A NEW CLASSIFICATION OF CONJUGATAE, WITH SPECIAL REFERENCE TO DESMIDS

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With 8 Tables and 2 Text-figures

CONTENTS

I. INTRODUCTION

Since the latter part of the 18th Century, thousands of references have been reported regarding Conjugatae, especially Desmids.

However, they were chiefly for Flora and very few for classification. This seems to be due to the fact that Conjugatae, particularly Desmids, have a very simple construction, for instance, in most of the species cells are unicellular or even in groups, namely, in merely unbranched filamants, and their basic characteristics are too scarce to be systematized. Therefore the classifications of them were possible only morphologically, with no further results brought out. No authorized fundamental system of classification had thus been reported till then, nor made any phylogenetic classification in detail.

In other words, a few attempts had been made systematically to classify these groups of algae but no remarkable results obtained except in suppotition

and at present, the situations thereof in phylogenetic classification of each family or geneus is not clarified yet.

The present writer, since 1927, has made an effort to clarify the Desmid-flora of Japan and its vicinity, and at the same time, has attempted to classify the Desmids on the phylogenetic sense.

Recently, the writer discovered that some definite characteristic features exist in the process of zygospore formation in conjugation, and he tried to classify these groups of algae from the phylogenetic standpoint. And, he could answer all questions and deficiencies, so far experienced in previous reports.

But, propagation of Conjugatae, especially Desmids, usualy takes place asexually so that the writer would rather supplement details of this thesis in future, because this classification is based upon the sexual propagation, which is rather an unusual case, and he is not well satisfied himself with the remarks and the observation herein noted.

However, in general, the writer believes that this new calssification would open a new way to the present standstill method of classification of Conjugatae.

Here the writer wishes to express his best thanks to the late Dr. M. MIYOSHI, Emeritus Professor of Tokyô University and to the late Dr. K. OKAMURA, Emeritus Prefessor of Tokyô Fisheries University, who gave him encouragement and aid throughout this study.

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II. HISTORICAL REVIEW

During about 250 years, since the 18th Century up to the present, thousands of references have been reported in regard to Conjugatae, especially Desmids (Ord. *Desmidiales*) yet a few papers have treated those algae from the taxonomical standpoint and most of them are the reports of the flora in various places of the world.

The following are the prominent studies which have dealt with the classi-

fication of Desmids or the flora studied from taxonomically; and from those studies we can recognize the bases or tendency of classification as well as changes of study of these groups of algae.

At first, in 1848, J. RALFS included all kinds of Desmids in one family "Desmidiaceae" in "British Desmidiaceae" and he arranged the species into 20 genera, including 2 genera of Chlorophyceae (*Pediastrum* and *Senedesmus*) by the forms of their cell-walls (filamentous or unicellular) and the characters of zygospores (existence of projections on the surface of the spore) but, the rank of each genera is not arranged systematically.

M. C. COOKE issued "British Desmids" in 1887 and he set them in one family *Desmidiaceae* belonging to Order *Zygophyceae* and he classified them into two sections, viz. *Leiosporae* and *Cosmosporae*, by the existence of projections on the surface of zygospores, and he established two new subsections in Section *Leiasporae* by the characters of forms of division and striae etc. of the cell-wall, but no attention was paid to systematic rank.

In 1892, W.E. TURNER classified the Indian Desmids in "Fresh-water Algae of E. India" and he established Cohors *Conjugatae* in Class. Chlorophyllophyceae and divided Ord. *Desmidieae* in it, thus describing 536 species belonging to 24 genera, 56 subgenera, 5 sections and 2 subsections chiefly by the morphological character of cell-wall.

In 1899, G. S. WEST issued "On variation in the Desmidiaceae, and its Bearings on their Classification" and he studied precisely the variation of 19 species of Desmids; and he adduced some evidence of relationships which exist between them. In this paper, he also cleared his hypothesis on the conception of the evolution of Desmids, illustrating the phylogeny of the genera of Desmids.

In 1901, C. E. BESSEY issued "The Mordern Conception of the Structure and Classification of Desmids" and he established 3 tribes, *Desmidieae*, *Arthrodieae* and *Cosmarieae*, in the key of the tribes by the character of the cell—filamentous or unicellular of cell, comparative length of the cell and the degree of depth of isthmus—and moreover he classified 23 genera in the key by the form of the cell and chromatophore etc., and he manifested the phylogeny of Desmids conclusively by showing a scheme.

In 1904, W. and G. S. WEST published "Monograph of the British Desmidiaceae" Vol. I and they set up one family in Order *Conjugatae* and divided into 2 subfamilies, *Saccodermae* and *Placodermae*, and moreover he subdivided in the former family 2 tribes, *Gonatozygae* and *Spirotaeniae*, and in the latter family 3 tribes, *Penieae*, *Closterieae* and *Cosmarieae*, and set up 31 genera in total. And, they showed the phylogeny of Desmids and expressed the opinion that the origin of Desmids came from "Ancestal filamentous Conjugates", and most of them developed from "Debarya Desmidioides" into two races but no basic argument is stated. This classification of both Prof. WEST above mentioned, is chiefly based upon the character of existence of division and the pore of the cellwall and the point of division of the cell-wall, numbers of layers of cell-membranes, and the comparative length and the form of the cell.

In this treatise, the present author believes that the following points are very important and interesting from the taxonomical standpoint; in the first place, there is no question that both *Docidium* and *Pleurotaenium*

belong to Tribe *Cosmarieae* but their origin is a question and in the second, both *Desmidium cylindricum* GREY. and *Hyalotheca dissiliens* (SM.) BRÉB. form zygospores in one side of conjugating cells and this fact shows that these two species are the ancestral types of *Conjugatae* in the third, they supposed that the origin of both genera *Gonatozygon* and *Genicularia* came from some filamentous ancestors.

In 1916, G. S. WEST, in "Algae" Vol. I, divided Order *Conjugatae* into 2 families, *Zygnemaceae* and *Desmidiaceae*, and he further classified the former into 2 subfamilies, *Zygnemeae* and *Spirogyreae*, and the latter into 2 subfamilies, *Saccodermae* and *Placodermae* and again subdivided *Saccodermae* into 2 tribes, *Gonatozygae* and *Spirotaenieae*, and *Placodermae* into 3 tribes, *Penieae*, *Closterieae* and *Cosmarieae*. And he discussed the following three hypotheses, viz. the first one is that the unicellular Desmids are primitive and that the *Zygnemaceae* have been derived from them, and the second is that the *Desmidiaceae* are not a natural family and that the *Spirotaenieae*, and even the *Gonatozygae*, may have removed from them, and the third is that the *Desmidiaceae* are a homogenous group and that all Desmids primarily arose from filamentous ancestors. Consequently, WEST supported the third hypothesis as it seemed on the whole to be the most probable.

In 1922, F. OLTMANNS classified Conjugatae into 3 families, *Mesotaeniaceae*, *Zygnemaceae* and *Desmidiaceae*, in "Morphologie u. Biologie der Algen" and the two races are developed from the *Zygnemaceae*, one is *Debarya-Zygnema-Spirogyra-Sirogonium* and the other is *Zygogonium-Muogeotia-Mesocarpus*.

In 1924, G. M. SMITH described the species of 22 genera under the one family *Desmidiaceae* in his "Phytoplankton of the Inland Lakes of Wisconsin" but neither taxonomical base nor the rank of genera are referred to but they are merely arranged and described after the order of the key.

In 1927, G. S. WEST and F. E. FRITSCH published "Treatise on the British Freshwater Algae" and he established the Group Conjugatae and classified 2 series, *Euconjugatae* and *Desmidiaceae*, and the former series is again divided into *Mesotaeniales* and *Zygnemales*, and the following 4 families, *Mesotaeniaceae*, *Gonatozygaceae*, *Zygnemaceae* and *Mougeotiaceae*, belong to those subseries, and the latter series is again divided into the subfamilies, *Peniae*, *Closterieae* and *Cosmarieae*. In this publication, one of the most interesting opinions is "A fairly close affinity between the Saccoderm Desmids and the *Zygnemales* is apparent, but the relation of the highly specialised Placodermae to the others is by no means evident. There is no indication of how the complex wall-structure of the latter has been arrived at, and the possibility of an origin distinct from that of the other two series must be envisaged", and "one cannot feel sure that the undoubted resemblances are not due to homoplasy. The writer is therefore unable to share wholeheartedly either the view of G. S. WEST and LÜTKEMÜLLER as to the close relation of Saccoderm and Placoderm Desmids, or those of OLTMENNS who regards the *Mesotaeniaceae* as decended from the ancestral type from which both the *Zygnemales* and Placoderm Desmids originated along separate lines." Thus, the authors classified the Desmids into two series, *Euconjugatae* and *Desmidiaceae* (Placoderm Desmids), and subdivided the former into *Mesotaeniales* (Saccoderm Desmids) and *Zygnemales* by means of the morphological characters of

the cell, viz. unicellular or colonial, numbers of pieces of the cell-wall, presence of pores of cell-membrane and the forms of chromatophores.

