy or polyandry, and after the examination of hundreds of examples, we can confirm Bennett's statement that the former is rather more frequent, the ratio of the frequency of polygamy to polyandry being about 1.6 : 1.

During conjugation the filaments frequently assume a darker colour, this being most marked in *Spirogyra angolensis*, in which species they become blackish- or brownish-purple.

¹ Bennett and Murray, A Handbook of Cryptogamic Botany, p. 266.

² Cf. *Z. cruciatum* in West, Sulla Conj. delle Zygn., l. c., t. 13, f. 13; also *Spirogyra*, sp. in Borge, Siber. Chlorophy., Bih. t. Sv. Vet.-Akad. Handl., Bd. 17, Afd. 3, No. 2 (1891), t. i, f. 2.

³ West, l. c., t. 12, f. 1.

Normal conjugation depends to a certain extent on the general surroundings of the filaments, many hindered and consequently irregular examples being met with in every gathering in an active state of conjugation. On rare occasions hybrids are produced, one species of *Spirogyra* conjugating with another of different thickness; examples of this are *S. maxima*, var. *inaequalis*¹, and some smaller species gathered in 1893 on Mitcham Common, Surrey (Figs. 70 and 71). Several abortive attempts at hybridism were seen in this gathering, the two examples figured being the only two observed with thick-walled zygospores. These spores were of variable form and dimensions, and were present in both filaments.

In contradiction to Cooke, we find scalariform conjugation to be much commoner than lateral conjugation, as may be gathered from the following table.

Species.	No. of gatherings of scalariform conjugation examined during the past few years.					No. of gatherings containing lateral conjugation examined in same period.		
<i>S. affinis</i> ...	...	...	...	1	...	...	...	3
<i>S. angolensis</i> ...	...	...	...	1				
<i>S. arcta</i> ...	...	...	...	2				
<i>S. bellis</i> ...	...	...	...	6	...	...	...	1
<i>S. calospora</i> ...	...	...	...	1				
<i>S. cataeniformis</i> ...	...	...	...	4				
<i>S. communis</i> ...	...	...	...	5				
<i>S. condensata</i> ...	...	...	...	9				
<i>S. crassa</i> ...	...	...	...	9	...	...	...	1
<i>S. cylindrospora</i> ...	...	...	...	1				
<i>S. decimina</i> ...	...	...	...	3				
<i>S. dubia</i> ...	...	...	...	—	...	...	...	1
<i>S. fusco-atra</i> ...	...	...	...	1				
<i>S. gracilis</i> , and v. <i>flavescens</i> ...	...	...	...	13	...	...	...	1
<i>S. Grevilleana</i> ...	...	...	...	4				
<i>S. inflata</i> ...	...	...	...	1	...	...	...	2
<i>S. insignis</i> ...	...	...	...	4				
<i>S. Jurgensii</i> ...	...	...	...	2	...	...	...	1
<i>S. longata</i> ...	...	...	...	13				
<i>S. Lutetiana</i> ...	...	...	...	1				
<i>S. majuscula</i> (<i>S. orthospira</i>) ...	...	...	...	2				
<i>S. maxima</i> (<i>S. orbicularis</i>) ...	...	...	...	1				

¹ Wolle, Freshw. Alg. U. S., Pl. CXXXVIII, Figs. 5 and 6, and Pl. CXLII, Figs. 5 and 6.

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Species.	No. of gatherings of scalariform conjugation examined during the past few years.				No. of gatherings containing lateral conjugation examined in same period.			
<i>S. neglecta</i> v. <i>ternata</i>	...	...	1	...	...	...	1	
<i>S. nitida</i>	...	...	17	...	...	...		
<i>S. porticalis</i>	...	...	3	...	...	...		
<i>S. setiformis</i>	...	...	2	...	...	...		
<i>S. Spreeiana</i>	...	...	1	...	...	...		
<i>S. tenuissima</i>	...	...	—	...	...	...	16	
<i>S. varians</i>	...	...	6	...	...	...	4	
<i>S. velata</i>	...	...	1	...	...	...		
<i>S. Weberi</i>	...	...	7	...	...	...	1	
<i>S. Welwitschii</i>	...	...	1	...	...	...		
Total	...	...	123	...	...	...	32	

Lateral conjugation is much rarer in *Zygnema* than in *Spirogyra*, and although it is figured in various works, we have never yet seen an example of it. It is figured by Schmidle¹ in this genus in a species which he names *Zygnema* (*Zygogonium*) *Heydrichii*, but of which he gives no proper diagnosis².

