A monograph of the Plasmodiophorales.

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(With 14 figures in the text and plates 5—11.)

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Preface.

The increasing interest which is being paid to the systematic study of the lower fungi has as a natural result produced the description of many new species. Frequently new forms have been recorded on comparatively little real evidence, and certainly without sufficent regard for those species which have already been described. This is in part due to the very extensive literature which already exists, and to the inaccessibility of much of it to many workers.

The Plasmodiophorales have, within recent years, attracted a number of workers, whose results, while not always harmonising in the more intricate details, still agree in the essential facts concerning the life-history of the various members of the group. It seemed, therefore, to the writer that a review of what has already been written and an endeavour to sift what has been definitely proved from what is more conjectural, or even in the light of recent studies has been proved to be inaccurate or untrue, might be of service to the general student of mycology as well as to those who are specially interested in the lower groups.

The systematic position of the Plasmodiophorales, and the fact that the members shew a remarkable similarity among themselves makes them particularly interesting to those who wish to elucidate the origin of the fungi among the most primitive organisms known. This fact is well illustrated by the difference of opinion among systematic botanists as to whether the Plasmodiophorales should be included in the fungi at all. Some consider that they are allied to the Protozoa, some to the fungi, while the idea that they represent a group intermediate between the two is not by any means without supporters. It is for this reason that the group is left out of many text-books of Mycology and Zoology, and no critical systematic account of the members has been published.

Recent discoveries in the group, moreover, have not been made use of in certain modern text-books which still describe as species of the Plasmodiophoracea, organisms which have been transferred to other groups, or physiological effects which have been mistaken for living organisms. Mixtures of two or more life-histories have been described as a single species which has then been used as evidence of relationships between the two groups of organisms of which that species was composed, and the introduction of such 'species' has tended to obscure the characters of both families.

The very limited distribution of the majority of the species, and the fact that many have only been recorded on a few occasions renders it difficult for any one investigator to be able to study the bulk of the species, and few type collections of slides even have been preserved. Up to the present no critical study has been possible, and authors have had to rely for their description upon published figures, some of which are by no means accurate. The present writer is in the fortunate position of having been able to study representative slides of all the recognised species with the exception of *Sorodiscus Karlingii*, and his descriptions of the appearance of the spore masses, as well as the most minute details of the myxamoebae is based upon these slides rather than upon the published results, though of course these have been thoroughly compared in each case. In addition he has published elsewhere [1]) critical accounts of *Plasmodiophora Brassicae, Sorosphaera radicalis, Ligniera Junci* and *Sorodiscus radicicolus.* He has also been able to study the complete series of slides upon which BLOMFIELD and SCHWARTZ'S paper on *Sorosphaera Veronicae* was based.

For the gift of slides of the other species he wishes to thank Prof. RÉNÉ MAIRE and Prof. O. WINGE. For permission to reproduce certain figures he is indebted to the Council of the Royal Society of London, the Ministry of Agriculture and Fisheries, the Department of Agriculture of the Irish Free State, Dr. G. H. PETHYBRIDGE, Prof. V. H. BLACKMAN F. R. S., and Prof. O. WINGE. Finally his thanks are due to Mr. J. RAMSBOTTOM O. B. E. and Miss G. LISTER for their helpful criticism. A summary of this paper has been published in the Supplement of the Hong Kong Naturalist, Oct. 1932 p. 29.

Introduction.

The first species of the Plasmodiophoraceae to be described was *Plasmodiophora Brassicae*, the organism causing Finger and Toe disease of cabbages and other Crucifers. Owing to damage done to crops in the neighbourhood of Leningrad, the Russian Gardeners' Association offered a prize in 1872 for a study of the cause. At first no response was made to this offer and it was repeated in 1875 and again in 1877. In 1873 WORONIN began his study of the fungus and completed his work in 1877. The results were then published in a series of Russian papers which received but little notice, and it was not until 1878 when a more complete account in German had appeared that any general notice was taken of these results.

Shortly after, in 1892, EYCLESHYMER, working in the United States also studied the nature of an organism causing what was called Club root of Cabbages, and shewed that it was due to the same fungus.

It was from these investigations that the study of the group began. Shortly after an investigation of the cytology of the organism was made by NAWASHIN, and it was found that the behaviour of

[1]) See bibliography p. 246.

the nuclei was different from what was then known to occur in the majority of other plants. Subsequent work by a number of students of mycology demonstrated the existence of other species which differed from *Plasmodiophora Brassicae* in the arrangement of the spores and in certain other features and a number of other genera were formed. Several of these genera have since been removed from the family since they did not really shew close similarity.

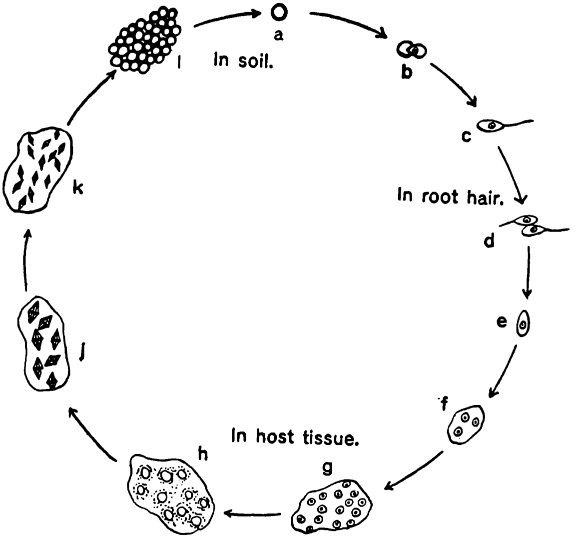

Fig. 1. Life-cycle of a typical member of the Plasmodiophoraceae.

The life-history of the organisms included in the family is simple. The spores are generally liberated into the soil where they pass the winter in a state of quiescence. In the spring the spore wall cracks and a small motile body escapes to which the name swarm spore has been applied, but in view of its behaviour it would be better to call it a swarm cell [1]). The swarm cell is generally spherical in shape with a single anterior flagellum about equal in length to the diameter of the swarm cell. The swarm cells move actively about in the water surrounding the host plant and in this position they fuse in pairs. The details have, however, only been seen in culture conditions. Two swarm cells meet and the flagella are withdrawn, the protoplasts then become amoeboid and coalesce together. A nuclear fusion follows and the swarm cell again becomes flagellate and in this state penetrates the host cell. There appears to be a relation between the amount of moisture present and the behaviour of the swarm cell, if there is plenty of water the infection is by flagellate bodies, while in the absence of excess

[1]) A glossary of technical terms will be found on p. 251.

of moisture they may remain amoeboid. There is some evidence that if external fusion is not achieved it may take place within the host tissue, and this certainly does occur in species in which spores germinate within the host cells, and infection in galls is spread. It also occurs in *Plasmodiophora Brassicae* where an intermediate stage is interpolated. Within the host cell motion becomes less active and the amoeboid organism migrates into the root proper since it has the power of penetrating the cell wall. This migration may occur while the nucleus remains quiescent, but sometimes the nucleus has already divided before the organism has finally reached a point suitable for further development. This multinucleated amoeboid structure is termed a myxamoeba.

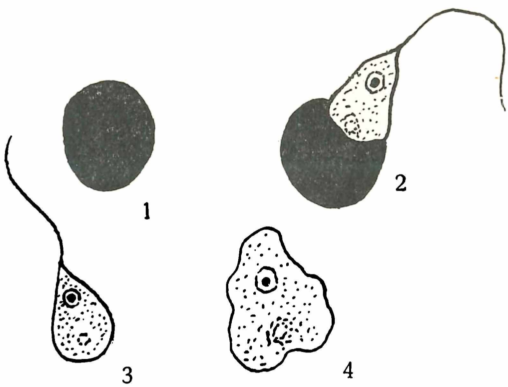

Fig. 2. Germination of the spore. 1. Spore. 2. Swarm cell emerging from the spore. 3. Mature swarm cell. 4. Amoeboid swarm cell.

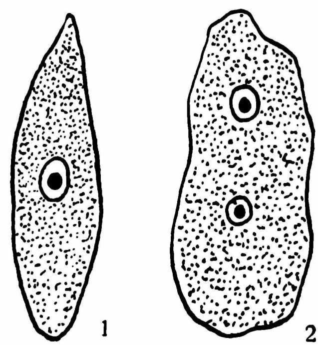

Fig. 3. Development of myxamoeba. 1. Swarm cell after fusion. 2. Myxamoeba containing two nuclei.

When the myxamoeba has reached a cell suitable for it to mature in, the nucleus divides up into a large number by a process of simple division to which the term protomitosis is generally applied. During this division the nuclear membrane is retained throughout the whole process which consists in the formation of the chromatin into a ring in the centre of which lies a karyosome. This karyosome is one of the most characteristic features of the resting nucleus and is far more easily seen than the chromatin which except during division lies around the nuclear membrane. A spindle is formed in such a way that the chromatin ring lies across the equator of the spindle. The ring then splits into two rings which pass towards the respective poles. Meanwhile the central karyosome has become drawn out and finally divides into two approximately equal parts. Owing to the appearance which these nuclear divisions give when viewed from the side certain terms have been coined to describe the stages. The stage in which the chromatin is arranged as a ring with the karyosome in its centre has been called the "cruciform" or "Saturn stage", and the later condition in which the chromatin rings have separated and the karyosome has almost divided is spoken of as the "double anchor" or "dumb-bell stage". The division is completed by the invagination of the nuclear membrane to form the membranes of the daughter nuclei. During this division most workers agree that no separate chromosomes are differentiated, although Horne has given an account of

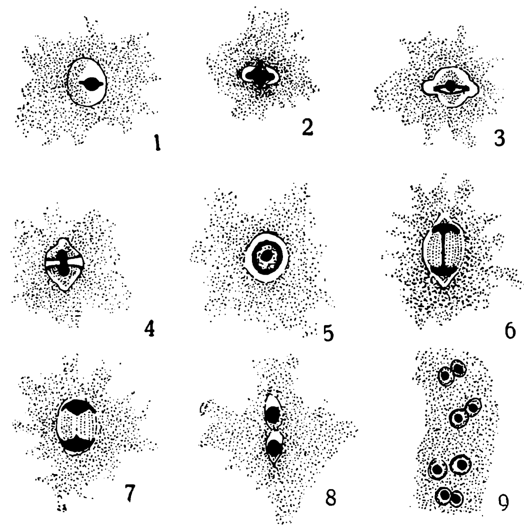

Fig. 5. Stages in Protomitosis in *Ligniera Junci*. 1. The early formation of the ring. 2—3. Cruciform stage seen in side view and slightly oblique. 4. Split of the chromatin ring and elongation of the karyosome. 5. Saturn stage, polar view. 6. Double anchor stage shewing the karyosome almost divided. 7. The karyosome split and the chromatin forming around it. 8. Re-formation of the nuclear membranes of the daughter nuclei. 9. Daughter nuclei at the end of the division.