In 1927, H. PRINTZ classified these groups of algae in ENGLER's "Die Naturlichen Pflanzenfamilien" Bd. 3. as two families, *Desmidiaceae* and *Zygnemataceae*; and subdivided the former into two series, *Saccodermeae* and *Placodermeae*, and the latter into three series, *Zygnemeae*, *Zygogonieae* and *Mesocarpeae*. The author carried on this classification basing it upon the unicellular cell or filamentous cell the number of young plants which germinate from a zygospore and the morphological difference of zygospore-formation.

In 1933, G. M. SMITH published "Freshwater Algae of the Unfted States" and placed these groups of algae in Chlorophyceae and divided them into three families, *Zygnemataceae*, *Mesotaeniaceae* and *Desmidiaceae*, under the Order *Zygnemales* basing upon the characters of the presence of pores on cell-membrane and forms of chromatophores etc.

In 1936, "Syllabus der Pflanzenfamilien" of ENGLER-DIELS Abteil. *Conjugatae* was classified into two Reihe, *Desmidiales* and *Zygnematales*, and again subdivided the former into two families, *Mesotaeniaceae* and *Desmidiaceae*, and the latter into two families, *Zygnemataceae* and *Mesocarpaceae*.

In 1937, W. KRIEGER classified Desmids in "Die Desmidiaceen. in RABENHORST's Kryptogamen-flora", and he placed Reihe Desmidiales under the Class *Conjugatae* and established three families, *Mesotaeniaceae* (Desmidiaceae saccodermae), *Desmidiaceae* (Desmidiaceae placodermae) and *Gonatozygaceae*, including 30 genera.

In short, the Class Conjugatae especially Desmids has hitherto been classified based on the external morphological charecters and therefore, the phylogenetic classification has not yet almost been done.

III. NEW SYSTEM OF CLASSIFICATION

1. Bases

The classification of Conjugatae especially Desmids has hitherto been done only from the morphological point of view.

The present author, since 1927, has made an effort to clarify the Desmid-flora of Japan and its surrounding areas, and at the same time he has traced the process of zygospore-formation in all the Desmids genera existing. Through such studies it was found that the Conjugatae in general can be divided into two forms by the position of the spore formed regardless of its shape, and that they are characterized by the type of cell-wall cleavage in gametes. Namely, in the first, characteristic features of the position of zygospores two different groups are existing, in one group all the zygospores being formed within or connecting gamete—the writer named those spores "Endozygospore"—and in another group all the zygospores are formed outside of gametes—the writer named this type of spore "Exozygospore" and those two groups were named "Endozygospore group" and "Exozygospore group" respectively. (Table 1.) As to the Endozygospore group three following divisions are made: 1. "Fused section"—the cell-wall of gametes is united when they conjugate and zygospore is formed inside of them, 2. "Middle section"—zygospore formed in the middle of conjugation-tube grown from gametes, 3. "Secund section"—contents in one gamete transferred into the other gamete through conjugation-tube and the zygospore formed in the latter. On the Exozygospore group we can recognize,

during the period of zygospore being performed, the two different types, in one type the cell-wall of each gamete is perforated and in the other type the cell-wall of each gamete dividing into semicells, but these two types of spore-formation are identical in the position of zygospore in relation to gamete. Therefore, no distinction is necessary between them.

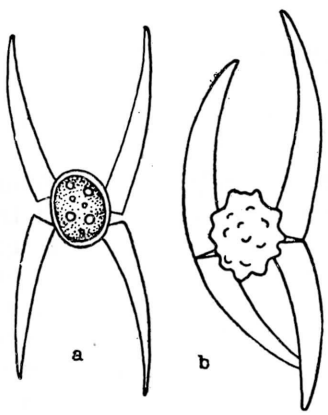
As for the second characteristic features on the type of cell-wall cleavage two different groups can be recognized: In the former, the cell-wall of gamete does not divide at all in conjugation and in the latter, the cell-wall of gamete always divides into semiceils. The writer named the former group "Undivided group" and the latter "Divided group."

As to the Undivided group tow more following distinctions are made: 1. "Connected section" in which both gametes connect still after the zygo-spore-formation, 2. "Pored section" in which both gametes isolate, with pore on each cell-wall.

The Divided group is also separated into two parts: 1. "Fissured section" the cell-wall of gamete with fissure, semi-cells are not completely separated, 2. "Separated section" the cell-wall of gamete are completely separated into two semicells.

The combination of these characters of zygospore-formation is theoretically 20 in all, but actually only 6 combinations exist and the remaining 14 combi-nations may have existed once or extinct at present and no report has been made yet. (*cf.* Table I.)

Among these 6 combination, *Gynmozyga moniliformis* EHR., *Desmidium cylindricum* GREV. and *Hyalotheca dissiliens* (SM.) BRÉB. which belong to A3-bl Type ought to be considered as the remain of ancestral type and Prof. WEST also explained these species were "ancestral type in conjugation".



Textfig. 1. Two of the Separated Types of cells in *Closterium*

In some species of *Closterium* the fissures of semicells do not separete each other and slightly connect on the opposite side of each connective phase. (Text fig.1 b)

The writer explains that this fact shows the phylogenetic process which has developed from Fissured section to Separeted section and as no actual connection is existing, it belongs to a different type of Separated section.

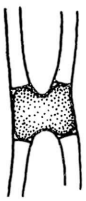
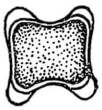
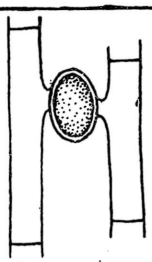
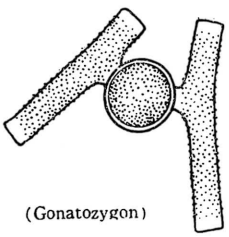
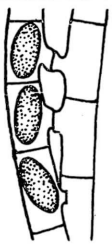
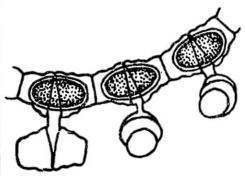
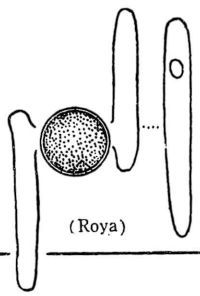
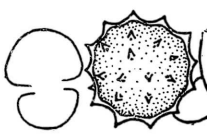
Thus, the writer attempted to combine these features cross-check, such as A2-a1, B1-a2, – named "Cross-check Method"– which was adapted to all species of *Conjugatae*, and arranged them in accordance with the rank of each group. Thus he obtained the new method on phylogenetic classification of *Conjugatae*.

2. Method And its Application

Before entering this chapter the writer thinks it better to summarize the results of the previous chapter as follows:

I. From the position of zygospore in conjugation:

Table 1. TYPES OF ZYGOSPORE-FORMATION IN CONJUGATAE

		Types of Cell-division of Gametes in Conjugation			
		a Group-CELL UNDIVIDED		b Group-CELL DIVIDED	
		1. Connected section	2. Pored section	1. Fissured section	2. Separated section
A Group-ENDOZYGOSPORE	1. Fused section	 (Mougeotia)	 (Cylindrocystis)	—	—
	2. Middle section	 (Zygnema)	 (Gonatozygon)	—	—
	3. Secund section	 (Spirogyra)	—	 (Gymnozyga)	—
B Group-EXOZYGOSPORE		—	—	 (Roya)	—
		—	—	—	 (Cosmarium)
		ZYGNEMALES	DESMIDIALES		

Note: A Group - Zygospore is formed within gametes or connects to gametes.
B Group - Zygospore is formed out of gametes and does not connect to gametes.
a Group - Cells of gamete are not divided into semicells in conjugation.
b Group - Cells of gamete are divided into semicells in conjugation.

A. ENDOZYGOSPORE GROUP (called "A group" hereafter)
   1. Fused section
   2. Middle section
   3. Secund section

B. EXOZYGOSPORE GROUP (called "B group" hereafter)

II. From the condition of the cell-wall of gametes in conjugation:

A. UNDIVIDED GROUP (called "a group" hereafter)
   1. Connected section
   2. Pored section

B. DIVIDED GROUP (called "b group" hereafter)
   1. Fissured section
   2. Separated section

At first, the writer adapted the above stated features to all species of *Conjugatae* in which zygospore-formation is observed and then grouped those species in each current genera in accordance with the same combination of features. In consequence, the writer found that the results were almost the same as those studies in the past only from the morphological point of view.

Table II shows the various Types of zygospore-formation of each genera in *Conjugatae* and each genus shown in this Table is then being arranged in Table III. In the same Table the morphological characters of each were from taken into consideration; vertical view of the cell, the presence or absence of constriction formed in the middle part of the cell. The reason being that these features have been employed only by a few phycologists in classifying Desmids.

