The Taxonomy of the Plasmodiophoraceae.

By

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(With 15 figures in the text.)

In recent years a great number of species and several new genera have been added to the family of *Plasmodiophoraceae.* Up to the beginning of this century the whole family consisted of practically only *Plasmodiophora* WOR., *Spongospora* WALLR., *Sorosphaera* SCHROET. and *Tetramyxa* GOEBEL, each genus being a monotypical one. In rapid succession, practically within the last two decades, *Ligniera* was described by MAIRE et TISON (1909—1911), *Sporomyxa* by LEGER (1908), *Sorodiscus* by LAGERHEIM and WINGE (1912), *Cystospora* by ELLIOT (1916), *Ostenfeldiella* and *Clathrosorus* by FERDINANDSEN and WINGE (1914 and 1920 resp.), *Trematophlyctis* by PATOUILLARD (1918), and quite recently *Membranosorus* by OSTENFELD and PETERSEN (1930). New species have from time to time been added to some of the above genera.

All these newer genera have been erected on mainly the following two characters: the shape of the spore masses and the relation of the spores to each other within these spore masses. These characters had served in establishing the four older genera and, as forms were found in which these two characters were combined into different patterns, the dividing arrangement shown was given the distinction of a generic character. Where these genera have not remained monotypical, species have been founded on certain minor characters as size, shape and membrane structure of individual spores and, to the same extent as is usual in current taxonomy of parasitic fungi, on difference in host plant.

Students of the *Plasmodiophoraceae* have, with regard to certain of the above genera, apparently realized that the morphological distinctions between them were of too low taxonomic value. Winge (1912, p. 17) writes with regard to *Sorodiscus*: "The similarity between *Sorodiscus* and *Sorosphaera* is" . . . "so great in fact, that it would seem most reasonable to unite them into one genus. As, however, the position of the spores at the maturity are considered of great importance for the definition of the genera of this family, we shall adopt Lagerheim's nomen nudum "*Sorodiscus*" since the spores" . . . „arranged themselves in spore cakes two layers thick". "Only occasionally a small lumen may be seen between the two layers of spores, and but rarely the sporeaggregations assume the form of a hollow sphere". Later, however, Winge has apparently somewhat changed his opinion in a more conservative direction. Asked by Ivimey Cook (1931, p. 318) regarding an eventual union of the two genera, Winge replied: "It seems to me that the spore masses are so characteristic in *Sorodiscus* that it would be wrong to put it in the same genus as *Sorosphaera*". *Ostenfeldiella* and *Clathrosorus* are thought by Cook (1926. p. 210) to be of doubtful taxonomical standing: "Both genera, so far as the evidence goes, appear to be closely allied to *Spongospora*".

Fitzpatrick (1930, p. 65) thinks it preferable, because of the too inadequate knowledge of the life history of *Clathrosorus*, not to recognise this genus. He adds that the organism is perhaps a relative of *Spongospora*. With regard to *Ostenfeldiella* he (l. c. p. 66) finds "but slight reason for including it in the group, and at best, its position is doubtful".

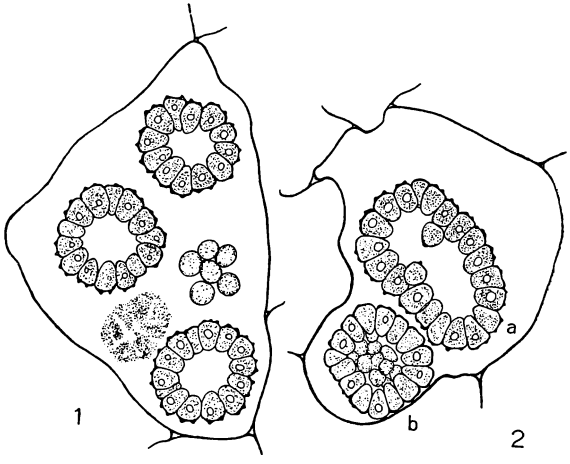
As far as can be judged from their description, Ostenfeld and Petersen (1930, p. 17) would seem not to be foreign to a similar opinion regarding the new monotypic genus *Membranosorus* created by themselves: "No doubt our plant is near to *Sorosphaera* and *Tetramyxa*, but we find it convenient to create a new genus for it".