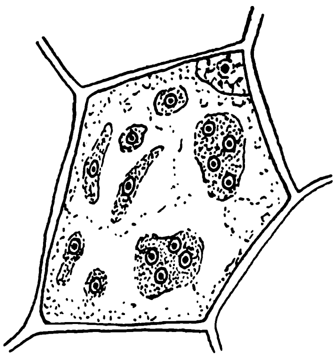

Fig. 4. Schizont formation in *Plasmodiophora Brassicae* shewing the fragmentation of the myxamoeba into a number of uninucleated parts.

the existence of four chromosomes during protomitosis in *Plasmodiophora Brassicae* and *Spongospora subterranea*; these observations, however, have not been confirmed by later studies.

Such a type of nuclear division takes place each time the nuclei divide during the somatic divisions within the myxamoeba, and as a general rule all the nuclei within the amoeba divide simultaneously. The myxamoeba may sometimes divide or fragment into smaller parts at any rate during the early stages in its development, though there is little evidence to shew that when two myxamoeba happen to reach the same cell, they fuse together into a single mass. There may be an association, but not complete co-ordination since in subsequent nuclear divisions the nuclei of the two associates will not necessarily divide at the same time. A gradual co-operation, however, is shewn, since in mature myxamoebae all the parts produce spores together. This may be because the stimulus for spore production is experienced by all the parts simultaneously. There is no evidence at all that these associations represent any reproductive phase or that during them any conjugation process occurs.

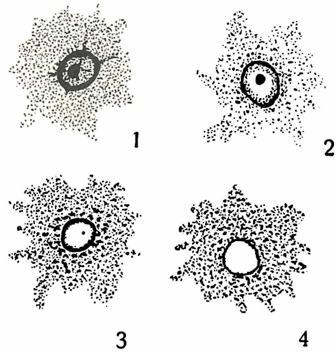

Fig. 6. The Akaryote stage in *Ligniera Junci*. 1. The radiation phenomena around the nuclear membrane. 2. Reduction in size of the karyosome. 3. Disappearance of the karyosome. 4. Migration of the chromatin outside the nuclear membrane.

The myxamoeba, then, is a multinucleated amoeba or, as it is frequently termed by workers in the group, a plasmodium, consisting of a mass of homogeneous protoplasm not surrounded by a wall, but containing a large number of nuclei. It is nourished at the expense of the host cell, and this is frequently shewn by disorganisation of the host nucleus, which sometimes becomes greatly enlarged, before finally disappearing completely.

When the myxamoeba has reached maturity, changes take place in the nuclei. This consists of the migration of all the stainable chromatinout from the nucleus into the surrounding cytoplasm. So complete is this process that it has been postulated, quite incorrectly, that fresh nuclei are formed *de novo* from this extruded chromatin. This stage in the life-history of the organism is spoken of as the "Akaryote stage".

Immediately following upon this condition the chromatin again passes into the nuclei and these immediately pass through two divisions during which separate chromosomes become differentiated. During the first of these two divisions the chromosome number is halved. The second, or homotypic, division is a perfectly typical mitotic division in which the karyosome is absent. In both these two divisions there is nothing to distinguish the nuclei form those of the higher plants and the stages described are entirely comparable with the heterotypic and homotypic divisions recorded for many flowering plants.

At the end of the second division furrowing appears around the daughter nuclei, walls are laid down and the content of each constitutes a spore. It is in the details of the formation of these spores that the genera are distinguished from one another. In *Plasmodiophora*, *Spongospora*, *Tetramyxa* and *Ligniera* no wall is developed around the whole plasmodium during spore formation, and therefore the individual spores are free after they have been differentiated. In the genera *Sorosphaera* and *Sorodiscus* each myxamoeba produces a single spore-ball or spore-cake and the whole is surrounded by a wall deposited around the myxamoeba during

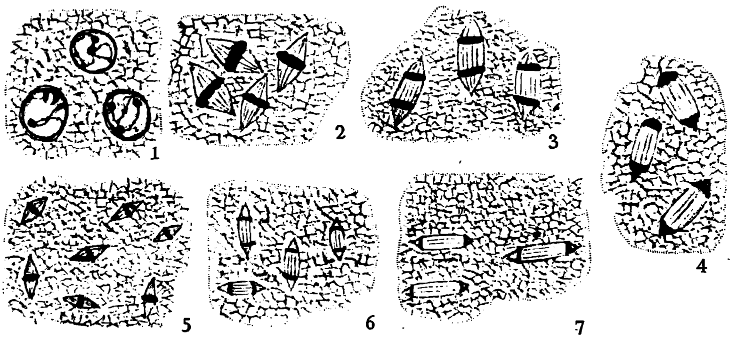

Fig. 7. Reduction division prior to spore formation in *Plasmodiophora Brassicae*. 1. Synapsis. 2. Heterotypic metaphase. 3. Heterotypic anaphase. 4. Heterotypic telophase. 5. Homotypic metaphase. 6. Homotypic anaphase. 7. Homotypic telophase.

spore formation. In the genus *Ligniera* there is a second type of reproduction by the formation of zoosporangia in which from four to eight zoospores become differentiated. Several zoosporangia may be formed in one myxamoeba.

The spores are shed when the host tissue disorganises, but germination may take place prior to this. The wall of the spore cracks and a single swarm cell emerges from each spore. This body may either migrate to the exterior, or, more frequently, make its way into another cell of the same host and finally produce another crop of spores. There is evidence that in many plants, particularly those in which the parasite produces hypertrophy, several complete life-cycles are passed through in the same organ during the year. It is during the winter that the host tissue generally dies and the spores come to be scattered in the soil.

They remain dormant for a considerable time and it has been found that spores two to three years old are capable of causing infection. It is also during the winter months that the fungus is scattered by the agency of man and animals especially by becoming incorporated in sticky soil which is carried about on the boots and feet. It is noticeable that most species occur in marshy damp soil.

The effect of the fungus upon the host plant differs in the various species, in most hypertrophy is caused which may be extensive, as in *Plasmodiophora* and *Sorodiscus*, or restricted to a small gall as in *Tetramyxa*, *Spongospora* and *Sorosphaera*. Only in the genus *Ligniera* is hypertrophy entirely absent. The species also differ in the organ which is attacked. In some it is the roots which become infected, in others infection occurs here but the parasite spreads from them to aerial organs. In *Plasmodiophora Fici-repentis* and *P. Diplantherae* it is the stem, while in *Tetramyxa parasitica* and *Sorosphaera Veronicae* the attack is restricted to that part of the stem just above the soil. In *Spongospora subterranea* both the roots and the potato tuber may become diseased.

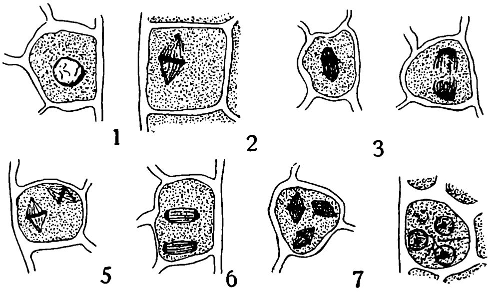

Fig. 8. Reduction division in Zoosporangia in *Ligniera Junci*. 1. Synapsis. 2. Heterotypic metaphase. 3. Heterotypic anaphase. 4. Heterotypic telophase. 5. Homotypic metaphase. 6. Homotypic telophase. 7. Metaphase of third division. 8. Formation of zoospores.

Plasmodiophoraceae Zopf.

Zopf (1884): Die Pilzthiere oder Schleimpilze. Breslau p. 74.

Mycelium wholly lacking, thallus consisting of naked amoeboid protoplasts, termed myxamoebae, which fragment into uninucleated, or multinucleated schizonts capable of amoeboid movement. Myxamoebae multinucleated, nuclei dividing by a simple form of mitosis termed protomitosis in which separate chromosomes are not differentiated, and in which the nuclear membrane and karyosome persists throughout the division. Nuclei before spore formation passing through a chromatin extrusion stage termed the Akaryote stage. A typical meiosis occuring before spore formation. Myxamoebae forming uninucleated spores which may be free or arranged in a definite system enclosed in a membrane. Nuclei in spores, haploid. Spores on germination producing swarm cells. Swarm cells uniflagellate at anterior end, pyriform and enclosed in a very delicate membrane. Swarm spores fusing in pairs, either before or after becoming amoeboid. In an amoeboid state they reinfect host cells foming myxamoebae. Myxamoebae diploid. The organisms included in the family chiefly attack the cells of Phanerogams and possibly Pteridophyta, in most genera causing hypertrophy and the formation of galls.

The family name Plasmodiophoraceae was used first by Zopf in 1884 to include two genera *Plasmodiophora* and *Tetramyxa* and placed in the Monadineae Zoosporeae, a group proposed by Cienkowski. Later in 1886 Schroeter established the family Phytomyxinae to include a new genus *Phytomyxa* which he had described. Into this family he placed four genera, *Plasmodiophora*, *Phytomyxa*, *Tetramyxa* and *Sorosphaera*. Later it was shewn that *Phytomyxa Leguminosarum* and *P. Lupini* were bacteria and the genus was removed from the Phytomyxinae. Reviewing the situation in 1909 Maire and Tison pointed out that since the genus *Phytomyxa* had been removed the name Phytomyxinae was unsuitable for the family, and proposed to revert to the older name given by Zopf. In the family thay placed five genera, *Plasmodiophora*, *Tetramyxa*, *Sorosphaera*, *Ligniera* and *Molliardia*. Later in 1911 Osborne added *Spongospora* and in 1912 Winge added *Sorodiscus* to the number of genera.

These genera will be considered in detail in the following pages and reasons will be given for altering and combining certain new genera in the older ones and excluding, one, *Molliardia*, from the recognised list. The genera are distinguished from one another by the arrangement of the spores and the following key is based upon this feature.

Key to the genera of the Plasmodiophoraceae.

I. Myxamoebae giving rise to spores only.
   a. Spores at maturity not arranged in a definite system, but lying freely in the host cell. 1. *Plasmodiophora* p. 189.
   b. Spores at maturity arranged in a definite system.
      A. Spores arranged in a spore-ball or spore-cake.
         1. Spore-ball enclosed in a common membrane.
            '. Spore-ball spherical or ellipsoidal, hollow containing a single layer of spores. 2. *Sorosphaera* p. 198.