Seeing Table III we notice that the Type A2-a1 is common to the genera *Geniculatia, Gonatozygon, Mesotaenium, Cylindrocystis* and *Penium.*

The same Type, however, is not found in the genus *Netrium,* but it is expected that this Type will be found in the genus in future. The two genera, *Genicularia* and *Gonatozygon* in which no other Type is to be found except A2-a1, are believed to have been derived from an ancestral form which is different from the other genera of Desmids. This particular ancestral form of algae is believed to have a close phylogenetic relation to the genus *Zygnema* in Order *Zygnemales,* if we take consider the fact that the genus shows A2-a1 Type into our condideration. These two genera therefore belong to an other independent genus because they also possese peculiar characters in other points. The writer therefore entirely agree with Dr. KRIEGER who established new family *Gonatozygaceae* by his own unique system.

The Type A1-a1 is represented by genera *Mesotaenium, Cylindrocystis, Netrium, Penium, Closterium, Hyalotheca* and *Desmidium,* but these 7 genera, excepting *Netrium,* have other respective Types in addition to the Type A1-a1. In other words, among these six some not only belong to this A1-a1 Type but also have relation to the Type A2-a1, although in the same species the Type is definite. This fact shows that one genus has a close phylogenetic relation to the other Type because these each have common Types.

On genus *Roya,* to the best of the writer's knowledge, only B1-a2 Type is known now but A1-a1 Type also may be discovered in some species in this genus sometime in future, or the latter may have already become extinct.

The Type B1-a2 is represented by only a small number of species in Conjugatae, and as far as the writer knows, they are two species in *Roya* (*Roya obtusa* (BRÉB.) W. & G. S. WEST var. *montana* W. & G. S. WEST; *Roya obtusa* (BRÉB.) W. & G. S. WEST var. *anglica* (G. S. WEST) KRIEGER), one species in *Hyalotheca* (*Hyalotheca cylindricum* GREV.) and four species in *Closterium* (*Cl. Lunula* (MÜLL) NITZSCH.; *Cl. Ehrenbergii* MENEGH.; *Cl. attenuatum* EHRENB., *Cl. aciculare* WEST). It is also observed that exceping genus *Roya*, the other two genera also have A1-a1 Type in addition to B1-a2.

At persent, the Type A3-b1, represented by further smaller number of species, is known in some species of three genera; one species of *Gymnozyga* (*Gymno moniliformis* EHRENB.), in one species of *Desmidium* (*Desm. Aptogonum* BRÉB.) and in one species of *Hyalotheca* (*Hy. dissiliens* W. and G. S. WEST).

This Type is believed to be in the course of evolution together with the forms showing A1-a1 and B1-a2 Type. However each of these three genera possesses not only A3-b1 Type but also A1-a1 or B2-b2 Type, and it also proves that these three genera are placed phylogenetically close relation.

The majority of Desmids (about 99 %) shows B2-b2 Type, which even from the morphological standpoint, is believed to be a highly speciallized group. This Type is seen in 18 genera, the species numbering some 2500.

It is noted here that excepting one species in the genera *Gymnozyga*, *Penium* and *Closterium* all other 16 genera shows only B2-b2 Type.

The fact that this Type has a great number of species and their structures are very complicated, also shows this Type is more highly specialized than the others.

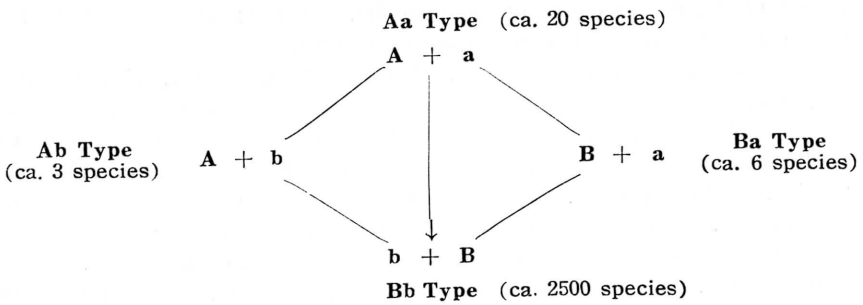
The Types of Desmids are interpreted as above, and it is important enough to show the direction of those Types changed from one Type to another as, A2-a1 → A1-a2 → B1-a2 → A3-b1 → B2-b2.

The phylogenetic keenship of the genera was measured by the number of species which hold the same Type in common with species in other genera.

By this interpretation, the direction of differentiation among Desmid genera is clearly shown.

In Table IV where the Desmid genera are arranged through the Type of sporeformation, the direction of the Desmid evolution is depicted, and in the Table, Aa Type denotes that this group combines the A and the a factors.

Table IV. **RELATION TO THE 4 TYPES OF ZYGOSPORE-FORMATION**



A denotes the factor of ENDOZYGOSPORE GROUP: Zygospore formed within gamete or connected to the feature of gametes.

B denotes the factor of EXOZYGOSPORE GROUP: Zygospore formed out of gametes.
a denotes the factor of UNDIVIDED GROUP: Cells not divided into semicells.
b denotes the factor of DIVIDED GROUP: Cells divided into each semicells.
Arrow denotes the direction of evolution of Types.

Through the same means, Ab, Ba and Bb combinations can be depicted. In the combination of Ab and Ba, the "A" or the "a" factors are transformed from Aa respectively and the "b" or the "B" from the Bb. The structures of the Bb Type are more complexed than those of Aa Type (for instance, the shapes of zygospore in the Aa Type are all spherical or elliptical and the faces are flat, but on the contrary, those of the Bb Type are spherical or polygonal and on the face of them are many projections such as spines, mammiform or furcate etc. (*cf.* Table II) and the external appearance of the cell-wall of the Aa Type is simply cylindrical, elliptical or oblong etc. but those of the Bb Type are not only elliptical or semilunate but also stellatus, polygonal etc. and some of them are furnished with various projections, spine, mammiform, granula and others more com plexed).

Moreover, special attention should be paid for the fact that the number of species ranking as the Ab and the Ba Type is only 9 species among thousands of Desmids existing, while the Aa is approximately 20, the rest of them being about 2500. Therby, it is not too far to say that the Bb group has much more evolved features than the Aa group.

Referring to the Desmid genera representing each group above, it may be resonably concluded that *Genicularia*, *Gonatozygon*, *Cylindrocystis* and others included in the Aa are primitive forms and *Euastrum*, *Staurestrum*, *Micrasterias* and others included in Bb are ones more highly evolved. And one species in *Gymnogyga*, one in *Desmidium*, one in *Hyalotheca* included in Ab and four in *Closterium*, two in Roya included in Ba, are all in the intermediate process of developement.

Besides the above-stated combinations, the writer referred to the following two morphological characters in making the Table III; a comparison between the genera which have constrictions in the middle parts of cells exist or not, and a comparison between the Type which is circular or compressed in the vertical view of the cell. Although not much importance has been attached to them by phycologists, but the writer thinks it important to classify those groups of algae.

As to the former chracter of constriction, it became clear that there is a boundary between Fam. *Closteriaceae* and Fam. *Hyalothecaceae*, and the genera before and behind this boundary do not belong to the singular type of conjugation, namely, some species in these genera are included in the double type of conjugation.

As to the latter character, it may be noticed that the vertical view of the cell is circular in the groups which seem to be primitive and, on the contrary, it is compressed in the groups which seem to be more developed. A boundary can be drawn between Tribe *Docidieae* and Tribe *Sphaerozosmeae*.