The genus *Ligniera* Maire et Tison was erected, as well known, to include those forms of the *Plasmodiophoraceae* which do not cause hypertrophy of their respective host plants and which showed a more loosely arrangement of the spore masses. Fitzpatrick (l. c. p. 65) "is wholly disinclined to accept it as valid". And he transfers its present species to the genus *Sorosphaera*, "even though in some the tendency to form definite spore balls" . . . "as for instance *L. verrucosa* Maire et Tison — is much less evident than in the type species *S. veronicae* Schroet.".

There exists thus in some quarters a tendency to doubt the advisability of splitting up the family into the present great number of genera. Apparently, however, the "taxonomic value" of the characters employed has not been questioned so far.

The peculiarities of the taxonomic structure of the *Plasmodiophoraceae* was brought to our attention recently when studying the galls of a Veronica caused by a member of the family. While a number of spore masses in these galls undoubtedly must be classified — according to the present system — as belonging to a "*Sorosphaera*" of the *S. veronicae*-type, other sori displayed equally typical *Spongospora*-, *Ligniera*-, *Clathrosorus*- or *Sorodiscus*-characters.

The fungus had infected a specimen of *Veronica americana* SCHWEINF. on which it had caused gall formation on subaerial adventitious roots of the main axis and on the petioles. As in all respects similar deformations have been described in great detail by WINGE (1912) on *V. chamaedrys* and by TROTTER (1916) on *V. hederaefolia*, a description will not be given here. Suffice it to mention that the Veronica-plant grew in a small brook on a mountain slope near La Veta in Colorado (U.S.A.) where it was collected by the senior writer in the later half of August 1931. Part of the material was fixed in ZENKER'S fluid; the following description of the spore aggregations and spores is based exclusively on fixed material.

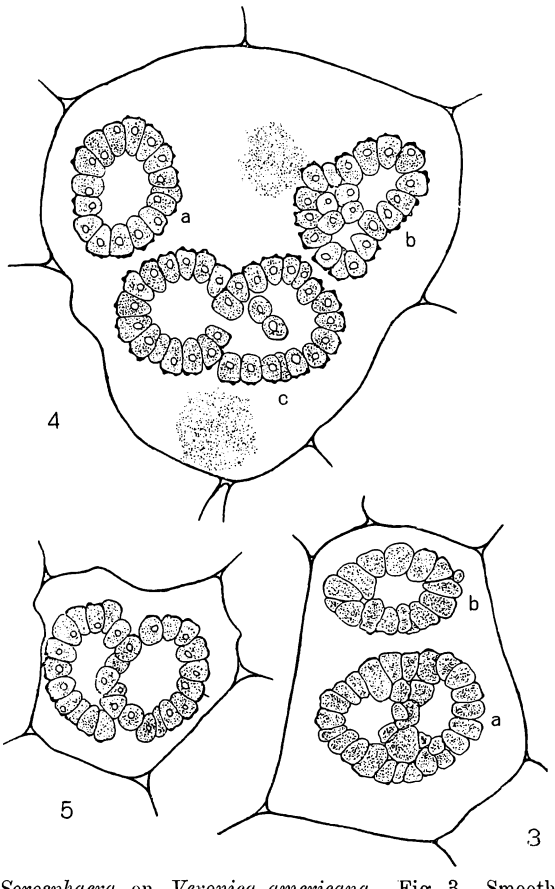


Sorosphaera on *Veronica americana*. Figs. 1 and 2. Spore-aggregations of *Sorosphaera*-type. Observe that warts may be present or absent. All figures were drawn with the aid of a camera lucida at a magnification of ×800; all reduced 1/4 for printing.