''. Spore-ball ellipsoidal, never hollow, but composed of two closely applied layers of spores 3. *Sorodiscus* p. 203.

2. Spore-ball not enclosed in a common membrane, irregular in outline, more or less solid, but traversed by fissures. 4. *Spongospora* p. 208.

B. Spores not forming a spore-ball, but associated in tetrads, becoming broken up owing to the absence of a common membrane. 5. *Tetramyxa* p. 216.

II. Myxamoebae giving rise to both spores and zoospores.

a. Spores at maturity not arranged in a definite system, but aggregated together; not enclosed in a common membrane. 6. *Ligniera* p. 221.

Genus I. *Plasmodiophora* Woronin.

Woronin (1877): Arb. d. St. Petersburg Naturf. Gesellsch. Vol. 8 p. 169—201.
Pringsheim (1878): Jahrb. f. Wiss. Bot. Vol. 11 p. 548—574.

Spores not aggregated together into a spore-ball or spore-cake nor enclosed in a common membrane. Myxamoebae generally large, completely filling the host cell. When mature myxamoebae producing a large number of spores. Spores on germination each producing a single swarm cell which reinfects the host. Conjugation occurring between swarm cells outside the host plant. Reduction division taking place between the akaryote stage and the formation of spores. The organisms cause hypertrophy of the host tissues.

Three species are considered to belong to this genus.

Key to the species.

I. Swarm cells giving rise to zoosporangia in which secondary zoospores are formed. *P. Brassicae* p. 189.

II. Swarm cells not giving rise to zoosporangia but producing myxamoebae direct.

a. Spores small, 1.5 μ diam. Myxamoebae small, up to 25 μ in length. *P. Fici-repentis* p. 193.

b. Spores large, 4.5 μ diam. Myxamoebae large, up to 200 μ in length. *P. Diplantherae* p. 194.

I. *Plasmodiophora Brassicae* Woronin.

(Text-Figs. 4 and 7 and Pl. 5 Figs. 1—3.)

Woronin (1877): Arb. d. St. Petersburg Naturf. Gesellsch. Vol. 8 p. 169—201.
Woronin (1878): Pringsh. Jahrb. f. Wiss. Bot. Vol. 11 p. 548—574.

Spores spherical 1.6—4.3 μ diam, with thin hyaline membrane with no sculpturing. Spores on germination each producing one swarm cell which infects the host. Swarm cell uniflagellate 2.5—3.5 μ diam. These producing zoosporangia within the root hairs, in which zoospores are formed. Zoospores devoid of flagella, 1.5 μ diam. Zoospores conjugating in pairs during migration into the cells of the root, forming myxamoebae. Myxamoebae large 100—200 μ diam, containing many nuclei; producing at maturity spores.

The organism causes hypertrophy of the roots of various wild and cultivated species of Cruciferae, particularly species of the genus *Brassica.* It occurs widely throughout the world in temperate climates. In this country is is known under various popular names, Finger and Toe disease, Club Root, Anbury; in the United States as Club Root; in France as hernie; in Italy as ernia; in Germany as Kropfkrankheit; in Holland as Knolvoet and in Denmark as Kaalbrok.

The organism has been very extensively studied and it is only possible to give a brief summary of the work which has been done. After the original discovery by Woronin in Russia and Eycleshymer in the United states many others investigated this important plant disease. In 1892 Waaker studied the effect of the organism upon the host tissue. In 1893 Nawashin commenced his study of the cytology using material sent to him by Woronin. The results were of the greatest importance since they indicated the special type of nuclear division associated with the vegetative part of the life-cycle. In his study, however, he made an incorrect interpretation of the number and nature of the divisions after the Akaryote stage and failed to observe that this was a reduction division. In 1905 Prowazek reinvestigated this problem and was able to shew that a perfectly typical meiosis occurred.

In 1909 Maire and Tison compared the life-history of this species with *Sorosphaera Veronicae* which they had been studying and shewed the close similarity between them. Based upon these results they may be said to have been largely responsible for placing the group on a sound systematic basis. Further work by Favorski in 1911 and Lutman in 1913 repeated much previous work and added slightly to our knowledge of the behaviour of the nuclei. In 1917 Chupp published an account of the method of infection and discussed the position of a karyogamy, a point which had not been so far satisfactorily proved. The following year Kunkel gave a very full account of the effect of the fungus on the host tissue and shewed the way in which the tumours arise.

In 1927 Jones gave an account of his work in culturing the fungus and suggested that the previous observations upon the life-history were erroneous. His observations have not been confirmed. In 1930 Horne expressed the opinion that protomitosis did not occur in the Plasmodiophoraceae, but that during the vegetative part of the life-cycle, chromosomes to the number of four were present. He further postulated that a karyogamy occurred between the vegetative and reproductive stages. In the same year Cook and Schwartz gave an account of the cytology and method of infection. Finally in 1931 Milovidov published a further study of the cytology, and failed to support Horne's view that any chromosomes were differentiated during the vegetative part of the life-cycle.

The life-history of this species has, therefore, been studied in considerable detail and it seems reasonable to consider that the accounts are substantially correct. From the author's own observations the life-cycle may be conveniently divided into three phases; (a) the infection of the host by the parasite; (b) the growth of the organism at the expense of the host, and (c) the multiplication of the fungus by the development of spores within the host cell.

The swarm cell penetrates through the cell wall of the root-hair, losing its flagellum during the process, and then when inside assumes an amoeboid shape. It grows and migrates up the root-hair and its nucleus divides mitotically. Walls are finally formed around the nuclei cutting the multinucleated amoeba into a number of separate zoosporangia which measure 6—6.5 μ in diameter. The nucleus of the zoosporangium divides into four or eight parts by typical mitosis, and around each a tiny mass of cytoplasm collects. The wall of the zoosporangium, which is quite thin, collapses, and the zoospores escape. Each zoospore is a spindle-shaped body 1—1.5 μ in length and from 0.5 —0.7 μ in diameter. After escaping these zoospores fuse in pairs. This fusion may either take place in the root-hair, or the individuals may migrate into cells of the cortex and fusion may occur there.

The body formed as a result of nuclear fusion is the myxamoeba which then continues to increase in size accompanied by protomitotic nuclear division. The myxamoebae are capable of slow movement, of the same sluggish character which occurs in the true Amoebae, the motion being achieved by the extension and contraction of blunt pseudopodia. Many remain in the cortical parenchyma, but some migrate into the cambial cells. In the cambium they increase their attack, since in the subsequent meristematic activity of that tissue the parasite is distributed to many cells. As a rule it is the medullary ray tissue which suffers most from the fungus.

After a while the myxamoeba reaches a suitable cell for development with a plentiful supply of food material, and it increases rapidly until it completely fills the cell. Coalescence of two or more myxamoebae is sometimes seen in this species. Occasionally the myxamoeba fragment into uninucleated or multinucleated schizonts, but the existence of two or more amoebae within the same cell is rare. When the myxamoeba has devoured all the available food it begin to reproduce. This is prefaced by a typical Akaryote stage in which nearly, but not quite all the stainable material passes out from the nuclei.

With the reconstitution of the nuclei a spireme stage is observed followed by the formation of a spindle upon which separate chromosomes, probably eight in number, are arranged across its equator. These chromosomes separate and pass to the poles. This heterotypic division is immediately followed by a second division in which only four chromosomes are present. Accurate counts of the chromosomes are difficult owing to the extremely small size of the nuclei, but from comparative measurements it has been found that the metaphase plate of the second division is exactly half that of the first, shewing that the quantity of chromatin is halved during the first division.

With the reformation of the nuclei after the second division the protoplasm divides up around them and walls are laid down. No wall is deposited around the whole myxamoeba in this species. The spores so formed are usually spherical 2—3 μ in diameter, although occasionally oval spores 4—6 μ have been found. The mature spore has a thin smooth wall with no superficial markings upon it. The spores remain within the host cell until the disorganisation of the host tissue. There is no evidence in this species that germination occurs within the host.

During the winter the host tissue disorganises and the spores are shed into the soil. Here they remain during the next few months and may retain their vitality for several years. Under suitable conditions of temperature and moisture the spores germinate. The wall cracks and there emerges a swarm cell. It is oval and pyriform 3—3.5 μ in length by 1.5—2 μ in diameter. The posterior end is not irregular or amoeboid, as described by Woronin, but perfectly smooth. At the anterior end there is a single flagellum about equal in length to the swarm cell. Infection can only take place if germination has occurred close to the host plant, and it has been found that the swarm cell cannot travel a distance of more than five inches to its host. The swarm cell penetrates the root hairs without external fusion and in this species fusion is delayed until after infection has occurred.

It has been found that infection is most active in acid soils and this knowledge forms the basis of soil treatment against the disease since cabbage plants grown in infected soil which have been planted in a liberal dusting of lime are not as a rule attacked. In the presence of an alkali the swarm cells die rapidly and do not seem to have the power of infection or penetration of even the thin wall of a root-hair. In addition to the use of lime, mercuric compounds, quinine, and even carbon disulphide have been successfully employed. It is not intended here to give an account of the very extensive work which has been done in this direction.

2. *Plasmodiophora Fici-repentis* Andreucci.

(Pl. 5 Fig. 4.)

Andreucci (1926): Archivio Botanico Vol. 2 p. 18—28.

Spores spherical 1.55 μ diam, membrane thin, hyaline and not associated into fours. On germination swarm cells are produced. Swarm cells pyriform with one flagellum, 2.7 μ in length, giving rise to amoebae of variable shape up to 6×24 μ in size. Myxamoebae formed by the aggregation of amoebae together, later fragmenting into irregular parts, but finally forming spores. Myxamoebae sometimes becoming enclosed in cysts forming fresh myxamoebae. Cysts 9.15—45.7 μ in diameter.

The organism causes tumours of irregular shape, usually rounded and coral-like, up to 5 cms. in diameter. It has been found on large and small branches of *Ficus repens* in a garden, at Siena, Italy.

This species has only been recorded by Dr. Andreucci from one locality and the present author has only seen dried specimens of the galls, which were unsuitable for studying the internal structure. It may be distinguished from *P. Brassicae* by the smaller spores and by the fact that it attacks the branches rather than the roots of the host plant. The galls are woody, hard and brownish grey in colour.

According to the observations made by Andreucci the life-history consisted of the germination of the spores to produce swarm-cells, these became amoeboid and united to form a plasmodium which again divided into uninucleated particles. When mature the plasmodium produced spores which were not arranged in a definite system. If these spores were placed in water small oval flagellated swarm cells were produced. No fusion of these bodies was observed.