Scalariform conjugation being far more predominant, we may say that lateral conjugation is the exception rather than the rule, and in view of this we may regard it with some amount of truth, as brought about by conditions unfavourable to conjugation in the natural or scalariform way. It may be thus considered to a certain extent as abnormal, and to what extent this abnormality is carried may be gathered from a consideration of Fig. 68 (drawn from an example from Mitcham Common, Surrey), in which specimen conjugation has taken place through the ends of the cells, and the conjugating cells have become genuflexed near their junction.

¹ W. Schmidle, Zur Entwicklung einer *Zygnema* und *Calothrix*, Flora, 1897, Bd. 84, Heft 2.

² This species seems to us to be only a *Zygnema spontaneum* with lateral conjugation. Nordstedt only found aplanospores when he described the species, but we have since found the zygospores (cf. Figs. 60 and 61) produced by scalariform conjugation (Journ. Bot., Feb. 1897, p. 40). The zygospores seen by Schmidle and produced by lateral conjugation agree in every way with those we saw in *Zygnema spontaneum*; moreover, the plants are of the same dimensions.

That it is not a perfectly normal condition is also proved by the numbers of failures where lateral conjugation was attempted¹.

Against the sexuality of the Zygnemeae only two plausible objections can be raised ; these are the phenomena of *lateral* and *cross-conjugation*. It is clear that in the case of lateral conjugation sexual differentiation of the individual cells and not of the whole filaments must have taken place, and concerning this Bennett and Murray² state, 'that there is some differentiation of this kind would appear from the fact that when lateral conjugation takes place in a group of four cells the zygospores are formed in the two centre cells, which may be regarded as female.' This we find to be the case, as may be seen from the figures of *S. furgensii* and *S. inflata* (Figs. 72 and 73). Under certain conditions why should not this individual differentiation take place? Why should not the cells in a filament of *Spirogyra* or *Zygnema* be considered in a sense as only partially developed, further physiological changes taking place just antecedent to conjugation, which give the cells the characters either of a germ-cell or a sperm-cell? We see no reason for regarding the filaments as sexual until conjugation is about to commence, and then instead of the reproductive cells being specially cut off (as in *Temnogametum*), the contents of the individual cells undergo a profound physiological change, being imperceptibly converted into isogamous gametes. Also if the conditions of environment be such (as in an isolated filament) as to render it impossible for the whole of the cells of one filament to become of one sex, why should not individual sexuality of each cell be assumed? In some cases scalariform and lateral conjugation occur in the same filament³, and within a few cells of each other. We have mentioned that a filament engaged in conjugation has the vigour of all its cells largely augmented, and may not the activity of the changes converting the ordinary vegetative

¹ West, Sulla Conj. delle Zygn., l. c., t. 12, f. 8.

² Bennett and Murray, Cryptogamic Botany, p. 267.

³ Petit, Spirogyra des envir. de Paris (Paris, 1880), Plate I, f. 13.

cells into reproductive cells be so far modified at different parts of the same filaments that differentiation of sex is brought about? Regarding the cells in this light, each one may be considered as an individual plant; and why not? Each individual cell is capable of living apart from its neighbours, obtaining its own nourishment from the surrounding medium, and its life is in no way dependent upon the other cells of the filament. Moreover, if we allow that the Zygnemeae are comparable to the filamentous Desmidiaceae, we find that the latter readily dissociate into separate cells, which are not at all affected by their isolation (cf. p. 30 supra). The only important function of the assumption of a filamentous condition seems to us to be in the greater facility for conjugation afforded by the entanglement of the gregarious filaments.