When microtome sections of *Veronica americana*, infected with the species of the *Plasmodiophoraceae* were studied, it was found that the spore masses exhibited wide variation in form, size, and number per host cell. Using the arrangement of the spores in the spore mass as a basis of classification, these forms, with much intergra-

dation, fall into three groups, to wit, the hollow sphere type, more or less flattened ellipsoids, and irregular spongelike masses.

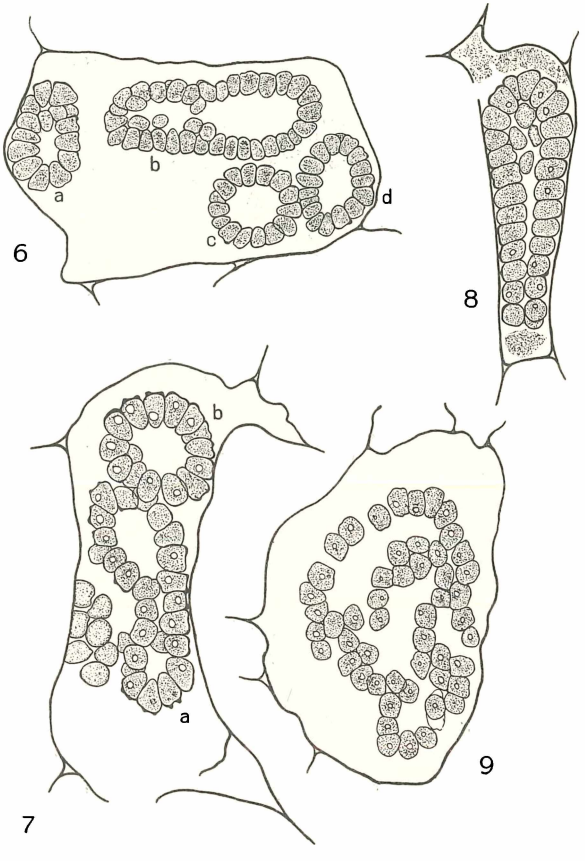
Most frequently the spores were arranged in isodiametric, hollow spheres having in median section from 12—16 spores (fig. 1). Masses of this type containing a larger number of spores per median section (20—30) were usually flattened, forming regular or irregular ellipsoids (figs. 3 b, 4 a, 6 a, 12 a, 13, 14). The spores of many of the masses of this type were crowded out of the periphery and projecting either singly or in clumps into the lumen of the mass. In the much flattened and irregular ellipsoid shown in fig. 7 a, one spore is out of line and pushed into the lumen, and here the lumen is so narrow that a double plate of spores is formed. In fig. 2 a, two spores are out of the regular order of the usual hollow ellipsoid; in 6 b, a small clump of spores occurs on the inner wall and in 4 b one end of the lumen is almost filled with the clump of spores. In the largest spore masses of this ellipsoidal type the lumen is divided into compartments by bands of spores which extend across the lumen or by clumps of spores joining within the spore mass cavity. Such spore masses usually may be recognized by their irregular surface. The smallest lumen of this form is divided into two parts and



Sorosphaera on *Veronica americana*. Fig. 3. Smooth spore-aggregations of *Sorosphaera*-like arrangement. Figs. 4 and 5. Deviations from the strict *Sorosphaera*-type; spores smooth or warted. × 800.

may appear to be formed by the linking of two spheres or ellipsoids (figs. 4c and 5). In fig. 3a the inner band of spores appears to have been formed by the joining of two opposite projecting masses. As the number of spores contained in the spore mass increases, the number of divisions of the lumen increases. In the spore mass figured in fig. 4c which in section has 31 spores, the division of the lumen into three parts is indicated, and in fig. 15b such a division is still more evident.