Namely, some species of *Cosmarium*, for instance, *Cos. moniliforme* (TURP.) RALF; *Cos. pseudoconnatum* NORDST.; *Cos. globosum* BULNH.; *Cos. Cucrbita* BRÉB.; *Cos. viride* (CORDA) JOSHUA; *Cos. cylindricum* RALFS; *Cos. subexcavatum* NORDST.; *Cos. isthmus* WEST; *Cos. orbiculatum* RALFS etc., belong to

Table III. SYSTEMATIC ARRANGEMENT OF DESMIDS (DESMIDIALES)

BY "THE CLASSIFICATION OE CROSS-CHECK METHOD"

Families	Tribes	Genera	Types of Zygospore-formation	Constriction in the middle of Cell	Vertical view of Cell
Gonatozygaceae	Gonatozygeae	Genicularia	A2-a1 (Aa Type)	No constriction	Circular (sometimes angular, rarely elliptic)
〃	〃	Gonatozygon	A2-a1 (Aa Type)		
Mesotaeniaceae	Mesotaenieae	Mesotaenium	A2-a1, A1-a1 (Aa Type)		
〃	〃	Cylindrocystis	A2-a1, A1-a1 (Aa Type)		
〃	〃	Netrium	? A1-a1 (Aa Type)		
Closteriaceae	Penieae	Penium	A2-a1, A1-a1 (Aa Type) / B2-b2 (Bb Type)		
〃	Closterieae	Closterium	A1-a1, B1-a2 (Ba Type) / B2-b2 (Bb Type)		
〃	〃	Roya	? B1-a2 (Ba Type) / Ab Type		
Hyalothecaceae	Hyalotheceae	Hyalotheca	A1-a1, B1-a2, A3-b1 (Ab Type)	With constriction	Compressed (sometimes radiating, rarely circular)
〃	Gymnozygeae	Desmidium	A1-a1 (Aa Type) / A3-b1 (Ab Type)		
〃	〃	Gymnozyga	A3-b1, B2-b2 (Ab Type / Bb Type)		
Cosmariaceae	Docidieae	Pleurotaenium	B2-b2 (Bb Type)		
〃	〃	Docidium	B2-b2 (Bb Type)		
〃	〃	Triploceras	B2-b2 (Bb Type)		
〃	Sphaerozosmeae	Sphaerozosma	B2-b2 (Bb Type)		
〃	〃	Onychonema	B2-b2 (Bb Type)		
〃	Cosmarieae	Cosmarium	B2-b2 (Bb Type)		
〃	〃	Oocardium	B2-b2 (Bb Type)		
〃	〃	Cosmocladium	B2-b2 (Bb Type)		
〃	〃	Arthrodesmus	B2-b2 (Bb Type)		
〃	〃	Xanthidium	B2-b2 (Bb Type)		
〃	〃	Staurastrum	B2-b2 (Bb Type)		
〃	Euastreae	Ichthyocerus	B2-b2 (Bb Type)		
〃	〃	Tetmemorus	B2-b2 (Bb Type)		
〃	〃	Euastrum	B2-b2 (Bb Type)		
〃	〃	Micrasterias	B2-b2 (Bb Type)		

NOTE: The following genera are omitted from this table, because of the zygospores are not fully described hitherto. viz., *Ancylonema, Phymatodocis , Spirotaenia, Spondylosium, Streptonema.*

the circular group and yet the writer supposes that Genus *Cosmarium* is originally develoved from Genus *Docidium* and the vertical view of the cell of *Docidium* is circular, and the fact that this circular type is also found in some species of *Cosmarium* in which the vertical view of the majority of species is compressed shows that these several species of *Cosmarium* indicate the relationship between the circular type and the compressus type, and it can be proved that Genus *Cosmarium* ranks between these two types. That is to say, even among to the highly developed genus of *Cosmarium* there are a few species which still keep the primitive character.

Besides these characters mentioned above, an additional consideration on the configuration of chromatophores and cell-membrane was taken, and the TableIII was got. Seeing this Table, we notice that the origin of these two genera, *Genicularia* and *Gonatozygon*, is originally different from that of other Families, and its origin may probably be descended from Genus *Zygnema*. Therefore, the writer has no objection to Dr. KRIEGER who established the new Family *Gonatozygaceae*.

As for the Family *Mesotaeniaceae* or Saccoderm Desmids, it belongs to the Aa Type (partly emended) and no objection is raised as to the organization of this family.

The six genera from *Penium* to *Gymnozyga* are the intermidiate forms between *Mesotaeniacece* and *Cosmariaceae* of which mention shall be made afterwards, and the writer prefers to established the two new Families *Closteriaceae* and *Hyalothecaceae*.

Therefore it is reasonable to classify them into the Aa and the Bb Types. In other words the Aa and the Bb types are common to both groups, but besides this the former has the strong character of the Bb and the latter that of the Ab character; moreover, between these two groups the distinct differentiation can be recognize by the presence of the constriction in the middle part of the cell.

Next, fifteen genera from *Pleurotaenium* to *Micrasterias* are all Bb Types and there is none common to other Types, and the writer prefers establishing a new Family *Cosmariaceae*, taking also other morphological characters into consideration.

From those respects, the phylogenetic classification of *Desmidiales* can be shown in Table VII, and although in some genera the type of zygospore formation is still left unknown, but the foundamental principle may not be changed. That is to say, the formation of so-called Desmids is supposed to be descended from the four different origins; Fam. *Hyalothecaeeae* developed from the Mougeotiaoides algae through the Spirogyraoides algae combined with the Debaryaoides algae; the other algae, originated from that of Debaryaoides, developed into the *Closteriaceae* through the *Mesotaeniaceae*; the *Closteriaceae* furthermore developed into *Cosmariaceae*, separated into two directions of and the Tribe *Euastreae*, finally developing into Genus *Micrasterias*; the others entered the Tribe *Cosmarieae* and being divided into *Cosmarium* through Genus *Docidium* and the others, developed till they formed *Onychonema*, *Cosmocladium* and *Staurastrum*, again separating into the three directions, the majority of Desmids' genera *Micrasterias* and *Staurastrum* being most highly evolved. Lastly, one group of the *Gonatozygaceae* seems

differentiated from the Zygnemaoides algae.

As a result of the reseaches above, the Order *Desmidilaes* constitutes the following five Families, out of which three Families were newly established by the writer.

1. *Gonatozygaceae* KRIEGER 1937
2. *Mesotaeniaceae* OLTMANNS 1904
3. *Closteriaceae* OKADA 1949
4. *Hyalothecaceae* OKADA 1949
5. *Cosmariaceae* OKADA 1949

3. Key to the New Families (Desmidales)

The Order *Desmidiales* is divided into the five Families above, and they are indicated by the following keys:

1 { The Type of zygospore-formation is only A2-a1, cells joined to filamentous, no constriction in the middle of cell ·····*Gonatozygaceae*
The Type of zygospore-formaiion is not A2-a1, majolity species cells solitary, constriction exists or not····· 2

2 { The Type of zygospore-formation is A2-a1 and A1-a1, cells solitary, no constriction in the middle of cell ····· *Mesotaeniaceae*
The Type of zygospore-formation is not only A2-A1 and A1-a1 but also the species wth other Types or entirely lacking these Types ····· 3

3 { The Type of zygospore-formation is only B2-b2, cells solitary, with constriction in the middle of cell ·····*Cosmariaceae*
The Type of zygospore-formation is not only B2-b2 but also the species with other Type····· 4

4 { The Type of zygospore-formation is A3-b1, some species also with A1-a1 or B1-a2, cells joined to filamentous, constriction shallow or not ····· ····· *Hyalothecaceae*
The Type of zygospore-formation is not only A1-a1 and B2-b2 but also A2-a1 or B1-a2, cells solitary, no constriction in the middle of cell ····· ····· *Closteriaceae*

ABBREVIATION: **A** denotes Endozygospore group and within this group **1** indicates Fused section, **2** for Middle section and **3** for Secund section; **B** denotes Exozygospore group, no division within it. **a** denotes cells of gamete not divided in conjugation, and within this group **1** indicates Connected section and **2** for Pored section; **b** denotes cells of gamete divided in conjugation and within this group **1** indicate Fissured section and **2** for Separated section. Therefore, for instance, A2-a1 indicates the combination of Types as to the Connected section in Undivided Cell and the Middle section in Endozygospore group.

4. Description of the New Families

The following 3 families are newly established and described.

Fam. **Closteriaceae** OKADA, *fam. nov.* 1949.

Cellulae solitariae lunares vel elongato-fusiformes, sine constrictione vel interdum paullulo constrictae, in varia parte vel fere in media divisae, vulgo corporum medio suturiferae, interdum sine sutura, membrana porosa vel epo-

rosa, aspectu verticali circulari; chromatophoro axiali, a centro radiatim exanso et longitudinaliter plurilineato, pyrenoideis 1 usque numerosis, in chromatophoro immersis vel diffusis.

Zygosporae globosae, ellipsoideae, late ellipsoideae, tetrahedrales, hexahedrales vel octahedrales, laeves, interdum porosae vel papillosae.

The types of zygospore-formation of *Closteriaceae* belong to the Endozygospore Group (Fused section) and Exozygospore Group (Separated section and Pored section).

Fam. **Hyalothecaceae** OKADA, *fam. nov.* 1949.

Cellulae breviter cylindricae, doliformes etc., filamenta longa efformantes, leviter vel vix constrictae, in parte media (cellularum) divisae, membrana porosa, aspectu verticali circulares vel ellipticae, triangulares vel tetragonae; chromatophoro axiali, utrinque 1, a centro radiante, pyrenoideo 1 in centro sito. Zygosporae globosae, ellipsoideae, laeves interdum conico-papillosae.

The types of zygospore-formation of *Hyalothecaceae* belong to the Endozygospore Group (Fused section and Fissured section) and Exozygospore Group (Pored section and Separated section).

Fam. **Cosmariaceae** OKADA, *fam. nov.* 1949.