Before considering cross-conjugation it will be as well to consider some examples of *interrupted conjugation*. A keen observer is continually coming across instances in which conjugation has by some means been brought to an abrupt termination before the proper formation of the zygospores has taken place, and in these cases the spores formed are very variable. It may be that something has caused a cessation of the activity along the whole filament, or that conjugation has been stopped between two cells only. Fig. 69 is an illustration of the latter, the forcible pressure of a second male conjugating-tube having narrowed the channel of communication to such an extent that union of the contents of the gametes was rendered impossible. The former is, however, much the most frequent. Sometimes the spore in the germ-cell is not of its true form¹, and occasionally two spores, one large and one small, are present in place of the normal one² (Figs. 75 and 76). When the conjugation has by some influence been hastened, a zygospore is often produced from only a portion

¹ Cf. *Spirogyra Groenlandica*, Rosenvinge in Öfvers. K. Vet.-Akad. Förh., 1883, No. 8, t. viii, f. 1-11.

² West, Sulla Conj. delle Zygn., l. c., T. XIII, Figs. 27, 28; binate spores in *Spirogyra communis*. A. Hansgirg, in Hedwigia, 1888, Hefte 9 u. 10, T. X, f. 6; binate spore in *Spirogyra Weberi*.

of the contents of the cells, and in these cases the spore is generally in the female filament (Fig. 74). Some examples have a spore in each conjugating cell (Figs. 77–80), and as a rule that in the female cell is of larger size. Occasionally the spores are of equal size (Fig. 78), and in rare cases the largest spore is in the male (?) cell.

All this leads up to cross-conjugation, which is the only other objection to sexuality. By *cross-conjugation* we mean scalariform conjugation with the formation of perfectly normal zygospores in each of the conjugating filaments, and we have seen but a solitary example of this amongst the thousands of conjugating specimens examined. This was a specimen of *Spirogyra gracilis* (Fig. 81) found in a gathering of Desmids obtained from a mass of *Utricularia minor* in a bog near Bowness, Westmoreland. As will be seen from the figure, there are two female cells and one male cell in one filament, and two male cells and one female in the other; moreover, the zygospores in each filament are perfectly normal, and the conjugation is complete and also normal. Now this is explicable, as in the case of lateral conjugation, by supposing that each individual cell has assumed sexuality. That the sexual condition of the filaments is the same in both lateral and cross-conjugation is proved by the occurrence of the former in both male and female filaments, which are also conjugating in a scalariform manner¹.

As a rule examples with zygospores in both filaments only exhibit a *false cross-conjugation* (Fig. 64), the zygospores in one filament being smaller than those in the other. This fact tends to prove that numerous attempts at cross-conjugation result in failures, normal zygospores not being produced, and together with its extreme rarity serves to show to what degree it is abnormal.

From the foregoing statements we have shown that lateral and cross-conjugation *are* explicable from a sexual point of view, and that there is no reason to regard the Zygnemeae as otherwise than sexual.

¹ Petit, in Bull. Soc. Botan. France, févr. 1874, t. xxi, Pl. I, f. 2.

Other minor observations have also been brought forward as a proof of this sexuality, such as the comparative lengths of the cells and the relative thickness of the male and female conjugating-tubes. These are, however, of little value, although it is certainly a fact that in the majority of instances the female conjugating-tube is shorter and thicker than the male (Figs. 66, 67, 79–81); also the female cells are often so swollen that all trace of a conjugating-tube is lost¹ (Figs. 67 and 81).

In a gathering of *Spirogyra velata* from a stream at Baildon, W. Yorks., several zygospores were noticed which did not assume a thick wall, but germinated immediately after their formation (Figs. 84 and 85).

The formation of spores without conjugation takes place not uncommonly in the Zygnemeae; these asexually-produced spores are called aplanospores, and are produced from the contents of a single cell. We have noticed them in *Zygnema leiospermum* (Fig. 83), *Z. pachydermum*² and *Spirogyra varians* (Fig. 82). They have been observed by Nordstedt³ in *Zygnema spontaneum* and by Wille⁴ in *Z. cruciatum*. In all cases the aplanospores are somewhat smaller than the zygospores, have a thinner membrane, and as a rule they are spherical, no matter what the form of the zygospore. We may also quote a remark made by Petit⁵ concerning *Spirogyra mirabilis*, in which species the spores are produced without conjugation. He writes: 'Cette très curieuse espèce ne conjugue pas et ne laisse voir aucun tube copulateur; à une certaine époque de la vie de la plante, les cellules se renflent vers le milieu, l'endochrome se partage en deux parties qui se concentrent sous forme de globule aux deux extrémités de la cellule; il se forme ainsi une différenciation entre les parties de l'endo-

¹ Petit, *Spirogyra* des envir. de Paris, Pl. IX, f. 10; West, *Freshw. Alg. W. Ireland*, Journ. Linn. Soc. Bot., Vol. xxix, T. XVIII, f. 5.