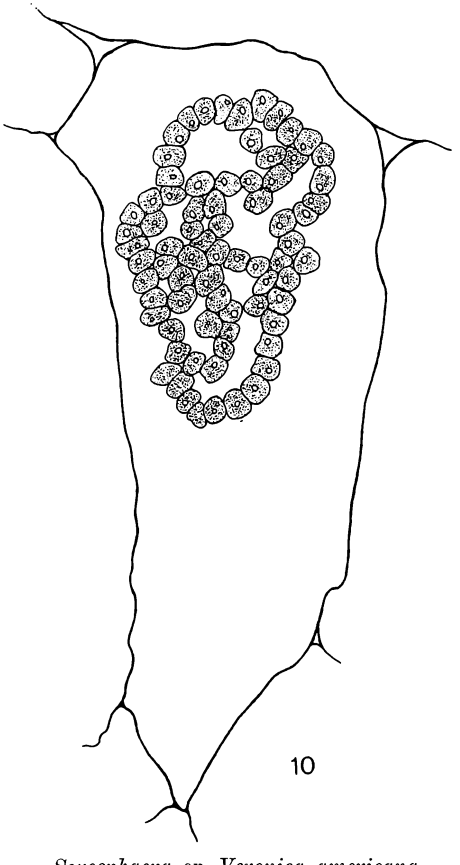
Involuntarily, upon seeing this latter irregular spore mass, one defines it as a spongelike structure rather than a hollow sphere or ellipsoid, and after observing the most peculiar form of spore mass, one may conclude that it is but a simple modification of this latter type.



Sorosphaera on *Veronica americana*. Figs. 6—8. Spore-aggregations rangeing from *Sorosphaera*-type to *Sorodiscus*- or *Ligniera*-type. Fig. 9. Spore-arrangement of *Clathrosorus*-type. × 800.

In many of the cells either occupying a portion of or the entire host cell, the spores were arranged in large irregular masses apparently derived from a single large plurinucleated plasmodium. Many spores formed these masses, the number in the outer layer of a median section varying from 30—60. Within the mass, the spores form bands or clumps which, joining, divide the lumen of the "large" hollow

sphere or ellipsoid into many small cavities. If the spores within the mass tend to form bands rather than clumps and these interlacing bands are few in number, the spore mass in section resembles an irregular net or knot with large cavities (figs. 15 b and 9). If, however, the spores of the spore masses form clumps rather than bands, the cavities are more numerous and smaller, the whole forming a spongelike structure (figs. 10 and 11). In conclusion, the spore masses of the species of *Plasmodiophoraceae* found in *Veronica* sp. may be arranged in a series showing a development from the very simple hollow spheres of figs. 1, 2 b through the simple, hollow ellipsoid (figs. 4 a, 13, 14, 15 a) through the irregular ellipsoid with spores within the lumen (figs. 2 a, 7 a) through the large irregular ellipsoids the lumen of which is divided into few cavities (figs. 3 a, 4 c and 5) to the large irregular many-spored masses with many cavities and conspicuously contoured surface. Yet we may divide these spore masses into three main groups, the hollow sphere, the hollow ellipsoid which is frequently so flattened as to form a double plate of cells (for in addition to fig. 7 a, the masses shown in figs. 8, 12 a, 13 and 14 closely approach the flattened plate), and the spongelike spore mass.