Cellulae solitariae, tympaniformes, disciformes, ellipsoideae, polyhedrales etc., cum isthmo, medio (i.e. isthmo) divisae, aspectu verticali ellipticae vel late ellipticae, interdum rhomboideae vel polygonae; chromatophoro axiali vel parietali, utrique 1 vel numeroso, lobato vel angulato, pyrenoideis 1–2 vel numerosis in centro sitis. Zygosporae globosae, ellipsoideae, late ellipsoideae, tetrahedrales, hexahedrales vel octahedrales, laeves, interdum porosae vel papillosae.

The types of zygospore-formation of *Cosmariaceae* all belong to the Exozygospore Group (Separated section).

5. Key to the New Tribes – 1.

Fam. **Hyalothecaceae.**

The Fam. *Hyalothecaceae* is divided into two new Tribes and they are indicated by the following key:

The Type of zygospore-formation is A1-a1, rarely B1-a2, A3-b1; on the conjugation of gamete, cells of gamates separate into two solitary cells each other, and not formed filaments·····Tribe *Hyalotheceae*

The Type of zygospore-formation is A3-b1, rarely A1-a1; on the conjugation of gametes, cells of each gamete does not separate into two solitary parts each other and remains as filamentous jointer···Tribe *Gymnozygaeae*

6. Description of the New Tribes – 1

Tribe. 1. **Hyalotheceae** OKADA, *tribus nov.* 1949.

Cellulae plerumque parvae filamenta longa formantes; filamenta saepe torta, saepius vagina gelatinosa cincta; tempore conjugatione gametes utrinque sexus inter se liberi, filamenta longa non formantes. Typi formationis zygospoae A1-a1, B1-a2 et A3-b1.

Tribe 2. **Gymnozygeae** OKADA, *tribus nov.* 1949.

Cellulae plerumque parvae, filamenta longa formantes; filamenta torta, saepius vagina gelatinosa tecta; gametes utrinque sexus in tempore conjugatione etiam in filamento longo connexi. Typi formationis zygosporae sunt A1-a1, A3-b1.

7. Key to the New Tribes - 2

Fam. **Cosmariaceae.**

The Fam. *Cosmariaceae* is divided into four new Tribes and they are indicated by the following key.

1 { Vertical view circular ..... Tribe *Docidieae*
  { Vertical view compressed 2

2 { Cells filamentous. Vertical view elliptical ..... Tribe *Sphaerozosmeae*
  { Cells solitaly 3

3 { Apical margin obtuse, no projection in the central part of cell ..... Tribe *Cosmarieae*
  { Apical margin truncate or obtuse with median incision or emarginate, generally with profections in the central part of cell ... Tribe *Euastrieae*

8. Description of the New Tribes - 2

Tribe 1. **Docidieae** OKADA, *tribus nov.* 1949.

Cellulae vulgo mediocres, elongato-bacilliformes solitariae et filamenta non formantes, constrictione mediocriter evoluta; semicellulis margine laevibus vel undulatim elevatis, interdum spinulosis, aspectu verticali plerumque circularis. Typus formationum zygosporum est B2 - b2. Zgosporae globosae, lata ovatae, laeves.

Tribe 2. **Sphaerozomeaes** OKADA, *tribus nov.* 1949.

Cellulae parvae, filamenta torta vel non torta saepius gelatinoso-vaginata; semicellulis ellipsoideis, reniformibus, oblongisve, interdum subrectangularibus, constrictione profunda, sinu angusto, aspectu verticali oblongae, apicibus semicellularum appendices 1–2-pares cum proximis contiguas ornatis, chromatophoro axiali, in semicellulo 1, pyrenoideo 1 in centro semicellulae sito. Zygosporae globosae vel oblongae, leaves vel simpliciter spinosae. Typus formationum zygosporum est B2 - b2.

Tribe 3. **Cosmarieae** W. α G. S. WEST emnd. OKADA. 1949.

Cellulae mediocres vel parvae, solilariae, tympaniformes, ellipsoideae, vel polyhedrales, isthmo profundo, sinu angusto, semicellulae apice rotundatae raro retusae truncataeve; chromatophoro axiali raro parietali, pyrenoideis vulgo in centro semicellulae 1, raro pluribus, interdum numerosis et irregulariter dispersis. Semicellulae aspectus verticalis depressus (ellipticus, oblongus, vel fusiformis), triangularis, vel quadrangularis. Zygosporae vulgo globosae, interdum angulatae, ellipsoideae laeves vel mamillatae, spiuosae vel papillosae interdum porosae. Typus formationum est B2 - b2.

Tribe 4. **Euastreae** OKADA, *tribus nov.* 1949.

Cellulae vulgo mediocres vel majusculae, solitariae, bacilliformes, disciformes vel ellipsoideae, isthmo vulgo profundo, sinu angusto, semicellulae apice retusae vel truncato-rotundatae vel rotundatae; chromatophoro axiali, pyrenoideis

in utrinque semicellulae 1, vel numerosis, aspectu verticali depressae (rhomboideae, late ellipticae, oblongae vel fusiformes). Zygosporae globosae, ellipsoideae, oblongae, tetraheralis, spinosae, glochidiatae vel mamillosae, porosae vel laeves. Typus formationum zygosporum est B2 - b2.

IV. NEW CLASSIFICATION OF ORD. *ZYGNEMALES*

Concerning to the classification of Order *Zygnemales*, it has been carried chiefly on the characters of shape and the numbers of chromatophores or the configuration of zygospores etc. And no phylogenetic relationship has been shownyet.

The new classification of the author which he adopted in Ord. *Desmidiales* in the previous chapter, is also available for the Ord. *Zygnemales*.

Table V. SYSTEMATIC ARRANGEMENT OF ZYGNEMALES BY MEANS OF THE CROSS-CHECK METHOD

Families	Tribes	Genera	Types of Zygospore-formation
Mougeotiaceae	Mougeotieae	Mougeotia	A1 - a1
//	Zygogonieae	Zygogonium	A2 - a1
//	//	Gonatonema	?
Zygnemaceae	Zygnemeae	Debarya	A1 - a1, A2 - a1
//	//	Zygnema	A2 - a1, A3 - a1
//	Spirogyreae	Sirogonium	A3 - a1
//	//	Spirogyra	A3 - a1

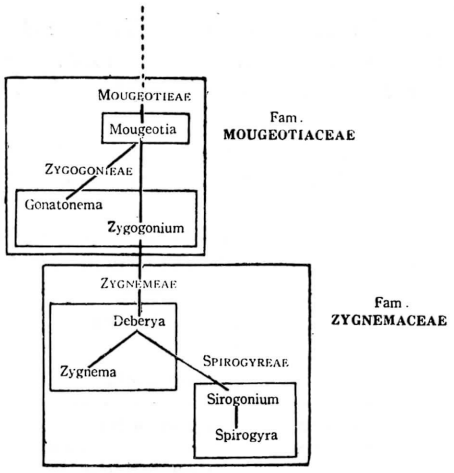
That is, as is shown on the Table V, (cf. Table II) in the A1-a1, Type, both gametes are fused to each other in the middle part of the cell and zygospore is performed, and the two genera *Mougeotia* and *Debarya* belong to this Type. Next, in another type, both gametes are connected with conjugationtube and zygospore is formed in the middle part of the gametes is shown as A2-a1 Type, and *Zygogonium*, *Gonatonema*, *Debarya* and *Zygnema* belong to this Type and among them two genera, exepting *Zygogonium* and *Gonatonema*, also possess the other Type, A1 - a1 or A3 - a1 in some species. Next, both gametes are connected with conjugation-tube and zygospore is performed in one part of gamete and in this case the contents of the cell are transformed from the other part of gametes, and to this Type the following 3 genera belong; *Zygnema*, *Sirogonium* andS *pirogyra*.

From these groupings, the writer considered that among them, those genera in which show the same Type indicate the phylogenetically close relationship and the groups of the same Type are originated from the same ancestor. In the Table V, the A1 - a1 Type is transformed gradually to the A3 - a1 Type through the A2 - a1 Type. This fact shows the direction of evolution of those groups of algae.

From these respects, applying the Type to each genus and arranging them, and the present writer obtained the result shown in the Table VI.

And, thus Fam. *Mougeotiaceae* is divided into two Tribes, *Mougeotieae* and *Zygogonieae*, and Fam. *Zygnemaceae* is divided into two Tribes, *Zygnemeae* and *Spirogyreae*. And these four Tribes are newly established.