An additional cystic stage was also observed. Hyaline cysts measuring from 9.15 μ to 42—70 μ in diameter or even up to 73 μ were found. These germinated to produce plasmodia. The wall of the smaller cysts is granular, while that of the larger is much thickened and marked with fine canals.

There are certain points in the life-history which seem to throw doubt on whether this species really belongs to the genus *Plasmodiophora.* Unfortunately the original work was not illustrated by any figures and the writer has been unable to obtain specimen slides from Dr. Andreucci to compare with the other species. It seems best, therefore, to retain this species in the genus until such a time as a more critical illustrated and comparative account is published.

3. *Plasmodiophora Diplantherae* (Ferdinandsen & Winge) Cook. nov. comb.

(Text-Fig. 9 and Pl. 6 Figs. 5—6.)

Syn. *Ostenfeldiella Diplantherae,* Ferdinandsen & Winge (1914): Annales Botany Vol. 28 p. 643—649.

Spores spherical, brown, 4—4.5 μ diam, with thin, hyaline, smooth membranes. Spores producing myxamoebae which grow to a large size, 125—200 μ in diameter, containing many nuclei. Myxamoebae forming spores within the host cells which increase in size from 35 μ to 200 μ in diameter.

The organism attacks *Diplanthera Wrightii*, a water plant belonging to the Naiadaceae, causing swelling on the stems in the area of the internodes, which as a result were swollen to give the appearance "of a string of pearls". It was found by Dr. Ostenfeld at St. Croix in the Danish West Indies. As a result of his examination Dr. Ostenfeld concluded that the causal organism was a species of the Plasmodiophoraceae and upon his return to Europe sent material to Ferdinandsen and Winge. Since the material had only been fixed in alcohol cytological details could not be made out, but the myxamoebae and spores were present in large numbers in the tissues. As a result of their study Ferdinandsen and Winge placed the organism in a new genus under the name *Ostenfeldiella Diplantherae*. Subsequent workers have doubted the validity of this species, and the present author obtained slides, through the kindness of Prof. Winge. From his observation he is satisfied that the organism is a species of the Plasmodiophoraceae but sees no reason for placing it in a separate genus. The spores are not arranged in a definite system, nor are they enclosed in a common membrane. In their shape and position, therefore they conform to that of the genus *Plasmodiophora*. It is therefore proposed to transfer this species to that genus under the name *Plasmodiophora Diplantherae*.

FERDINANDSEN and WINGE studied the effect of the fungus upon the host and shewed some interesting points. They found that only the internodes were infected and that the cells at the top of the internode were active and devoid of the fungus. They found that in the meristematic parts of the plant uninucleated amoebae were present and concluded that the myxamoebae divided soon after nuclear division, a feature rare in the Plasmodiophoraceae. Lower down the internode were large myxamoebae associated with swelling of the host tissue. In lower internodes many of the cells were filled with masses of spores.

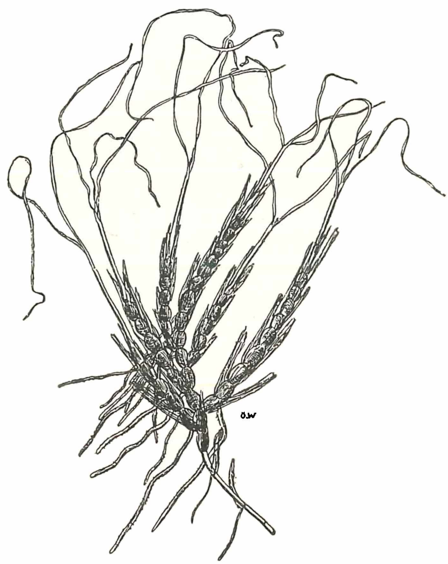

Fig. 9. *Plasmodiophora Diplantherae*. Habit of the fungus on the host (from FERDINANDSEN and WINGE).

The myxamoebae stimulate the host cell to increase in size and in this way very large myxamoebae are formed. The effect of these large cells is to cause the elements to stretch tangentially instead of increasing radially. The fungus is restricted to the central cortex and does not occur in the outer cortex or in the central cylinder.

In the slides I have examined the myxamoebae are mostly large, and contain many nuclei, though these are not sufficently well preserved to make out cytological details. In mature myxamoebae there are indications that the nuclei are passing through the Akaryote stage since they appear as almost empty areas, and the protoplasm around them shews greater avidity for stains. The spores, although a few are shrunken, shew the typical form of those of *P. Brassicae* except that they are larger. There appears to be no special reason for excluding this species either from the group as a whole nor for considering that it should be placed in a separate genus. So far as is known it has not been recorded from any other locality.

Species doubtful, or no longer recognised as belonging to the genus *Plasmodiophora*.

1. *P. Alni* (Woron.) Moell. (Ann. Sci. Nat. Bot. Ser. 5 Vol. 7 1867.)

This species was first described by Woronin under the name *Schinzia Alni*; it was subsequently places in the genus *Plasmodiophora* by Moeller and Schroeter. Later Maire and Tison examined the galls and found very fine hyphae in them, and gave the name *Frankiella Alni* (Woron.) Maire & Tison to the fungus.

2. *P. Elaeagni* Schroet. (Engler u. Prantl, Nat. Pflanzenfamilien Vol. 1 1897.)

Brunchorst gave the name to the organism which caused swelling on *Elaeagnus* similar to those on *Alnus*. Later Maire and Tison also observed similar galls on *Hippophae rhamnoides* and considered that the causal organism was a species of the genus *Frankiella* and called it *Frankiella Elaeagni* (Schroet.) Maire & Tison.

3. *P. Orchidis* Massee. (Ann. Bot. Vol. 9 1895.)

Massee considered that the "spot" disease of orchids was due to this fungus, later he retracted his view and stated that the disease was entirely physiological.

4. *P. Humuli* Kirk. (Fourteenth Rept. Dept. Agric, New Zealand 1906.)

The roots of hop plants in New Zealand were found with galls similar to those produced by *Plasmodiophora Brassicae* and Kirk concluded that the galls he observed were due to a similar fungus which he called *P. Humuli*. He never actually saw the fungus. Later Nicholls found similar swellings on hops in Tasmania and recorded that it was due to the same fungus without examining the tissues microscopically. Stevens in his "Fungi which cause plant disease" refers to another species *P. humili* Kirk which is presumably a printer's error.

5. *P. Halophilae* Ferdinandsen & Winge. (Zentralbl. f. Bakt., Parasit. u. Infektion. Vol. 37 1913.)

This organism was found by Ostenfeld attacking the petiole of *Halophila ovalis*; Ferdinandsen and Winge stated that they found an organism present which "had the morphological characteristics of the genus *Plasmodiophora*" but gave no further description.

6. *P. californicae* VIALA & SAUVAGEAU. (C. R. Acad. Sci. Paris Vol. 115 1892.)

This organism was described by VIALA and SAUVAGEAU as responsible for a disease of the vine in California. MASSEE later found that the disease was physiological. It seems likely that the accumulation of tannin in the cells was mistaken for either amoebae or masses of spores.

7. *P. Vitis* VIALA & SAUVAGEAU. (C. R. Acad. Sci. Paris Vol. 114 1892.)

Described by VIALA and SAUVAGEAU as causing the "brunissure" disease of the vine in Europe and the United States. MASSEE considered that the cause was physiological and that once again tannin had been used as evidence of spores.

8. *P. tomato* ABBEY. (Journ. Hort. Ser. 3 Vol. 30 1895.)

Stated in a letter in the Journal of Horticulture as the probable cause of a disease of tomatoes. ABBEY stated that he intended to give a description of the organism but apparently never did so.

9. *P. Tabaci* JONES. (Bot. Gaz. Vol. 81 1926.)

Described as causing a Mosaic disease of Tobacco, but BROOKS states definitely that this organism is not the cause of the Mosaic. There is reason the think that to this and other bodies found in the cells of plants suffering from Mosaic disease are due to protoplasmic bodies caused by degeneration similar to those described by HOLMES [1]) and SHEFFIELD [2]). The organism isolated in culture by JONES did not appear to shew sufficent characteristics to justify inclusion in the Plasmodiophoraceae.

10. *P. vascularum* MATZ. (Journ. Dept. Agric, Porto Rico Vol. 4 1921.)

This organism was described by MATZ as causing a disease of Sugar canes in Porto Rico. Later M. T. COOK transferred the organism to the genus *Ligniera* on the grounds that no hypertrophy to the host tissue was caused. The present author examined the organism recently and shewed that two distinct species were present in the cells neither of which were related to the Plasmodiophoraceae and referred them to a new genus *Amoebosporus*.

11. *P. theae* FITZPATRICK. (Lower Fungi, Phycomycetes New York 1931.)

This organism is mentioned by FITZPATRICK and is presumably the same as *Sorosphaera Theae* described by SPESCHNEW on the leaves of tea bushes in the Caucasus. Ducommet shewed that no organism

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[1]) F. O. HOLMES, Bot. Gaz. Vol. 86 p. 50—58 1928.

[2]) F. M. L. SHEFFIELD, Ann. Rpt. Biol. Vol. 18 p. 473—493 1931.

was present but that the apparent spores were due to tannin collecte in the cells.

Genus II. *Sorosphaera* Schroeter.

Schroeter (1886—1897): Cohn's Kryptogamenflora von Schlesien Vol. 3 p. 1—500.

Spores arranged in spherical or ellipsoidal hollow spore-balls. Individual spores ellipsoidal or pyriform. Spore-ball enclosed in a universal membrane, one spore-ball being produced by each myxamoebae. Spores on germination each producing a single swarm cell, swarm cells fusing in pairs producing fresh myxamoebae. Infection takes place either through the growing apex of the stem or through root-hairs; meiosis occurring just prior to spore formation. The organisms cause hypertrophy of the host tissue.

Two species are considered to belong to this genus.

Key to the species.

I. Spore-balls spherical, containing few spores.
S. Veronicae p. 198.

II. Spore-balls ellipsoidal, containing many spores.
S. radicalis p. 201.

The genus differs from *Plasmodiophora* in the spores being enclosed in a common membrane and in being aggregated together in a spore-ball. It differs from *Spongospora* in the shape of the spore-ball which is regular in outline and in having a common membrane. It differs from *Sorodiscus* in the spore-ball being hollow. Finally it differs from *Ligniera* in the common membrane, and in the hollow spore-ball, as in the latter genus there is no membrane and the spores are not arranged in a hollow spore-ball, further in *Ligniera* there is an additional method of reproduction by means of zoospores.

I. *Sorosphaera Veronicae* Schroeter.
(Pl. 6 Figs. 7—9.)

Schroeter (1886—1897): Cohn's Kryptogamenflora von Schlesien Vol. 3 p. 1—500.
Syn. *Tuburcinia Veronicae* Schroeter.