² West, *Alg. W. Indies*, Journ. Linn. Soc. Bot., Vol. xxx, p. 266, Pl. XIII, f. 9, 10.

³ O. Nordstedt, *De Alg. aq. dulc. et Char. Sandvic*, p. 17, T. I, f. 23, 24.

⁴ N. Wille, *Ferskv.-alg. Nov. Semlj. Öfvers. K. Vet.-Akad. Förh.*, 1897, No. 5, p. 63, T. XIV, f. 87.

⁵ Petit, l. c. p. 14.

chrome. Bientôt les deux globules se rapprochent vers la partie renflée de la cellule et finissent par se réunir en constituant ainsi la zygospore.'

The vegetative cells of the genus *Debarya* are like those of *Mougeotia*. The conjugating-tubes of *D. glyptosperma* are long, some of them very long, and when they do not happen to meet with a fellow they often become club-shaped. As the cell-contents pass into the conjugating-tube the chromatophore takes the form of a loop, and a peculiar change comes over the empty cells as the zygospore is being formed; they become very clear and refractive, and a series of striations parallel to the transverse septa become visible. After this has taken place the cells have the appearance of solidity, this appearance being possibly due to annular thickenings deposited inside the cell-wall on the receding of the protoplasm during conjugation; in any case this character stands out distinctly in both old preserved specimens and in living ones. The large size of the zygospore is also a noticeable feature.

In *D. laevis* the conjugating-tubes are shorter and thicker and the spores are proportionately smaller. We give a figure of a specimen of this plant which has conjugated in a remarkable manner (Fig. 58). It has two to four pyrenoids in each chromatophore.

Mougeotiopsis, a genus recently described by Palla¹, seems to us to differ in no way from *Debarya*, except in the absence of pyrenoids. This is certainly in itself an insufficient generic character, and might probably be caused by the conditions under which the plants were growing. Lagerheim² states that *Mougeotia laevis* belongs to *Mougeotiopsis*; it is, however, a true species of *Debarya*, and as stated above certainly contains pyrenoids. The zygospores of both *Debarya laevis* and *Mougeotiopsis calospora* are scrobiculate, which seems to further indicate the identity of these two genera.

¹ E. Palla, Ueber eine neue, pyrenoidlose Art und Gattung der Conjugaten, Ber. der Deutsch. Botan. Gesellsch., Jahrg. xii (1894), Heft 8, pp. 228-236, T. XVIII.

² G. Lagerheim, Ueber das Phycoporphyrin, Vidensk.-Selsk. Skrift., I. mathem.-natur. Kl., Kristiania, 1895, No. 5, p. 16 (Sep.).

Fam. II.—TEMNOGAMETACEAE.

This order, defined as follows, 'Ordo novus *Conjugatarum*, conjugatio solum inter cellulas speciatim abstrictas,' was instituted a short time ago¹ to include a West African plant differing in a marked way from all the genera of Conjugatae. The sole representative plant is *Temnogametum heterosporum*, which has a great superficial resemblance to some species of *Mougeotia*. The vegetative cells are precisely like those of the latter genus, each cell being provided with a more or less plate-like chromatophore, in which a single series of from one to six small globose pyrenoids is embedded.