Table VI. PHYLOGENY OF THE GENERA OF ZYGNEMALES



1. Key to the New Tribes

Fam. **Mougeotiaceae**

The Fam. *Mougeotiaceae* is divided into two new Tribes and they are indicated by the following key:

Type of zygospore-formation, Endozygospore (Fused section)-Undivided Group (Connected section) ..... *Mougeotieae*
Type of zygospore-formation, Endozygospore (Middle section)-Undivided Group (Connected section) ..... *Zygogonieae*

Fam. **Zygnemaceae**

The Fam. *Zygnemaceae* is divided into two new Tribes and they are indicated by the following key:

Type of zygospore-formation, Endozygospore (Fused section)-Undivided Group (Connected section), Endozygospore (Middle section)-Undivided Group (Connected section) and Endozygospore (Secund section)-Undivided Group (Connected section) ..... *Zygnemeae*
Type of zygospore-formation, Endozygospore (Secund section)-Undivided Group (Connected section) ..... *Spirogyreae*

2. Description of the New Tribes

Tribe 1. **Mougeotieae** OKADA, *tribus nov.* 1949.

Cellulae longe-cylindricae, filamenta longa formantes; chromatophoro axiali discoideo, zygosporis globosis vel depresso-tetrahedralibus, anglis rotundatis vel truncatis. Typus formationum zygosporum est A1-a1.

Table IL TYPES OF ZYGOSPORE-FORMATION OF GENERA OF CONJUGATAE

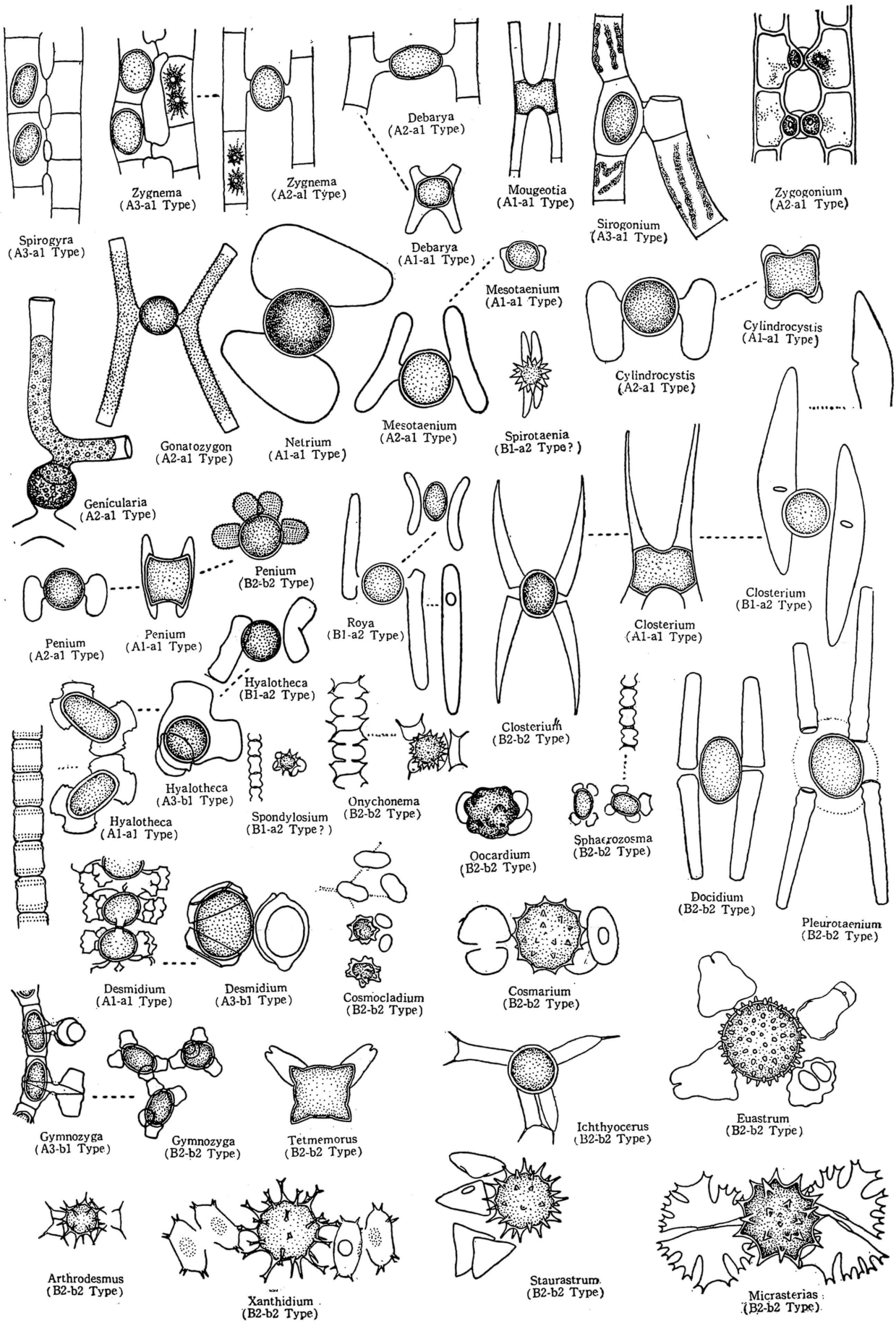
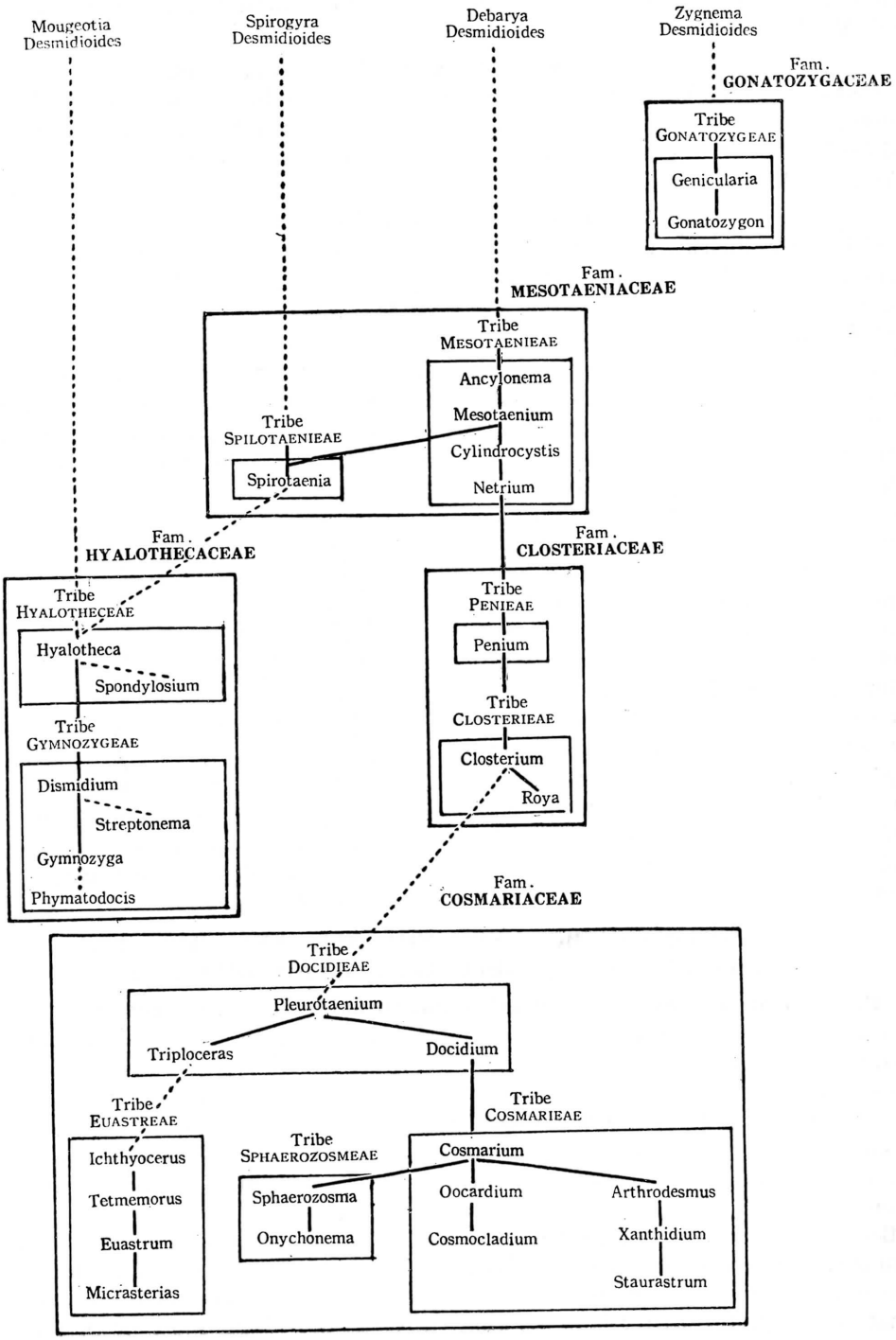


Table VII PHYLOGENY OF THE GENERA OF DESMIDIALES



Tribe 2. **Zygogonieae** OKADA, *tribus nov.* 1949.