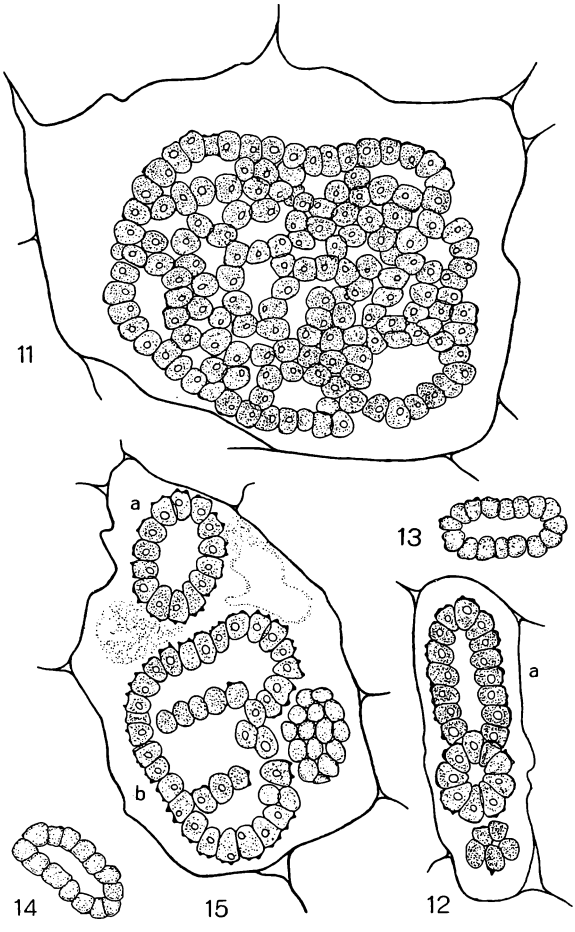


Sorosphaera on *Veronica americana*.
Fig. 10. *Spongospora*-type of arrangement. × 800.

Curiously enough, these three spore types are the basis of defining several genera of *Plasmodiophoraceae*, the hollow sphere, oval or ellipsoid spore mass being characteristic of *Sorosphaera* (sensu Schroeter, non Fitzpatrick), the flattened ellipsoid or double plate

of *Sorodiscus*, and the spongelike spore mass of *Chlathrosorus*; the more compact spore masses may be likened to the characteristic spore arrangement of *Spongospora*.

In various species of the genus *Ligniera* the spores are sometimes arranged in hollow spheres, but more often they occur in "indifferent" congregations, the form of which is by some authors attributed to lack of hypertrophy of the host cells and the subsequent crowding. It is convenient to recall here the descriptions given for instance by Maire et Tison (1911) of the aggregation types displayed by their species *L. radicalis*. They write (l. c. p. 234): "On trouve dans les cellules-hotesses une on plusieurs balles de spores;" . . . "de plus, il arrive parfois, mais rarement, qu'une ou deux tetrades demeurent isolées au moment de la formation des balles. Celle-ci sont pleines ou creuses, aplaties ou cylindriques, arrondies ou allongées suivant leurs taille et les conditions dans lesquelles elles se sont develloppées". The same description would apply also to the conditions found by the same



Sorosphaera on *Veronica americana*. Fig. 11. Spore-aggregation of *Spongospora*-type. Figs. 12—14. Spore-groups of *Sorodiscus*-type. Fig. 15 a. Spore-group intermediate between *Sorosphaera*-type and *Sorodiscus*-type. Fig. 15 b. Spore-aggregation of indeterminable type. × 800.

authors in *L. verrucosa* M. & T. (l. c. p. 235) with the difference that the spore-aggregations here more often may be in the shape of ellipsoid or globoid balls which seldom are flattened to disks or plates. Similar irregularities have been reported from other species of *Ligniera* as well by other authors. In our fig. 8 the host cell of which is little hypertrophied and much crowded, the much flattened or plate-like mass of spores is very characteristic of a *Ligniera*.

These types of spore masses appeared indiscriminately throughout the host in both stems and leaves. The three forms occurred in the same area of infection, separated from other infected regions or strands by normal host tissue, and the various forms were found in the same host cell. In fig. 6 and 7 the regular hollow sphere or the flattened ellipsoid occur, in fig. 15 the ellipsoid and the spongelike type.

In addition to these variable spore arrangements another interesting feature could be observed. The mature spores of the various types of spore masses are in a number of instances provided with slightly thicker walls, showing an unquestionably verrucose sculpturing (see figs. 1, 2, 4). This observation acquires a special interest as in view of the fact that the presence of verrucose walls has been made the main distinguishing characteristic for a species of *Ligniera*, *L. verrucosa* M. & T.