Spore-balls nearly spherical 18—28 μ diam. Spores ovoid, 8—9 μ long by 4—5 μ wide. Spore coat thin and smooth. On germination swarm cells fusing in pairs producing myxamoebae. Myxamoebae not aggregating together when associated in the same host cell. Mature myxamoebae each forming a single spore-ball.

Myxamoebae 20—30 μ diam, containing many nuclei, frequently forming schizonts when containing about eight nuclei. Schizonts developing directly into mature myxamoebae.

The organism causes hypertrophy of the cortical region of the stem and petiole, forming tumours up to 5 mm diam. It has been recorded on *Veronica hederifolia* and *V. triphyllae* in Germany; *V. hederifolia* in Denmark; in *V. arvensis* and *V. Chamaedrys* in France and in *V. Chamaedrys* in southern England. In all these countries it is considered very rare and local in distribution. In this country it is only known now from two localities near Sevenoaks, Kent.

Sorosphaera Veronicae was first described by SCHROETER in 1877 and was placed by him in the Ustilaginales under the name *Tuburcinia Veronicae*, later in 1886 he transferred it to the group Phytomyxinae and created the genus *Sorosphaera* for it. In 1895 ROSTRUP found the same organism in *Veronica hederifolia* in Denmark and replaced it in the Ustilaginales. In 1904 TROTTER found it in *Veronica arvensis* and, although he was doubtful of its systematic position, questioned that it was a member of the Ustilaginales, but also thought that it was not a member of the Mycetozoa. In 1902 MAIRE and TISON received material from Alencon but did not give any further description as the material only contained spores. Search for the fungus in 1903 was without result but in 1906 two more specimens were found. In 1907 they found more material of the fungus and commenced a critical study of the structure, the results of which were published in a preliminary paper in 1908 and in a fuller paper in 1909.

Meanwhile LAGERHEIM had also found material and according to WINGE "already in 1901 knew the correct systematic position of *Sorosphaera*". WINGE moreover states that the organism had been found on other species of *Veronica*, e. g. *V. saxatilis*, *V. acutellata*, *V. Beccabunga*, *V. Anagallis*, *V. aquatica*, *V. serpyllifolia*, *V. officinalis* though, as will be explained later, there is some question as to whether all these records are reliable.

In 1909 BLOMFIELD and SCHWARTZ found the organism in *Veronica Chamaedrys* in the neighbourhood of Sevenoaks, K. and published an account of the life-history and cytology in 1910.

The life-history of the organism agreed in the main points with that described in *Plasmodiophora Brassicae*. Actual infection has not been observed though it has been observed that the youngest amoebae are found in the neighbourhood of the growing apex of the stem. Healthy plants of *Veronica Chamaedrys* watered with a solution containing the spores of *S. Veronicae* have been found to become diseased. In such plants no myxamoebae have been met with in the roots and it is clear that infection does not occur in this way. On the other hand healthy plants grown associated with diseased ones seldom contract the disease and it has been suggested that the spores may have to pass through the body of a slug or other animal before germination generally takes place. Schwartz only obtained infection after "the sorospheres from dried tumours pounded with a pestle in water" had been used. It is possible that in this process the spore walls had been artificially cracked, and that some similar action may be required, such as the action of the gastric juices or an animal, before the spores can germinate.

The fungus enters the procambial strands and it is thought that in the course of cell division the myxamoebae may become distributed through the plant tissue. At about the eight nuclear stage the myxamoebae frequently form schizonts and in large hypertrophied cells as many as six schizonts may be found lying together. There is no evidence that these schizonts have the power of penetrating from cell to cell through the host tissue. During development the nuclei in the same myxamoeba divide simultaneously by a protomitotic division similar to that described in *Plasmodiophora Brassicae*, though Winge states that the ring is really a plate. The present author has been quite unable to confirm this statement and has seen examples in which the ring could be clearly seen with the karyosome lying freely within it. Although there is complete co-ordination among the nuclei in the same myxamoeba, myxamoebae in the same host cell do not behave alike and their nuclei do not all divide together.

During the Akaryote stage the chromatin is completely extruded and the nuclei appear almost entirely empty. This stage is followed by the separation of the protoplasm into uninucleated parts each of which is considered to be a spore mother cell. Within this cell the nucleus divides twice, during which a reduction division takes place. According to Maire and Tison eight chromosomes are differentiated during the first division and four during the second. These spore mother cells become heaped together and each divides up into four spores. A thin membrane is then laid down around the whole spore-ball and the individual spores become orientated into a single layer around a hollow centre. Each spore secretes around itself a separate wall. Winge states that around each spore a "collar-formed swelling" occurs.

The germination of the spores has not been critically observed, though BLOMFIELD and SCHWARTZ found that small active amoeboid bodies could be obtained by allowing a mixture of spores to remain for some time in a tube of sterile water.

Slugs appear very ready to feed upon these tumours and it is thought that by their aid and also by bacterial attack which sets in as soon as the tumours are mature, the spore-balls are scattered into the soil and germination occurs. Since, however, the infection takes place in those parts of the plant which are above the surface of the soil it is concluded that it either occurs at a very early stage as the stem apex is pushing through the soil or that the spores, or swarm cells, are carried by some external agency to a position suitable for infection.

The effect upon the host tissue is considerable. Since the fungus finds its way into the cambium schizonts get distributed throughout the meristematic tissue. In an early stage only slight bulging of the cells is noticed, after further growth of the parasite the nucleus of the infected host cells remains rounded and increases considerably in size, and although it is still capable of division it appears to lose its power of initiating the formation of a cell plate so that cells with several nuclei are found. Similar enlarged nuclei have been recorded by NAWASHIN in *Plasmodiophora Brassicae.*

In accounts of the existence of this fungus on plants of species of *Veronica,* mistakes have frequently been made where the internal structure of the galls have not been studied. By no means all the galls found on *Veronica Chamaedrys* in this country are due to *Sorosphaera Veronicae,* the majority are caused by an attack by Nematode worms, and these have frequently been sent to the present author as evidence of *Sorosphaera Veronicae* in other parts of the country. Galls produced in this way are difficult to distinguish externally from those caused by the fungus, and it is for this reason that some of the records given by WINGE of the existence of the parasite in a large number of species of *Veronica* are viewed with suspicion.

2. *Sorosphaera radicalis* [1]) COOK & SCHWARTZ. (Pl. 7 Figs. 10—11.)

COOK & SCHWARTZ (1929): Annals Botany Vol. 43 p. 81—88.

Spore-balls ellipsoidal or oval, with large central hollow, 20—57 μ long by 16—20 μ diam. Spores ovoid 4 μ long by 3 μ

[1]) Previously described as *Sorosphaera radicale* COOK and SCHWARTZ.

diam. Spore coat thin and smooth. Spores germinating to produce swarm cells which infect root-hairs. Myxamoebae developing exclusively in the root-hairs, each finally producing one spore-ball. Myxamoebae up to 60—20 μ in size, containing many nuclei. Schizont formation not occurring.

The organism occurs in the root-hairs of a number of species of the Gramineae, particularly *Poa fluitans*, *Monilia caerulea* and *Catabrosa aquatica*. It has been found in two localities, in damp meadows and marshes at Dunton Green, Kent and by the side of a large lake between East Grinstead and Crawley, Sussex. It causes swelling of the root-hairs, but since the fungus never enters further into the host no other damage is done and except for a slight reddening of the stem and leaf bases no external signs of the parasite are shewn by the host plant.

The life-history of this species agrees very closely with that of *S. Veronicae*. Actual germination of the spores has not been observed, though swarm cells 2—3 μ in diameter have been seen associated with diseased roots, and these had a single apical flagellum about the same length as the cell. They have been seen entering root-hairs and there to become amoeboid. Their further fate has never been followed owing to changes in the concentration of the liquid in which they were being kept, which seemed to exert a retarding influence upon their development. It is concluded, however, that these amoebae develop into the myxamoebae seen in the root-hairs. The myxamoebae are composed of very fine cytoplasm and the nuclei are extremely small, far smaller than in any of the other species of the family, and are quite unsuitable for cytological investigation. The myxamoebae do not generally fill the swollen root-hair even when mature but lie in the centre of it. They are irregular in shape and contain many minute nuclei. When mature a definite membrane is secreted around each of the myxamoeba whose nuclei then divide up into a large number around which a spore wall is laid down. The spores become arranged in a single layer around a large hollow sphere.

It is easy to distinguish the spore-ball of *S. radicalis* from that of *S. Veronicae*. It the former the ball is generally spherical, while in the latter it is ellipsoidal. Moreover the hollow space in the centre is much larger in *S. radicalis* and many more spores are present in the spore-ball. In *S. radicalis* the spore-ball is bright yellowish brown in colour.

When the spore-ball is mature it is liberated as a whole by the decay of the root-hair and the whole sorosphere is set free into the soil. Infection takes place at an early stage in the development of the root-hairs. No fusion of swarm-cells has been observed.

Species no longer regarded as belonging to the genus *Sorosphaera*.

1. *S. Junci* SCHWARTZ = *Ligniera Junci* (SCHWARTZ) COOK.
2. *S. graminis* SCHWARTZ = *Ligniera Junci* (SCHWARTZ) COOK.
3. *S. Theae* SPESCHNEW (Die Pilzparasiten des Tustranches. Berlin 1907).

This species are described by SPESCHNEW in 1907 attacking tea plants in the Caucasus. It was also known under the name *Plasmodiophora Theae*, q. v.

In a recent treatment of the Plasmodiophorales by FITZPATRICK the view is put forward that species referred to the genus *Ligniera* should be transferred to the genus *Sorosphaera* on the grounds that the only distinguishing feature was the fact that they caused no hypertrophy of the host tissue. This statement is incorrect since the absence of a common membrane and of a hollow central cavity among other features distinguish them clearly from this genus.

Genus III. *Sorodiscus* LAGERHEIM & WINGE.

WINGE (1912): Arch. f. Bot. Vol. 12 p. 1—39.

Spores arranged in flat spore-cakes two spores thick, without any hollow space between them. Individual spores urn-shaped, with an apical ring or collar. Spore-cake enclosed in a common membrane which disorganises when the spores are shed. One spore-cake is the produce of a single myxamoeba. Spores on germination giving rise to swarm cells which develop into myxamoebae, fusion of swarm cells has not been seen. Meiosis occurring before spore formation. The organisms cause hypertrophy of the host tissue.

Three species are considered to belong to this genus.

Key to the species.