Cellulae cylindricae, filamenta longa efformantes; chromatophoro axiali discoideo, zygosporis globosis vel ellipsoideis. Typus formationum zygosporum est A2-a1.

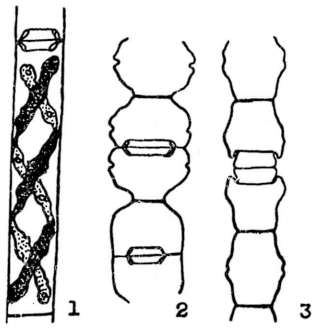
Tribe 3. **Zygnemeae** OKADA, *tribus nov.* 1949.

Cellulae cylindricae, elongato-cylindricae, filamenta longa formantes; Chromatophoro axiali discoideo vel stellato, in utrinque cellulo 1 vel 2, zygosporis globosis, ellipsoideis vel oblongis. Typi formationis zygosporae sunt A1-a1, A2-a1 et A3-a1.

Tribe 4. **Spirogyreae** OKADA, *tribus nov.* 1949.

Cellulae cylindricae, elongato-cylindricae, filamenta longa formantes,; chromatophoris parietalibus, in utrinque cellulo 1–7, interdum 12, filiformi-complanatis, spiraliter vel longitudinaliter positis. Typus formationum zygosporum est A3-a1.

The general characters of each tribe in Ord. *Zygnemales*, the shape of the cell is cylindrical, both ends of the cell connecting to those of the adjoining cell, and making a long filamentous shape, the types of zygospore-formation all belonging to Endozygospore. These facts show that in Ord. *Desmidiales* the type of zygospore-formation is seen in both Endozygospore and Exozygospore, and the Endozygospore type is seen in all the primitive species and these primitive species, cylindrical and filamentous, indicate that close relationship between the two groups. Moreover, so-called "replicate", one of the asexual reproduction of *Zygnemales*, is often seen especially in genus *Spirogyra*, and also recognized at *Desmidium* and *Gymnozyga* in *Desmidiales*, this fact also being remarkable and interesting from the phylogenetic point of view.



Textfig. 2. Replicate-form of Cell-wall
1. Zygnemales (*Spirogyra*)
2–3. Desmidiales (2. *Desmidium*; 3. *Gymnozyga*)

V. COMPARISON BETWEEN THE OLD AND THE NEW CLASSIFICATION, ESPECIALLY MAJOR DIFFERENCE

1) Position of Hyalotheca, Spondylosium, Desmidium and Gymnozyga

These genera are hitherto been considered more evolved group than *Cosmarium*, *Euastrum* and *Micrasterias* etc. and placed in higher position than the latter group by most of all phycologist such as TRUNER (1893), CARTER (1923), WEST (1923), SMITH (1924), KRIEGER (1933) etc. but on the contrary, from the result of the present study, they are all to be placed in such lower position than those of the latter group because they are recognized more primitive than the latter.

Because the type of zygospore-fomation transforms gradually from *Netrium*, *Penium*, *Closterium* to *Pleurotaenium*, *Docidium* by the degree of evolution, the four genera in question should be placed in the intermediate position. That is to say, the writer believes that the structure of the most of Desmids

is single-celled and not filamentous and therefore those filamentous Desmids are merely be placed in the last stage of all single celled genera, only from the convenience to classify all of Desmids by morphorogically.

That is to say, this classification has no phylogenetic sense. This is easily be recognized only from the morphological stand point and filamentous algae in Conjugatae is not always highly evolved than single-celled algae. It is clear that all the filamentous structured genera such as *Debarya*, *Spirogyra* etc. are recognized as the origin of Conjugatae; and moreover, the filamentous structure of *Hyalotheca*, *Spondylosium*, *Desmidium* and *Gymnozyga* is quite different from that of *Debarya*, *Spirogyra* in *Zygnemales*, the cells of the former genera having no cooperate cell-wall, being merely jointed by mucilage or processes to adjacent cells to form filamentous appearance.

2) Position of Genus Roya

Genus *Roya* was established by W. α G. S. WEST in 1896. The taxonomical position of this genus is placed near genus *Closterium* of *Placodermae*, at first, by the establishers and the difference between the two genera is in the numbers of chromatophores (*Closterium* 2, *Roya* 1), in the existence of apical vacuole (*Closterium* present, *Roya* none) and in the position of nucleus (*Closterium*- center of middle part of the cell, *Roya*- side of middle part of the cell). But, in 1910, Dr. LÜTKEMÜLLER observed that the cell-wall of *Roya* lacking the small pores and the structure of this genus is very simple, and he proposed that it may be placed near genus *Mesotaenium* in *Saccodermae*. According to this LÜTKEMÜLLER's opinion W. α G. S. WEST retracted their first opinion.

Thenceforth, Dr. KRIEGER (1933) followed this opinion and he included this genus into *Saccodermae* and placed it next to genus *Spirotaenia*, up to the present.

But, according to the result of the present study, the genus *Roya* ought to be placed next to the genus *Closterium* of *Placodermae*. The reason is, that one of the type of zygospore-formation of *Closterium* in which three types are included, so-called B1-a2 Type in which zygospore forms out of both gametes and arise with a pore in conjugation, is quite the same type in some species of *Closterium*, therefore, the genus *Roya* seems to be a small genus which separated and developed from the genus *Closterium*. Yet, because the type of zygospore-formation of the genus *Spirotaenia* has not yet been classified cleared, the relation between *Roya* and *Spirotaenia* or *Closterium* can not be settled.

The numbers and position of chromatophores is surely are important taxonomical character for those group of algae, but it is not always an important factor, for instance, in some individuals of *Cosmarium Subcucumis* SCHMIDLE, the chromatophores of one part of semicell suggest a parietal disposition whereas the other half looks an axile disposition. (*cf.* W. α G. S. WEST. Mono. Brit. Desm. Vol. II).

3) Establishment of the New Families and the New Tribes

The writer has advocated 5 families and 8 tribes in Ord. *Desmidiales*, in the chapter III in this thesis, but out of these 3 families and 6 tribes are

newly established (*cf.* p. 176) and, 4 new tribes are established in Ord. *Zygnemales*.

The taxonomical discussion of which has been carried on hitherto is limited chiefly to genus or species and neither families nor tribes are very few. This is partly due to the fact that most of the papers hitherto issued are that of Flora and arranged and described each species from morphological stand point of view, and as for the Families, they are merely summarized in one Family *Desmidiaceae* or two Families *Desmidiaceae* and *Mesotaeniaceae* and thousands of Desmids are included among them. And, the second reason, perhaps, no foudamental phylogenetic factors can be found by which discuss or classify the Family or Tribe of these group of algae.

VI. RESULTS OBTAINED

In short, on the classification of Conjugatae, the writer found the new foundamental factors which appear in the period of conjugation on the position of zygospore and the type of cell-division of gametes and he established the new method of classification called "Cross-check Method". Adopting this method he classified those groups of algae phylogenetically instead of by the old morphological method, and he established the phylogeny of Ord. *Desmidiales* as well as that of Ord. *Zygnemales* (*cf.* Table VI, VII and VIII).

Besides, he cleared the phylogenetic relationship of those groups of algae and he could settled the questions which were obscure and indefinite.

Adding to this contribution, the writer established and described the following 3 new Families and 13 new Tribes:

New Families — *Closteriaceae, Hyalothecaceae, Cosmariaceae.*

New Tribes — *Mougeotieae, Zygogonieae, Zygnemeae, Spirogyreae, Spirotaenieae, Mesotaenieae, Closterieae, Hyalotheceae, Gymnozygeae, Decidieae, Sphaerozosmeae, Cosmarieae, Euastreae.*

Table VIII. **NEW PHYLOGENETIC CLASSIFICATION OF CONJUGATAE**

CLASS **CONJUGATAE**

ORD. I. **Zygnemales**

FAM. I. MOUGEOTIACEAE

TRIBE 1. *Mougeotieae* OKADA

Gen. Mougeotia

TRIBE 2. *Zygogonieae* OKADA

Gen. Zygogonium; Gonatonema

FAM. 2. ZYGNEMACEAE

TRIBE 1. *Zygnemeae* OKADA

Gen. Debarya; Zygnema

TRIBE 2. *Spirogyreae* OKADA

Gen. Sirogonium; Spirogyra

ORD. II. **Desmidiales**

FAM. 1. GONATOZYGACEAE KRIEGER

Gen. Genicularia; Gonatozygon

FAM. 2. MESOTAENIACEAE OLTMANNS

TRIBE 1. *Spirotaenieae* OKADA

Gen. Spirotaenia

TRIBE 2. *Mesotaenieae* OKADA

Gem. Ancylonema; Mesotaenium; Cylindrocystis; Netrium

FAM. 3. CLOSTERIACEAE OKADA

TRIBE 1. *Closterieae* W. & G. S. WEST

Gen. Closterium; Roya

TRIBE 2. *Penieae* LÜTKEMÜLLER

Gen. Penium

FAM. 4. HYALOTHECACEAE OKADA

TRIBE 1. *Hyalotheceae* OKADA

Gen. Hyalotheca; Spondylosium

TRIBE 2. *Gymnozygeae* OKADA

Gen. Desmidium; Phymatodocis; Gymnozyga; Streptonema

FAM. 5. COSMARIACEAE OKADA

TRIBE 1. *Docidieae* OKADA

Gen. Pleurotaenium; Docidium; Triploceras

TRIBE 2. *Sphaerozosmeae* OKADA

Gen. Sphaerozosma; Onychonema

TRIBE 3. *Cosmarieae* OKADA

Gen. Cosmarium; Oocardium; Cosmocladium; Arthrodesmus; Xanthidium; Staurastrum

TRIBE 4. *Euastreae* OKADA

Gen. Ichthyocerus; Tetmemorus; Euastrum; Micrasterias

VII. SUMMARY

The Conjugatae especially Desmids has hitherto been classified and based primarily on the morphological characters. On the sexual reproduction in Conjugatae, the author found the foundamental fact that those groups of algae have definite characters on the position of zygospore formed regardless of its shape, and the type of cell-wall cleavage in gametes.