The conjugation is remarkable, owing to the fact that the reproductive cells are specially cut off from the rest of the plant; they are short, isogamous gametes, being about a quarter or a sixth part the length of the ordinary vegetative cells, and are cut off at intervals along the filaments. Some are cut off singly and others in pairs; in the former case the conjugation is scalariform, in the latter it is lateral. In scalariform conjugation the contiguous faces of the gametes become swollen, these swellings being merely short, rounded conjugating-tubes which finally unite (cf. Fig. 49), their union being followed by the bending towards each other and ultimate coalescence of the gametes to form a somewhat cruciate zygospore (Fig. 50). As previously mentioned², this zygospore at first sight very much resembles the central cell (or carpospore) of the five cells constituting the sporocarp of those species of *Mougeotia* belonging to the section *Staurospermeae*, but on closer examination the four contiguous cells are seen to possess their complete cell-contents, and to have taken no part in the formation of the zygospore. In the case of lateral conjugation, the pairs of cells become a little oblique or somewhat swollen on one side and then unite, this coalescence giving rise to an obliquely subcylindrical zygospore

¹ West and G. S. West, *Welw. Afric. Algae*, Journ. Bot., Feb. 1897, p. 37.

² West and G. S. West, *l. c.*

(Fig. 52), which has a considerable resemblance to the aplano-spore of some species of *Gonatonema* (e. g. *G. notabile*). Soon after the coalescence of the gametes the wall of the zygospore increases much in thickness.

One case was noticed in which a solitary gamete in one filament was conjugating with one of a pair in another filament (Fig. 51).

There is no perceptible sexual differentiation between these gametes, but owing to the fact that they are specially cut off, this family must be regarded as considerably removed from the other families of the Conjugatae, though it is not so highly specialized as the Mesocarpeae.

Fam. III.—DESMIDIACEAE.

The chromatophores in the Desmidiaceae are disposed more or less symmetrically in the two halves of the cell, either as central masses of chlorophyll arranged in relation to certain pyrenoids, or as parietal and somewhat pulvinate masses containing scattered pyrenoids.

In some genera these pyrenoids are definite; the majority of *Cosmaria* have either one or two in each semi-cell, and the great majority of *Staurostra* contain one large one in the centre of each semi-cell. In a paper published by Lutkemuller¹ entitled 'Beobachtungen über die Chlorophyllkörper einiger Desmidiaceen' the author demonstrates the irregularity of the pyrenoids in certain species. No doubt many irregularities are to be found in most Desmids, but as a general rule we find the central pyrenoids very constant in character. One of the species mentioned by Lutkemuller as very variable in this respect is *Cosmarium pyramidatum*, normal specimens of which should contain two pyrenoids in each semi-cell. Our experience of this species confirms his observations, but we may add that in this respect it is the most variable species that we have yet examined.

¹ Oesterreich. Botan. Zeitschr., 43. Jahrg. 1893, No. 1.

Specimens of *Cosmarium ornatum* occasionally have irregular pyrenoids, but we have not yet seen more than one example in a hundred. Amongst an immense number of examples of *Cosmarium sphagnicolum*, collected in early spring in N. Yorks. from moorland pools nearly filled with *Sphagnum cuspidatum* and *Ptilidium ciliare*, many variations were observed in the chromatophores, and the pyrenoids which were normally one in each semi-cell, varied from one to three (cf. Figs. 34–36). This variability of the chromatophores has been described in *Penium minutum*¹.

We figure four cells of *Hyalotheca neglecta* (Figs. 30–33), which show considerable variation in the pyrenoids, but these were only found after the examination of a very large number of filaments. This irregularity is usually found after rapid division, in the same way that abnormality of form is probably caused (cf. Fig. 39 of *Euastrum didelta*).

This subject is one concerning which much work is yet desirable, as several doubtful genera have been founded on the structure and arrangement of the chromatophores; e.g. *Pleurotaeniopsis*, *Pleurenterium*, &c.

Sexual (?) reproduction is by conjugation and formation of zygospores, the conjugating cells generally not being differentiated. Double spores are formed in *Closterium lineatum*, *Cylindrocystis diplospora* and *Penium didymocarpum*, and are analogous to those in the Mesocarpeae and homologous with those in the Zygnemeae. In some rare cases three (or even four) cells have participated in the formation of a zygospore². The zygospore is formed *between* the conjugating cells in all Desmids except *Desmidium cylindricum*. In this species it is formed *within* the female cell³ as in *Spirogyra*

¹ Cf. remarks by Lutkemuller under *Docidium baculum*. Also Journ. Bot., March, 1895, p. 65.