It is obvious from this description and from the literature that the aggregation of spores into masses, showing a certain arrangement, is governed by environmental conditions, hoc est in this case the constitution of the cell of the host plant. So we find that the *Sorosphaera veronicae* of *Veronica chamaedrys* develops the typical "*Sorosphaera*-balls", in *Veronica hederaefolia* the *Sorosphaera* forms flattened double-layered cakes concurrently with the "normal" spheres (Trotter, 1916) and in the present *Veronica americana* great variety of deviations from the *Sorosphaera*-arrangement is the rule. That the several types of spore aggregations described above belong to a single species of the *Plasmodiophoracae* must be taken for granted, if one does not want to assume the galls to be the result of a mixed infection in which organisms, belonging to several genera, had participated. While being theoretically possible, this is hardly likely to have happened in this case, vide the occurrence of several types of spore aggregations in a single host cell. It would in fact be solely a matter of subjective taste to ascribe the plasmodiophoraceous organism in *V. americana* to several species belonging to several genera.

The conclusion can thus hardly be escaped that a practical taxonomy of the members of the *Plasmodiophoraceae* can not profitably

be based on the characters which are being utilized for that purpose at present. It serves no useful purpose, in our opinion, under such conditions to retain a number of genera which are being distinguished by characters, showing such a great amplitude of variation even within the plasmodia derived from an infection by a single organism.

A plainly artificial classification, as is our present day classification in mycology, even if it is claiming to express phylogenetic relationships, cannot be maintained on characters which may vary to the extent that has been described above. It would thus seem only logical to drop those genera which have been founded on the types of spore arrangement that were found by us in the galls of *Veronica americana*. The following genera could thus be regarded as synonyms to *Sorosphaerae* SCHROETER 1886.

Spongospora BRUNCHORST 1887
Ligniera MAIRE & TISON 1911
Sorodiscus LAGERHEIM & WINGE 1912
Ostenfeldiella FERDINANDSEN & WINGE 1914
Clathrosorus FERDINANDSEN & WINGE 1920
Membranosorus OSTENFELD & PETERSEN 1930

As we have seen in the introductory remarks, there has already now and then been given voice to a feeling that several of the above mentioned genera should — for one reason or another — be abolished. Their life histories and general cytological behaviour far from militates against this proposal; in so far as the life history of the genera mentioned has been studied, a remarkable uniformity has as a matter of fact been reported to exist. The discrepancies noted in the literature regarding the interpretation of certain cytological features do not affect to any extent the taxonomical arrangement within the family.

There can be but little doubt entertained regarding the close relationship between *Sorosphaera* (SCHROETER) on the one side and the remaining genera *Plasmodiophora* (WOROIN), *Tetramyxa* (GOEBEL), *Sporomyxa* (LÉGER) and *Trematophlyctis* (PATOUILLARD). This relationship has been further strengthened by recent studies of the cytology of *Plasmodiophora* and several other members of the family. Only *Cystospora* (ELLIOT) would seem to stand apart because of its more complicated spore formation [1]). It seems to us that it would

[1]) MANN (1925) and HARTER and WEIMER (1929) seem to doubt the very existence of the genus *Cystospora*, while TAUBENHAUS (1918) has had ELLIOT's organism in pure culture.

be advisable to go even a step further than has been suggested above and thus to submerge all genera that are recognized at present — with the exception of *Cystospora* — into a single genus, as being in fullest accord with the life history data.