I. Spore-cakes large containing many spores.
  a) myxamoebae small. *S. Callitrichis* p. 204
  b) myxamoebae large. *S. Karlingii* p. 207
II. Spore-cake small containing few spores. *S. radicicolus* p. 206.

This genus differs from *Sorosphaera* in the arrangement of the spores. In the genus *Sorodiscus* they are aggregated into two flat layers without any appreciable hollow space between them. The whole spore-cake is derived from a single myxamoeba. It differs from the genus *Spongospora* in the presence of a common membrane and in the shape of the spore mass. It differs from the other genera in the same characters as have already been described in *Sorosphaera*.

No English species are known.

1. *Sorodiscus Callitrichis* Lagerheim & Winge.
(Text-Fig. 10 and Pl. 7 Figs. 12—13.)

Winge (1912): Arch. f. Bot. Vol. 12 p. 1—39.

Spore-cakes composed of two layers of spores closely appressed to one another, 30—40 μ in diameter, containing up to 200 spores. Spores urn-shaped, or hexagonal, 6—7 μ long by 4—5 μ diam. Spores producing amoebae which grow into myxamoebae. Myxamoebae up to 60—40 μ each producing one spore-cake, and containing many nuclei. Reduction division occurring prior to spore formation.

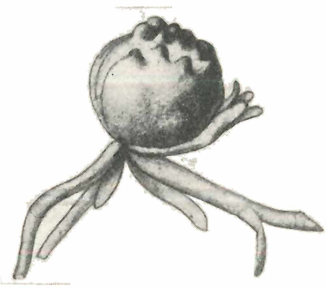

Fig. 10. *Sorodiscus Callitrichis*. Habit of the fungus on the host tissue (after Winge).

The organism has been recorded from Norway in *Callitriche vernalis* and in Sweden and Russia in *C. autumnalis*.

This species was probably first recorded by Kareltschikoff and Rosanoff in 1870. They mention an organism causing swellings on the stem of *Callitriche autumnalis*, but thought that the spore-cakes were cystoliths and compared them with those of the Urticaceae, though Rosanoff suggested that they might be remains of a parasitic mycelium. Later in 1907 Ostenfield found the fungus in *Callitriche autumnalis* in a stream near Ronnekro and in lake Ringsjo both near Skåne in Sweden. Lagerheim collected material both in 1893 and 1900 on *Callitriche stagnalis* growing in moist soil near Bjerkeng in Tromso, Norway, and although he made some study of his collections did not publish anything but eventually passed that material on to Winge who first gave a complete account in 1912.

The life-history of this species as described by Winge differs in several respects from that of the other members of the family. Infection of the host tissue has not been observed, nor has the presence of schizonts been demonstrated. Myxamoebae containing several nuclei have been seen in the cells, and owing to their distribution it is considered probable that the amoebae have the power of penetrating from cell to cell of the host. All the nuclei in the myxamoeba divide simultaneously and most often with their axes parallel. Winge considers that true protomitosis does not occur in this species but describes the occurrence of four chromatin masses at the equator of the spindle. Later the karyosome comes to lie in the centre and the chromatin around it in a thin plate. The further division has not been followed in detail. Surrounding the nucleus during division radiations of staining material are found, which are considered to be equivalent to centrosomal structures, although actual centrosomes have not been observed. This type of nuclear division continues until the myxamoeba is mature. Prior to spore formation a state comparable with the Akaryote stage is recorded. Radiation phenomena appear and the karyosome passes to the periphery of the nucleus, and two bodies having the appearance of centrosomes become differentiated at the poles of the radiations. The nuclear membrane disappears and the chromatin passes out along the radiation processes. Finally only a few lines of chromatin appear to be left within the nuclei.

This condition is followed by meiosis and spore formation. Nuclei are re-formed and chromatin travels towards an equatorial mass along spindle fibres. The nucleus itself also becomes spindle-shaped and finally an intranuclear spindle is formed. Winge states that the chromatin is aggregated into 16 chromosomes "presumably arisen by the splitting up of 8 chromosomes, for most often two and two lie near each other, and 8 chromosomes travel to both poles". This division is immediately followed by the second. Winge states — "This is a mitotic reduction-division which shews smaller nuclear division figures than the former and only 4 double chromosomes of which 4 halves travel to each pole". Finally the amoeboid mass becomes converted into spores by the deposition of cell walls. Prior to the laying down of these walls the individual spores are naked, and during this time their nuclei increase in size. Winge considers that the spore-cake is not formed until this stage. Finally he finds that "the spore-wall divides into two layers of which the outer one merges into that of the neighbouring spores, so that it givers one the impression of the spores being deposited in a common substance". The present author considers that this interpretation is incorrect and that a definite wall is laid down around the spore-cake and he has seen clear indications of this in slides sent him by Prof. Winge.

The effect upon the host plant is to cause hypertrophy, and globular galls 5—3 mm in diameter are produced. Only the epidermis and outer cortical layers remain free from the fungus. The vascular system is disorganised and may be destroyed. The cells of the inner cortex become greatly enlarged up to 150 μ in diameter, and contain several spore-cakes. In a single host cell various stages in the development of the fungus may be found.

2. *Sorodiscus radicicolus* Cook.

(Pl. 8 Figs. 14—16.)

Cook (1931): Annales Mycologici Vol. 29 p. 313—324.

Spore-cake composed of two layers of closely appressed spores. 12 μ wide by 25 μ in length, containing up to 50 spores. Spores rectangular or oval with the external wall produced into blunt spines. 3.8—4.2 μ by 3.2—3.6 μ. Spores germinating to produce swarm cells, swarm cells oval 3.5—2.5 μ with single apical flagella, these becoming amoeboid and fusing in pairs after migration into healthy host cells. Amoebae giving rise to myxamoebae up to 15—30 μ in size, each producing one spore-cake. Reduction division prior to spore formation.

The organism has been recorded on the roots of *Gynandropsis pentaphylla* (Capparidaceae) at Koster, about 100 miles from Pretoria, South Africa, collected by Dr. E. M. Doidge.

This species closely resembles the last but is distinguished by the size of the spore-cakes and spores. In the development of the myxamoebae the same general process is followed. The nuclei however, divide by a process of protomitosis in which a chromatin ring is formed with the karyosome in its centre. There is no evidence of separate bodies of chromatin material being formed at any stage during the division. The chromatin ring splits after the cruciform stage and the halves pass to the poles followed by the karyosome. During this division dark staining radiations are formed in the cytoplasm emanating from the poles of the spindle: no centrosomes are formed. All the nuclei in the same myxamoeba divide at the same time, although the planes of the protomitotic figures are not necessarily the same. The Akaryote stage is clearly seen in this species, and all stainable material passes out into the cytoplasm during the process, though there is no evidence that when the nuclei are reconstituted they do so on different sites. The nuclear membrane persists during the Akaryote stage. In spore formation the nuclei divide twice by a typical meiosis in which four chromosomes are present during the first division and two pass to the poles in the second. Spore mother cells are formed as in *S. Callitrichis* and these become converted into four spores after the second division. The spore-cake is made up of two layers of closely appressed spores each with a wall and the whole enclosed in a common membrane.

After a period of rest within the host the membrane disappears and the spores separate and germinate *in situ.* The wall cracks and a swarm cell emerges. It is almost spherical in shape with one apical flagellum. The flagellum, however, is soon lost and the swarm cell becomes amoeboid. In this condition it has the power of penetrating from cell to cell of the host tissue. In time it finds itself in the same cell as another swarm cell, and the two fuse together to form a zygote. The nucleus then divides protomitotically and a fresh myxamoeba is formed. The fate of spores which are shed into the soil by the disorganisation of the tumour has not been followed.

The effect upon the host plant is hypertrophy of the affected tissue. Galls are formed which vary from 3 to 15 mm. in diameter. They are convoluted and coral-like in appearance, and several may be attached to the same root. The host cells are not greatly enlarged by the influence of the fungus although their nuclei may become disorganised. In large galls at least two generations of the fungus may occur. Near the root itself young myxamoebae are found, further out spores, followed by swarm cells and the myxamoebae of increasing size shewing that infection of the outer tissue results from the germination of the spores formed in the older parts of the same gall. The host plants are not seriously affected by the presence of the fungus.

The widely separated occurrence of the two species of this genus suggest that it is very likely that further species will eventually be found in different parts of the world. As yet this is the only species recorded from Africa.

3. *Sorodiscus Karlingii* Cook sp. nov.

Karling (1928): Amer. Journ. Bot. Vol. 15 p. 475—496.

Spore cake composed of two layers of closely appressed spores, 15 μ wide and 70 μ in length, containing upwards of 100 spores. Spores spherical, angular in outline, with their apical ends produced into caps. Myxamoebae bacoming multinucleated, up to 90 μ diam.

The organism causes hypertrophy of the cells of *Chara contraria* and *C. delicatula* and was collected in a reservoir at Oberlin, Ohio, U. S. A.

In 1928 KARLING described, without name, an organism which should certainly have been referred to the genus *Sorodiscus*. KARLING, however, refused to name his organism because certain stages in the life-history were missing and unknown, and he therefore did not feel able to relate it to any known genus. Later in 1931 in a letter to the present author, he agreed to include the organism in the genus *Sorodiscus*. It was hoped that Dr. KARLING would, himself have published a note to this effect, but as he has so far not done so I propose to call this new species *Sorodiscus Karlingii* in his honour and in recognition of the work he has done in elucidating the life-histories of the lower (l. c.).

The extreme interest in this species lies in the fact that it is the only member of the Plasmodiophoraceae known to attack the cells of Thallophytes. According to KARLING the cells of the stipules, leaflets, spicules, nodal tissue and cortex are all affected, the fungus causing pronounced hypertrophy of the host cell which bulges out in a very noticeable way. In addition to causing hypertrophy the fungus stimulates starch formation, but in old cells there is a depletion of cytoplasmic content and nuclei.

The present author has had no opportunity of examining slides or material of this organism, but from the description and illustrations published by KARLING he has not hesitation is regarding the organism as a species of the genus *Sorodiscus*. KARLING's Text-Fig. 8 is strikingly similar to Pl. 7 Fig. 13 of *Sorodiscus Callitrichis*. It is unfortunate that the parasite has died out in culture and that no further material could be found by KARLING, but the amount already known appears to be sufficent for the organism to be relegated to the genus *Sorodiscus*.

Genus IV. *Spongospora* BRUNCHORST.

BRUNCHORST (1887): Bergens Museum Aarsberstnung 1886 p. 219—226.

Spores arranged in hollow or irregularly channelled spore-balls. Spore-ball not enclosed in a common membrane. Spores spherical, with thin smooth walls. Spores on germination giving rise to swarm cells which fuse in pairs producing myxamoebae. Myxamoebae producing one, occasionally more spore-balls. Infection taking place through the epidermal cells. Meiosis occurring before spore formation.