² Cf. *Staurastrum teliferum* in West, Freshw. Alg. W. Ireland, Journ. Linn. Soc. Bot., Vol. xxix, Pl. XXIV, f. 5; *Cosmarium rectisporum*, W. B. Turner, Freshw. Alg. E. India, K. Sv. Vet.-Akad. Handl., Bd. xxv, No. 5, T. X, f. 16e; also *Closterium Pritchardianum*, West and G. S. West, Freshw. Alg. S. of England, Journ. Royal Micr. Soc., Pl. VI, Fig. 5, December, 1897.

³ Ralfs, Brit. Desm., T. II, f. 1, e, f, g, h, i, k; Wolle, Desm. U. S., Pl. III, f. 4;

and *Zygnema*, although, as in most filamentous Desmidiaceae, the filaments break up before conjugation. So far as we know, this is the only case of differentiation of the conjugating cells met with in the whole of the Desmidiaceae. Boldt¹ figures a 'forma monstrosa' of *Hyalotheca dissiliens* with the zygosporangium in one of the cells, and Joshua² mentions a case where *Hyalotheca dissiliens* was conjugated like *Desmidium cylindricum*. Fig. 37 is also an approximation to this stage in an example of *Hyalotheca dissiliens*. What is this 'monstrous form' of conjugation in this species? Abnormal it certainly is as compared with ordinary conjugated examples, but is it not a case of reversion to some ancestral type of conjugation, represented at present by the Zygnemataceae, and which the Desmidiaceae have almost lost, the lingering remains of which are still found in *Desmidium cylindricum*?

Thus degeneration and loss of sexual differentiation of the conjugating cells have gone on hand in hand with the loss of the filamentous condition, the majority of filamentous forms dissociating before conjugation. An extreme morphological specialization has accompanied this loss of the filamentous condition, causing the large majority of this family of unicellular plants to be remarkable for their beauty and variety of form.

In the genus *Desmidium* conjugating-tubes are formed, and we have noticed rudimentary conjugating-tubes in some species of *Closterium*³ and in *Arthrodesmus octocornis*.

Conjugation seems to take place in many Desmids immediately after division and before the young semi-cells have had time to attain maturity⁴: for sexuality to exist

West and G. S. West, N. Amer. Desm., Trans. Linn. Soc. Bot., ser. 2, Vol. v, Pt. v, Pl. XII, f. 29.

¹ R. Boldt, Desm. fran Grönl., Bih. till Sv. Vet.-Akad. Handl., Bd. xiii, Afd. 3, No. 5, T. II, f. 33.

² W. Joshua, Notes on Brit. Desm., Journ. Bot., Vol. xx (1882).

³ In *Closterium Ehrenbergii* they are perforated protuberances at the base of the younger semi-cells; cf. West and G. S. West, Journ. Roy. Micr. Soc., 1896, p. 151.

⁴ West and G. S. West, l. c., pp. 151 and 153, Pl. III, f. 29; also W. Archer, in Quart. Journ. Micr. Soc., Vol. ii, p. 251.

under these conditions, the physiological change (previously referred to) from the vegetative to the reproductive cell must be immediately antecedent to conjugation.

Lateral conjugation is not unknown amongst filamentous Desmids. Ralfs describes¹ the conjugation of two adjacent cells in a filament of *Sphaerososma excavatum* as taking place between their flat ends, and we have seen an example of this in *Spondylosium pulchrum*, var. *planum*, from Orono, Maine, U.S.A. In these instances the filament does not fragment before conjugation, the zygospore filling up the space originally occupied by the two adjacent semi-cells of the conjugating cells.

Aplanospores are occasionally found in the Desmidiaceae; Bennett² mentions the occurrence of some spore-like bodies produced without conjugation in *Closterium*, and they are figured by Wallich³ and Turner⁴ in *Spondylosium nitens*. In a gathering of Desmids from the New Forest in which *Hyalotheca neglecta* was abundant, many of the cells contained aplanospores (Cf. Figs. 23-27); these were produced by the rounding off of the cell-contents and final assumption of a thick cell-wall. They differ in form from the globose zygospores, being elliptical, with rounded poles, and when mature their walls turn yellowish-brown.

PHYLOGENY.