The above genera are at present characterized by having spores remaining more or less free from each other or not arranged on a special pattern as *Plasmodiophora*, *Sporomyxa* and *Trematophlyctis* — or adhering together in dyads or tetrads — as *Tetramyxa*. *Sporomyxa* has been excluded by Fitzpatrick (1930, p. 65) from the *Plasmodiophoraceae* on the grounds that "it occurs in an animal host"; furthermore "its possession of ellipsoidal spores indicates lack of relationship. In any case our knowledge of its life cycle and cytology is insufficient to warrant its inclusion here". Such an exclusion might in our opinion be warranted, if further studies prove its cytology and general life history to be different in essential points; the circumstance that it attacks an animal host could hardly be taken as a serious objection. The deviation in spore shape would, neither, constitute, in our opinion, a valid reason for exclusion from the family of *Plasmodiophoraceae*. The senior writer has had the opportunity of studying an undoubted member of this family, probably closely related to, if not identical, with the *Trematophlyctis* of Patouillard, and which possesses spores resembling closely the *Sporomyxa*-type [1]). *Trematophlyctis*, according to Patouillard (1918 p. 87), "devait rentrer dans le Plasmodiophora, mais il diffère essentiellement de dernier par le mode particulier de dehiscence des sores". The genus and species created by Patouillard attacks the aerial parts — stems and leaves — of a *Leptodesmia*-shrub; the host tissue of these organs ruptures over the sori whereby the spores are set free. This distinction is, it would appear, of a wholly biological nature, and consequently it can not be used for the delimitation of a genus. With regard to the spores of *Trematophlyctis*, they are either rounded or "parfois anguleuses par pression mutuelles" (Patouillard l. c.). They may thus occur singly — though there are always many spores in a cell and a sorus — as in *Plasmodiophora*, or remain in rather close contact with each other as in several other genera. This condition leads over to for instance the *Ligniera verrucosa* M. & T., in which species "single" spores have been reported by Maire & Tison (1911, p. 235) to occur side by side with spores in single file or in non-descript aggregations. *Tetramyxa parasitica*

[1]) Unpublished data; the material was collected on young branches of an unnamed plant in Southern Madagascar in 1913 by the senior author.

is no exception from the present rule that the aggregation-type of the spore masses varies within wide limits. According to SETCHELL (1924, p. 243), the spores may be largely in fours but sometimes in twos and uneven higher numbers, and MAIRE et TISON (1911, p. 231) report that they — the spores — are "asses souvent disassociées ou associées en dyades". Even if thus a certain spore arrangement may be more prevalent than an other or others, the existence of all these variations that have been recorded in the literature from the relatively few cases of infection studied, tends to show that the aggregation-types found in *Plasmodiophora* and *Tetramyxa* are observed not infrequently also in other "distinct" genera. When it furthermore is realized, how far from stable the conditions are in *Sorosphaera*, *Ligniera*, etc., one can find but little justification for not abandoning the present concepts of classification in the *Plasmodiophoraceae*. We therefore would feel wholly justified to merge not only those genera that we already have listed above as synonyms to *Sorosphaera*, but to unite all hitherto described genera of the family — with the exception of *Cystospora* ELLIOT — into one genus which would, according to the nomenclatoric rules, have to be called *Plasmodiophora*. In so doing, we want to express the very close relationship between the various members of the family which has been amply proven to exist by recent cytological and biological studies. Those characters which up till now have served to distinguish genera would in several cases be used to determine species within an amended genus *Plasmodiophora*.

As species under an amended genus *Plasmodiophora* would, temporarily, have to be upheld, firstly those species which belong to formerly monotypical genera as *Plasmodiophora*, *Tetramyxa*, *Spongospora*, *Clathrosorus*, *Trematophlyctis*, *Ostenfeldiella*, *Membranosorus*, *Sporomyxa*, and secondly those species of *Sorosphaera*, *Sorodiscus* and *Ligniera* for which infection experiments have not proven their identity with previously described ones. It is strongly felt by us that the number of species recorded in the literature will be much reduced in the future. We base this belief on the following indications. It has already been proven that *Sorosphaera graminis* SCHWARTZ, *L. bellidis* SCHWARTZ, *L. menthae* SCHWARTZ, *L. alismatis* SCHWARTZ, and *L. pilorum* FRON & GAILLAT are but synonyms to *S. junci* SCHWARTZ. *Sorosphaera radicalis* MAIRE & TISON is according to COOK (1926) probably also identical with *S. junci* SCHWARTZ. *S. junci* is thus capable of infecting the roots of a great diversity of hostplants. A comparison between *Ligniera verrucosa* MAIRE et