The organisms cause hypertrophy of the host tissue.

Two species are considered to belong to this genus.

Key to the species.

I. Spore-balls large, spores small, closely packed together with small channels within the spore ball. *S. subterranea* p. 209.

II. Spore-balls small, spores larger, loosely packed together with large irregular channels in the spore-ball. *S. Campanulae* p. 215.

The genus differs from *Sorosphaera* in the absence of a common membra... and in the spores not being arranged in a single layer. It differs from *Sorodiscus* in the absence of a common membrane and in the existence of channels among the spores. It differs from the other genera in the same respects as *Sorosphaera*. The name *Spongospora* was given to this genus on account of the sponge-like nature of the spore-balls.

1. *Spongospora subterranea* (Wallroth) Lagerheim.

(Text-Fig. 11 and Pls. 8 and 9 Figs. 17—21.)

Wallroth (1842): Linnaea Vol. 16 p. 332.
Wallroth (1842): Beiträge zur Botanik Vol. 1 p. 11—123.
Lagerheim (1892): Journ. Mycol. Vol. 7 p. 103—104.

Syn. *Erysibe subterranea,* Wallroth (1842): Linnaea Vol. 16 p. 332.
Protomyces Tuber-solani, Martius (1842): Die Kartoffelepidemie der letzten Jahre oder die Stockfäule und Räude der Kartoffeln. München. 70 pp.
Rhizosporium solani, Rabenhorst (1844): Deutschlands Kryptogamenflora Vol. 1. Pilze. Leipzig. 614 pp.
Tubercinia scabies, Berkeley (1846): Journ. Hort. Soc. London, Vol. 5 p. 9—34.
Sorosporium scabies, Waldheim (1877): Apercu Systematique des Ustilaginees. Paris. 51 pp.
Spongospora solani, Brunchorst (1887): Bergens Museum Aarsberstnung, 1886 p. 219—226.
Spongospora scabies, Massee (1908): Journ. Board Agric. England, Vol. 15 p. 592—599.

Spore-balls irregular, 45 by 70 μ diam. not enclosed in a common membrane. Spores spherical, 4 μ diam. with smooth thin yellow walls. On germination producing uniflagellate swarm cells 2.5 by 3.5 μ which fuse in pairs producing myxamoebae. Myxamoebae irregular in shape up to 70 μ in length, giving rise to one, or occasionally more, spore-balls. Meiosis occurring prior to spore formation, nuclear fusion in the swarm cells. The organism causes the host tissue to become active, and either produces abnormal development of cork, with the final production of a scab, or the formation of a gall. This latter condition is rare upon the tuber but frequently occurs on the roots. Various species of *Solanum* are attacked but it is most common on the cultivated potato. The organism is world-wide in distribution.

No species of the Plasmodiophoraceae has been subject to so great diversity of opinion as to the correct position and therefore scientific name than this species. Even before the discovery of *Plasmodiophora Brassicae*, "Powdery Scab" of potatoes was known in this country. Wallroth was the first to collect it, in 1842, and named it *Erysibe subterranea.* Martius in the same year described and figured it under the name *Protomyces tuber-solani.* In 1844 Rabenhorst concluded that it was neither a species of the genus *Erysibe* nor *Protomyces* and placed it in a new genus under the name *Rhizosporium solani.* Berkeley in 1846 described it under the name *Tuburcinia solani,* although he knew that it had been previously placed in the genus *Protomyces* by Martius. The name was again changed by von Waldheim in 1877, who called it *Sorosporium scabies.* In 1886 Brunchorst found it in Norway and definitely referred it to the Mycetozoa, and despite the fact that he knew of several of its previous names preferred to make a new one for himself and called it *Spongospora solani,* a name by which it was known until 1908, despite that fact that Lagerheim in 1892 pointed out the identity of Wallroth's *Erysibe subterranea* and suggested the name *Spongospora subterranea.* In 1908 Massee in a series of papers called it *Spongospora scabies.* Johnson in a series of papers between 1907 and 1909 first called it *Spongospora solani,* but later, having established the identity of Wallroth's *Erysibe subterranea,* called it *Spongospora subterranea.* In 1911 Horne returned to the name given by Brunchorst and called it *Spongospora solani.* In 1913 Pethybridge cleared up the question by bringing forward further evidence of the identity of Wallroth's fungus, and both from figures of the spores and also from description of the development and fate of the warts, he shewed conclusively that it was the same fungus as that described by later workers, and he argued that the correct name was *Spongospora subterranea* (Wallroth) Johnson. In 1914 Melhus in America reviewed the nomenclature and came to the same conclusions and urged that the name used by Pethybridge should be adopted. Later Lagerheim's paper came to light and the name was again altered to *Spongospora subterranea*

(WALLROTH) LAGERHEIM, a name which should be generally accepted for this fungus.

While this difficulty was being experienced regarding the name of the fungus investigations concerning the structure were also being carried out. In 1911 OSBORNE and HORNE published preliminary accounts of the cytology simultaneously. Later in the same year OSBORNE published a fuller account while HORNE described his results in a paper before the British Association for the Advancement of Science. Assording to these results the nuclear division during the vegetative part of the life-cycle is protomitotic. In 1915 KUNKEL described the development of the spores and stated that one swarm cell was liberated from each spore. In 1930 HORNE gave a completed account of his study of the cytology commenced in 1911 and stated that the cytological configurations in this species differed from that previously described and that protomitosis did not occur. He stated that the number of chromosomes in the vegetative part of the life-cycle was half that found just prior to spore formation and concluded that a fusion took place at this point in the life-history.

In the host tissue the earliest stage is the appearance of an amoeba which increases in size accompanied by nuclear division. When it has reached the six to eight nuclei stage schizonts are cut off. These have the power of penetrating from cell to cell of the host tissue and in this way a considerable area of infection is brought about. The nuclei at this stage divide, according to the present author's observations, by a protomitosis essentially similar to that described in other species. No chromatic radiations occur and the nuclear membrane remains during the whole division. Within the nucleus the karyosome persists and divides into two in the way usually found in the group. The chromatin is at first arranged in a ring around the periphery of the nuclear membrane and this ring is, as far as he can see, completely uniform, shewing no indication of fragmentation into individual chromosomes. HORNE, however, states that four chromosomes can be made out in this ring. The ring splits and the halves pass to the poles of the spindle and come to surround the karyosomes, after which the nuclear membranes of the daughter nuclei are completed. When the myxamoebae are mature the nuclei pass through an Akaryote stage in which all the stainable material passes out from the nuclei. The new nuclei are, however re-constituted on the same sites as the original ones. The present author can find no evidence that any nuclear fusion takes place at this stage, and the nuclei immediately pass to a synaptic condition associated with spore formation. In the metaphase of the first division a number of separate chromosomes are differentiated which Horne states are eight in number, though the present author is uncertain upon the point. These separate into two groups of four. Horne finds that a third division sometimes occurs although again the writer can see no evidence of this in his preparations.

Finally around the nuclei small mass of cytoplasm are cut off by cell walls and the spores are formed. As has already been satated these are arranged in masses having the appearance of a

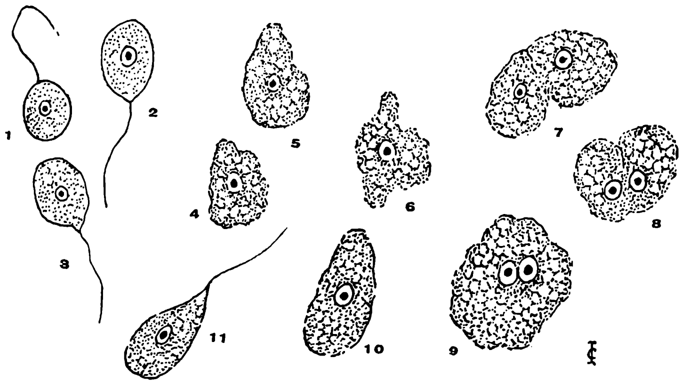

Fig. 11. *Spongospora subterranea.* Stages in the germination of the spores.

sponge with irregular channels running through the mass. The shape of the spore mass is neither regular nor the same in different individuals.

The germination of the spores and the infection stages have been subject to much controversy. In 1907 Johnson described eight swarm cells escaping from each spore of the spore-ball, while in 1910 Massee briefly stated that the spore gave rise to only one swarm cell. In 1915 Kunkel further studied the problem and found only one swarm spore. A recent investigation by the present author has confirmed this view and, since it has not been published elsewhere will be given in detail here.

Potato agar was employed, and the spores were floated on to the surface of the agar before it had quite hardened, as Kunkel found this assisted the organism to burst the spore coat. After a day or two a small quantity of sterile potato extract was added.

This was prepared in the same way as for normal potato agar except that the agar was omitted. The swarm cell escaped by wriggling through the broken spore coat and being already provided with a flagellum swam actively about in this liquid medium. Kunkel found that he could not observe a flagellum in the swarm cells he germinated. Those here described possessed a quite definite flagellum about equal in length to the swarm cell. It seems probable that the presence of a flagellum depends upon the amount of liquid present at the time of liberation, and that in dryer media the swarm cell immediately becomes amoeboid. These swarm cells fused in pairs, the flagellum if present at the time was withdrawn and the two conjugated by their anterior ends. The contents of the one is absorbed by the other, which for a time becomes more rounded. For a while the two nuclei remain side by side without fusion, but later complete nuclear fusion takes place. The zygote may subsequently become flagellate again (Text-Fig. 11 [1—11]).

In examining young roots of infected potatoes, uninucleated amoebae were found, which were quite comparable with those produced after fusion of the swarm cells in the culture medium. It is thought probable that in nature the swarm cells fuse before entering the host tissue.

It will be seen that in this species there is no question but that nuclear fusion of swarm cells occurs, and this precluded the suggestion that fusion during the growth of the myxamoebae can take place, unless it is assumed that two fusions occur in the life-history, therefore there must be some other explanation to the view put forward by Horne that the chromosomes are doubled between the somatic and sporogonic phases. In the present author's opinion four chromosomes are not differentiated during the somatic nuclear divisions, but eight chromosomes appear at the heterotypic division and that these are reduced to four during the homotypic division and the chromosome number again becomes diploid in the fusion of the swarm cells.