In all probability the Zygnemaceae have arisen along two distinct lines from some ancestral filamentous sexual Conjugates. The Mesocarpeae may have been developed through *Debarya* along one of these lines, and from them *Temnogametum* probably struck off at some early stage. Along the other line the remainder of the existing Conjugates

¹ Ralfs, Brit. Desm., p. 67.

² A. W. Bennett, in Annals of Botany, Vol. vi, No. 21, April, 1892.

³ G. C. Wallich, Desm. Low. Bengal, Ann. Mag. Nat. Hist., Ser. iii, Vol. v, 1860, T. VII, f. 10, 11.

⁴ W. B. Turner, Freshw. Alg. E. India, K. Sv. Vet.-Akad. Handl., Bd. xxv, No. 5, T. XVIII, f. 7, 8.

were probably developed, and at a short period before the Zygnemeae became differentiated into the two distinct groups represented by *Spirogyra* and *Zygnema*, the Desmidiaceae were probably evolved by retrogression. The view that the latter may have been evolved in this way is confirmed by the occasional reversion of *Hyalotheca* to its ancestral mode of conjugation, the remains of which are still found in *Desmidium*

TABLE OF PHYLOGENY.

cylindricum. *Pleurodiscus*, which conjugates like a *Zygnema*, was probably evolved from the *Zygnema* group just after its differentiation from the *Spirogyra* group, *Pyxispora* being evolved from *Zygnema* by the assumption of a rudimentary sporophyte-generation, thus placing it on an equal level of specialization with the Mesocarpeae. *Zygnema* can be connected with *Debarya* by the subgenus *Zygogonium*, and

a parallelism of modification has gone on in the reproduction of *Spirogyra* and certain filamentous Desmids, as shown by the obsolete *Rhynchonema* and the laterally conjugated *Spondylosium*.

We cannot but regard the Mesocarpeae and the Pyxisporeae as the most highly specialized families of the Conjugatae, the formation of the sporocarp being a faint indication of an 'alternation of generations'¹.

There is a little retrogression in the Mesocarpeae, certain plants of this family (placed under a distinct genus—*Gonatonema*) producing spores only asexually. The accompanying phylogenetic table has been drawn up to graphically illustrate the conclusions we have arrived at.

DESCRIPTION OF PLATES IV AND V.

Illustrating Messrs. West's paper on Conjugatae.

PLATE IV.

Figs. 1-9. *Gonatonema Boodlei*, West and G. S. West. From Mitcham Common, Surrey. $\times 520$.

Figs. 10-15. *Gonatonema tropicum*, West and G. S. West. From Huilla, Angola, W. Africa. $\times 520$.

Fig. 16. *Mougeotia* sp. Showing organ of attachment. $\times 120$.

Figs. 17-19. *Mougeotia* sp. Showing short lateral branches. $\times 120$. From Frizinghall, W. Yorks.

Figs. 20, 21. *Spirogyra* sp. With rhizoids; from Hanka Deela, Somaliland. $\times 120$.

Figs. 22-33. *Hyalotheca neglecta*, Racib. $\times 520$. From the New Forest, Hants. 22, vegetative filament with wide gelatinous sheath; 23-27, showing formation of aplanospores; 28-29, zygosporos; 30-33, single cells with irregularity of pyrenoids.

Figs. 34-36. *Cosmarium sphagnicolum*, West and G. S. West. $\times 520$. From Mossdale Moor, Widdale Fell, N. Yorks. 34, with normal pyrenoids; 35 and 36, with irregular pyrenoids.

¹ The Mesocarpeae afford a better example amongst the lower Algae of a sporophyte-generation and a rudimentary alternation of generations than that shown by the Oedogoniaceae.

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Fig. 37. *Hyalotheca dissiliens* (Sm.), Breb. A peculiarly conjugated example from Thursley Common, Surrey. $\times 250$.

Fig. 38. *Euastrum binale* (Turp.), Ehrenb. Showing tendency to assume a filamentous condition; from Thursley Common, Surrey. $\times 250$.

Fig. 39. *Euastrum didelpha* (Turp.), Ralfs. Specimen from Wrynose, Lake District, abnormally divided. $\times 220$.