Tison on the one hand and *Sorosphaera junci* Schwartz on the other shows that both species display the same variability in spore-arrangement within the aggregations as well as no appreciable differences in the measurements of the individual spores. The only difference between the two consists in the presence of a verrucose sculpture of the membrane of *L. verrucosa*. The authors (Maire et Tison 1911, Cook 1926 and Fitzpatrick 1930) seem to be in agreement regarding this sculpture as providing a character of distinctive species-value. In our opinion, which we base on the rather common occurence of warts on the spores in spore aggregations in the galls of *Veronica americana* (see figs. 4, 7) while being absent in others in the same host cell, this verrucose character cannot be used in delimiting species. The character in question must, when it occurs, be considered as a response to some environmental condition, and in all events as of a non-genotypic order. On morphological grounds *L. verrucosa* can thus not be regarded as a "valid species".

The question then arises with which, if any, of the already described species *L. verrucosa* might be identified. As already mentioned, it shows a high degree of morphological similarity with *L. radicalis* Maire et Tison. On the other hand, it cannot be distinguished from the "*Sorosphaera*" present in the *Veronica americana*-galls. The only difference, which we have been able to find, consists in the circumstance, that our *Sorosphaera*, like *S. veronicae*, causes deformation of the aerial organs of a species of *Veronica*, while *L. verrucosae* infects the root tissues of another species of *Veronica* (*V. arvensis*) without causing hypertrophy of invaded cells. From a pathological point of view, it is conceivable that one and the same species may give rise to a different reaction in different tissues of one and the same host plant. It is also possible that one so called strain or physiological race of one species of parasite is specialized on subterranean organs, while another, morphologically indistinguishable one, might be able to attack only subaerial organs of one species of host; we could thus perhaps best regard *Sorosphaera veronicae* Schroeter and *Ligniera verrucose* M. & T. as "vicariating" strains or races of one species. To us it would seem most natural to consider the two as identical; infection experiments are necessary before such a conclusion is warranted on other than purely morphological grounds. The question of species becomes still more complicated when one extends the comparison to include *L. radicalis* M. & T. This species attacks root tissues of *Callitriche stagnalis* without causing deformations. On the same species of host plant

Sorodiscus callitrichis LAGERH. & WINGE causes gall formation on aerial shoots. Now, the variability of *L. radicalis* M. & T. is wide enough (see above) to include also the flattened type of spore aggregation that so far has been supposed to provide a characteristic of the genus *Sorodiscus*. Moreover, the measurements of the individual spores in the two species under consideration are so similar, that the two species can not be separated on characters based on size. On morphological grounds, in view of the variability of the aggregation-types, the two species must be considered identical. It has already been mentioned, that *L. radicalis* probably is identical with *Sorosphaera junci* SCHWARTZ. If this be the case, *Sorodiscus callitrichis* LAGERH. & WINGE would also be identical with that species, as *L. verrucosa* M. & T. does not, in our opinion, differ from *L. radicalis* on one side, nor from *Sorosphaera Veronicae* SCHROETER on the other. A very suggestive supposition is thus arrived at, namely that all these species are in reality identical. In any event, there are no morphological criteria by which they could be held apart.

With this discussion we have endeavored to show the unsatisfactory condition of present day taxonomy in the *Plasmodiophoraceae*. It is felt by us that experimental work in this family will materially reduce the number of species recognized now and prove their host range to be much wider than is thought at the present time. As we have exemplified, it is impossible to delimit genera or species on the characters utilized at present for that purpose. Although we would feel justified in uniting all accepted genera of the *Plasmodiophoraceae* into one large genus, such action is deferred, until more evidence of an experimental nature has been accumulated in favour of the opinion expressed by us in this paper.

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