According to these two factors, the author proposed a new method of classification named "Cross-check Method" and he attempted to classify those group of algae. And, he succeeded in classifying them phylogenetically.

These two factors are again divided into 4 different types, 2 types by the position of zygospore and the other 2 by the process of gametes cell-wall cleavage. (*cf.* Table I).

The four groups are featured as follows:

- Endozygospore group ..... Zygospore formed within gamete.
- Exozygospore group ..... Zygospore formed outside of gamete.
- Undivided group ..... Gamete cell-wall, in conjugation, not divided into semicells.
- Divided group ..... Gamete cell-wall, in conjugation, divided into semicells.

The further distinction made in each group are as follows.

ENDOZYGOSPORE GROUP (called "A group" hereafter)

1. Fused section ..... Gamete cell-wall united and zygospore formed inside.

2. Middle section……Zygospore formed in the middle part of conjugation-tube.
3. Second section……Contents of cell in one gamete transfered into the other gamete through conjugation-tube, and zygospore formed in the latter.

EXOZYGOSPORE GROUP (called "B group" hereafter)

1. In the zygospore formation, each gamete cell-wall is perforated.
2. In the zygospore formation, each gamete cell-wall is divided into semicells.

These two types of zygospore-formation was identified in the position of zygospore in relation to gamete, thence, no distinction is necessary.

UNDIVIDED GROUP (called "a group" hereafter)

1. Connected section…Gametes connected still after the zygospore-formation.
2. Pored section ……Gametes isolated, and with pore on cell-wall.

DIVIDED GROUP (called "b group" hereafter)

1. Fissured section…Gamete cell-wall with fissure and semicells not completely isolated.
2. Separated section…Gamete cell-wall completely separated into two semicells.

The combination of these sections of zygospore-formation is theoretically counted 20 Types, but actually we find only 6 combinations or Types existing.

Table II shows the various Types of zygospore-formation of each genera in Conjugatae, each Type represented by the genus or genera referred to.

The genera represented in Table II are then arranged in Table III in accordance with the Type; in the same Table a consideration was made as to the morphological characters of each form such as vertical view of the cell as well as the presence or absence of constriction formed in the middle part of the cell.

Seeing Table III we notice that A2-a1 Type is shared by the genera *Genicularia, Gonatozygon, Mesotaenium, Cylindrocystis* and *Penium.*

The same Type, however, is not found in the genus *Netrium,* but it is expected that this Type will be found in the genus. The two genera, *Genicularia* and *Gonatozygon,* where no other Type is found than A2-a1, are believed to have derived from an ancentral form which is different from the other genera of Desmids. This particular ancentral form of algae is believed to have a close phylogenetic relation to the genus *Zygnema* in order *Zygnemales,* when we consider the fact that the genus shows A2-a1 Type.

The Type A1-a1 is represented by genera *Mesotaenium, Cylindrocystis, Netrium, Penium, Closterium, Hyalotheca* and *Desmidium*; among these 7 genera, excepting Netrium, each genus has species which shows another Type than A1-a1.

The Type B1-a2 is represented by only a small number of species in Conjugatae, and to the best of the writer's knowledge, they are 2 species in *Roya,* one species in *Hyalotheca,* and 4 species in *Closterium.* It is also noticed that genus *Roya* shows only B1-a2 Type, but other two genera also show A1-a1 Type in addition to B1-a2. The Type A3-b1, represented by further smaller number of

species, is seen, at the present moment in one species of *Gymnozyga*, one species of *Desmidium* and one species of *Hyalotheca*. But all these three genera show also another Type, i.e. A1-a1.

The Type A3-b1, which is seen in one species of each *Gymnozyga*, *Desmidium* and *Hyalotheca*, is believed to stand in the course of evolution together with the forms showing A1-a1 and B1-a2 Type. However each of these 3 genera possesses not only A3-b1 Type but also A1-a1 or B2-b2 Type, and this again convinces the author that these 3 genera are placed phylogenetically close to those genera which show the latter two Types.

The majority of Desmids (about 99%) show B2-b2 Type, which, with their morphological features, is believed to cover a highly speciallized group.

The present B2-b2 Type is seen in genera of as many as 16 and the species numbering some 2500.

It is noted here that excepting only one species in the genus *Gymnozyga*, all other 16 genera show strictly B2-b2 Type.

The multitude of the species and complicated structural characters possessed by the present group of genera as well as their types of spore-formation are altogether sufficiently conducive to call them a highly specialized group which is also the main trunk of Desmids phylogenetic tree.

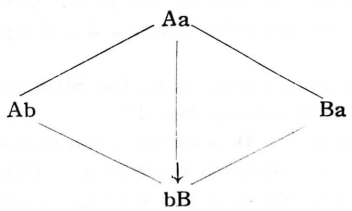
The grouping of Desmid form is interpreted as above and it is important enough to note the change from one Type to another as, A2-a1 → A1-a2 → B1-a2 → A3-b1 → B2-b2.

The phylogenetic keenship of the genera was measured by the number of species (in a given genus) which shares the same Type with species in other genera. By this interpretation, the order and the direction of differentiation among Desmid genera set up clearly.

In Table IV, where the Desmid genera are arranged by the Type of zygospore formation, the direction and succession of Desmid evolution are diagramatically depicted, and in the Table each factor is represented as follows:

Endozygospore group ..... A
Exozygospore group ..... B
Undivided group ..... a
Divided group ..... b

then you will interprete the combination of Types and the changees of the factors indicated as below:



The direction of evolution (shown by the arrow) is suggested from the fact that Bb Type (shows the combination of b and B factors) has much more specialized chacters than Aa.

Consequently, the two Types Ab and Ba will be placed in the middle of evolutionary change.

If we take the Desmid genera representing each Type as made above, it is stated that *Genicularia, Gonatozygon, Cylindrocystis* and others which are all included in Aa are generalized form, and *Euastrum, Staurastrum, Micrasterias* and others are included in Bb are specialized. One species of each *Gymnozyga, Desmidium* and *Hyalotheca* to included in Ab; 4 species of *Closterium* and 2 species of *Roya* are in Ba. As to the number of species in each Type we count about 20 in Aa, approximately 9 each in Ab and Ba, and some 2500 in Bb.

The combination of major types of zygospore-formation, with additional consideration on the constriction and vertical view of the cells, as well as configuration of chromatophores and constriction of cells produced a phylogeny of Desmids (*cf.* Table III & Table IV) and thus systematized the new classification of Desmids (*cf.* Table VIII).

The Order *Zygnemales* was also classified in the same principle in *Desmidiales* as presented in Table V. Using the same symbol of zygospore-formation as in *Desmidiales* it was found that A1-a1 Type includes the genera *Mougeotia* and *Debarya*; A2-a1 Type is seen in *Zygogonium, Gonatonema, Debarya* and *Zygnema* but in the latter two genera there are found also some forms which show A1-a1 or A3-a1. The species in *Zygnema, Sirogonium* and *Spirogyra* show A3-a1 Type. The phylogenetic construction of *Zygnemales*, with the same consideration of zygospore-formation types as in Desmidiales, is shown in Table VI, and the classification will be presented as in Table VIII.

With the basic knowledge of the "Cross-check" as presented in this report the author proposes here the following 3 new families and 13 new tribes.

New Families — *Closteriaceae, Hyalothecaceae, Cosmariaceae.*

New Tribes — *Mougeotieae, Zygogonieae, Zygnemeae, Spirogyreae, Spirotaenieae, Mesotaenieae, Closterieae, Hyalotheceae, Gymnozygeae, Docidieae, Sphaerozosmeae, Cosmarieae, Euastreae.*

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