Fig. 40. *Tetmemorus granulatus* (Breb.), Ralfs. Specimen from the New Forest, Hants, one semi-cell branched. $\times 250$.

Fig. 41. *Mougeotia* sp. Showing branching; from near Lindley Reservoir, W. Yorks. $\times 250$.

Fig. 42. *Mougeotia uberosperma*, West and G. S. West. With immature spores. $\times 520$.

Fig. 43. *Mougeotia uberosperma*, West and G. S. West. With mature spores. $\times 520$.

Fig. 44. *Mougeotia parvula*, Hass. From Black Hill, near Settle, W. Yorks. $\times 520$.

Fig. 45. *Mougeotia recurva* (Hass.), De Toni. Three cells conjugating together; from Borrowdale, Lake District. $\times 520$.

Fig. 46. *Mougeotia angolensis*, West and G. S. West. From Pungo Andongo, Angola, W. Africa. $\times 250$.

Fig. 47. *Mougeotia nummuloides*, Hass. From Scarf Gap Pass, Lake District. $\times 250$.

Fig. 48. *Mougeotia capucina* (Bory.), Ag. Example from New Forest, Hants, with two carpospores. $\times 250$.

PLATE V.

Figs. 49-52. *Temnogametum heterosporum*, West and G. S. West. From Huilla, Angola, W. Africa. $\times 250$.

Figs. 53, 54. *Pyxispora mirabilis*, West and G. S. West. From Huilla, Angola, W. Africa. $\times 520$.

Fig. 55. A hybrid specimen from Strensall Common, N. Yorks.; conjugation taking place between two species of *Mougeotia*. $\times 400$.

Figs. 56, 57. *Mougeotia irregularis*, West and G. S. West. From Pungo Andongo, Angola, W. Africa. $\times 350$.

Fig. 58. *Debarya laevis* (Kutz.), West and G. S. West. Peculiarly conjugated example from Mitcham Common, Surrey. $\times 220$.

Fig. 59. *Debarya laevis*. Mature zygospor showing the scrobiculations. $\times 520$.

Figs. 60, 61. *Zygnema spontaneum*, Nordst. Mature zygospor produced by scalariform conjugation; specimens from Huilla, Angola, W. Africa. $\times 520$.

Figs. 62, 63. *Zygnema pectinatum* (Vauch.), Kutz. 62, $\times 120$; 63, $\times 220$.

Fig. 64. *Spirogyra condensata* (Vauch.), Kutz. $\times 120$.

Fig. 65. *Zygnema pectinatum* (Vauch.), Kutz. $\times 120$.

Fig. 66. *Spirogyra maxima* (Hass.), Wittr. $\times 100$. Conjugation between three cells.

Fig. 67. *Spirogyra* sp. From Huilla, Angola, W. Africa. $\times 120$.

Fig. 68. *Spirogyra inflata* (Vauch.), Rabenh. $\times 220$. From Mitcham Common, Surrey.

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- Fig. 69. *Spirogyra condensata* (Vauch.), Kutz. $\times 250$.
Figs. 70, 71. Hybrids from Mitcham Common, Surrey. $\times 250$. Conjugation between two species of *Spirogyra* of different thickness.
Fig. 72. *Spirogyra inflata* (Vauch.), Rabenh. $\times 100$.
Fig. 73. *Spirogyra Jurgensii*, Rabenh. $\times 100$.
Figs. 74, 75. *Spirogyra bellis* (Hass.), Crouan. $\times 140$.
Fig. 76. *Spirogyra velata*, Nordst. $\times 220$.
Figs. 77, 78. *Spirogyra bellis* (Hass.), Crouan. $\times 140$.
Figs. 79, 80. *Spirogyra velata*, Nordst. $\times 220$.
Fig. 81. *Spirogyra gracilis* (Hass.), Kutz. forma. $\times 350$.
Fig. 82. *Spirogyra varians* (Hass.), Kutz. $\times 520$. Aplanospore.
Fig. 83. *Zygnema leiospermum*, De Bary. $\times 520$. Showing aplanospore.
Figs. 84, 85. *Spirogyra velata*, Nordst. Two zygospores germinating immediately after formation. $\times 220$.

G.S. West ad nat. del.

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