The effect of the parasite upon the host plant varies greatly. Normally corky scabs are produced upon the potato tuber, whence the name Powdery Scab, or Corky Scab, was given to it. In certain instances, however, the development of the fungus does not stop at the time the potatoes are lifted but continues or resumes its activity when the potatoes are stored in the clamp. Under these conditions small warts appear, which have a general similarity to those caused by *Synchytrium endobioticum*, and have doubtless been sometimes mistaken for this fungus. Similar galls may be caused upon the roots of the potato. The normal scab first appears as slightly raised pimples and slight discoloration, and when such potatoes are cut the infected area is generally purple. When the organism is mature the scab bursts and the spores are scattered. The fungus does not attack those parts of the plant which are above the soil.

As regards the behaviour of the tissues themselves, a cork cambium is formed below the seat of injury though amoebae may be found in the layers below this. It is the host cells containing starch which are chiefly sought out by the organism. The cells themselves are not much increased in size as a result of the fungus, but the nuclei shew remarkable lobing and indentations and frequently become applied to the surface of the myxamoebae. With the growth of the parasite the host nucleus disintegrates. Multinucleate host cells are not generally found.

The distribution of the disease is interesting. After being recorded in England in 1842, it was found in the Netherlands, Belgium, Norway, France, Sweden and Germany. Later it was found in the United States and Canada, probably as a result of shipments of potatoes from Europe. In 1891 Lagerheim found it at Quito, in Ecuador, and since South America is probably the native home of the potato, it suggests that the disease first reached Europe from South America, spread through Europe, and from thence into North America. It occurs most commonly in countries with a heavy rainfall and in Great Britain it is chiefly met with in Western counties and in Wales.

In the British Isles and North America it is known as Powdery or Corky Scab, in France as gale ordinaire; in Italy as crosta, in Germany as Pulverschorf; in Holland as poederschurft and in Denmark as pulverskurv.

With regard to preventative measures against attacks of this fungus little has been done. No immune varieties of potato have been found. Lime increases the attack of the fungus, but acids, or acid producing ubstances like flowers of sulphur have been found to give the best results. Superphosphates of lime, copper sulphate and formalin reduce the disease but have an adverse effect upon the yield of tubers. Well drained soils are less susceptible to the disease than those which are heavy and waterlogged. The disease can be transferred from field to field upon the boots of labourers and upon farm implements. Many wild species of *Solanum* are also attacked and may act as a source of infection.

2. *Spongospora Campanulae* (Ferdinandsen & Winge) Cook **nov. comb.**

(Text-Fig. 12 and Pl. 9 Figs. 22—23.)

Syn. *Clathrodorus campanulae* Ferdinandsen & Winge (1920): Annals Botany Vol. 34 p. 467—469.

Spore-balls irregular 25—50 μ diam. not enclosed in a common membrane. Spores spherical, 4—5.5 μ diam. with slightly verrucose walls. Spores germinating to produce myxamoebae. Myxamoebae irregular 30—50 μ diam. when mature, multinucleate and developing singly in host cells. Myxamoebae giving rise to one spore-ball. Meiosis occurring prior to spore formation.

Fig. 12. *Spongospora Campanulae.* Habit of the fungus on the host (after Ferdinandsen and Winge). $\times$ 1/2.

The organism causes hypertrophy of the host tissue by stimulating cells in the neighbourhood of infection to active division. The infected cells are not hypertrophied, and the myxamoebae do not fill the host cell. The fungus attacks the roots of *Campanula rapunculoides.* It has been collected on one occasion only, from a garden in Soro, Sealand, Denmark.

A brief account of this species was given by Ferdinandsen and Winge who were only able to examine material which had already been fixed in Carnoy's Fluid. In section they were able to study the growth of the organism. The host cells contained many multinucleated myxamoebae which became more numerous in the direction of the central cylinder. The central cylinder is distorted but not actually parasitised. In the myxamoebae they were able to make out the nuclear division and found that a protomitosis occurred during the increase in size of the myxamoeba. At the commencement of spore formation, the nuclei passes through an Akaryote stage which was followed by two divisions which are stated to be a heterotypic followed by a homotypic division indicating that meiosis takes place prior to the formation of spores. The spore-ball is rather irregular in shape, with an uneven surface and traversed by large and small cavities. The individual spores are not solidly connected together, and have a finely warted coat.

Through the kindness of Prof. Ö. Winge the present author has been enabled to examine slides of this fungus and to confirm the observations set out above. The species shews very close similarity of the genus *Spongospora*, and it has been suggested by some writers that the galls of *Campanula rapunculoides* were due to *Spongospora subterranea.* This it incorrect, the species under consideration is quite distinct, differing chiefly in the less close association of the spores, the larger cavities within the spore-ball and the smaller number of spores aggregated together. It is, however, similar, and should be placed in the same genus, there being no clearly marked features by which the two genera can be separated from one another. It is proposed therefore to place this species in the genus *Spongospora*, distinguished from *S. subterranea* by the characters given in the diagnosis.

Genus V. *Tetramyxa* Goebel.

Goebel (1884): Flora Vol. 67 p. 517—521.

Spores aggregated in groups of four, not enclosed in a common membrane, but free and frequently becoming separated from one another. Spores spherical with smooth walls. Spores on germination giving rise to swarm cells which eventually re-infect the host tissue. Infection taking place through the cells of the gall and through the exterior as well. Meiosis occurring before spore formation.

The organisms cause hypertrophy of the host tissue.

One species is regarded as definitely belonging to this genus although a second in which the spores are unknown is considered here for convenience.

The genus is separated from all the others by the arrangement of the spores in groups of four, though this primary system is frequently lost owing to the very slight connection between the spores, and spores in pairs or singly are frequently found. *Tetramyxa parasitica* has been known for many years, but as yet is in-completely studied, being very local and rare in distribution. It was the second genus of the Plasmodiophorales to be recognised.

1. *Tetramyxa parasitica* GOEBEL.
(Pl. 10 Figs. 24—26.)

GOEBEL (1884): Flora Vol. 67 p. 517—521.

Spores spherical 3.5 μ diam. on germination producing swarm cells which fuse in pairs to produce myxamoebae. Swarm cells frequently amoeboid and devoid of flagella. Myxamoebae small 15—30 μ diam. containing many nuclei. Spore tetrad arising from myxamoeba, each nucleus of which before reduction division being the nucleus of the tetrad.

The organism causes hypertrophy of the host tissue, producing galls up to 15 mm. diam. It attacks the stalks of *Ruppia rostellata*, *Zannichellia polycarpa*, and *Z. palustris*. It has been recorded from Finland, Warnemunde, in Germany, France and Great Britain.

This organism was first collected by HISINGER on the coast of Finland at Fagervik and in the island of Ramsjö, in 1884, but no account was given of the find and the systematic position was not discovered. In the same year GOEBEL found similar tumours on the stalks of *Ruppia rostellata* growing in some of the Baltic rivers near Warnemunde and from a study of the structure of the organism concluded that it was closely allied to *Plasmodiophora Brassicae*. In 1887 HISINGER re-examined his material and found that in addition to *Ruppia rostellata*, which up to that time had been the only Phanerogam in which the parasite had been found, the fungus also occured in *Zannichellia polycarpa*.

In 1909 LIGNIER found it in France at Ouistreham and at Grayke growing on *Ruppia rostellata* and at the same time found in the former locality a small quantity attacking *Zannichellia palustris* var. *pedicellata* CLAV. MAIRE and TISON therefore regard the record by HISINGER of *Zannichellia polycarpa* with some suspicion.

In Great Britain it has been found in three localities on *Ruppia*. BOYD [1]) recorded it at Chapelton, West Kilbride in Scotland in 1897, and more recently it has been found near West Porlock in Somerset by Mr. HADDON in 1922 [2]). There is also a specimen

[1]) BOYD, D. A., Exhibited a specimen on *Ruppia rostellata* to the Glasgow Natural History Society, collected in a shore pool from this locality on August 16 th 1887. Proc. Nat. Hist. Soc. Glasgow Vol. 2 NS. p. XXXVI, 1886—1898, published 1890.

[2]) The organism has appeared in a number of successive years during September and October but recently the host plant has become scarce and the parasite has disappeared.

of *Ruppia rostellata* with the disease upon it in the Father Reader Herbarium, now in the University of Bristol, collected near Lymington, Hampshire in 1885 [1]). (This latter collection, therefore is in reality the first British specimen of this species to be collected.)

The earliest stage found is that of a small spindle shaped amoeba containing a single nucleus, this increases in size and the surface becomes less regular. Nuclear division occurs and the myxamoeba is formed. The nuclear division in the myxamoebae is protomitosis and all the nuclei divide together. In the division a chromatin ring is formed and a small central karyosome comes to lie across the chromatin giving the typical "cruciform stage". Later the chromatin ring separates into two and the daughter nuclei are re-formed exactly in the same way as has already been described. At about the six nuclei stage schizonts are formed, which for a time may remain closely associated together. Their individuality however, may be recognised by the fact that the nuclei in different schizonts do not divide simultaneously. After the myxamoebae are mature they pass to the spore stage. The Akaryote stage is poorly shewn in this species, but the present author has observed stages in which the karyosomes are absent from the nuclei. A condition of complete nuclear extrusion has not been observed in this species.

In spore formation the myxamoebae come to lie around the periphery of the host cell and separate into uninucleated portions. Asters appear at the poles of the nuclei and this is followed by the fragmentation of the karyosome and division of the chromatin into a number of separate chromosomes. Their actual number has not been counted with any degree of reliability but is probably about eight. The second division follows immediately and in the metaphase of this a smaller number of separate chromosomes are formed, which are thought to be four. At the end of this division walls are laid down around the nuclei enclosing a part of the cytoplasm. Where these walls touch one another they become loosely joined together and it is this which causes the appearance of the spores in groups of four. It is interesting to note that the four spores which are so grouped together have nuclei which are the product of a single nucleus. The association of these spores together is not very strong and they soon become separated and may be found singly, in pairs or in threes lying in the host cells.

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[1]) I am indebted to Prof. O. V. Darbishire for permission to publish observations made from his slides from material collected by Mr. Haddon at West Porlock, and also for the record of the fungus in the Father Reader Herbarium.

The spores frequently germinate at once while still within the host cell producing a swarm cell. The swarm cell is devoid of a flagellum and immediately becomes amoeboid. In this condition it migrates from cell to cell of the host making its way to the younger parts of the gall. During this migration the swarm cells fuse in pairs. During this process they may become almost euglenoid in shape. Fusion occurs by the two becoming associated by their anterior ends, and the contents becomes aggregated into a single amoeboid mass. Finally the nuclei unite. The zygote amoeba again becomes spindle-shaped, but is larger than before fusion, and it does not now seem to be able to penetrate through the wall of the host cell.

Frequently after the fungus has become mature the gall disorganises and the spores are shed into the soil or water in which the plants are growing. No details of the spores are known under these conditions, but it is probable that the swarm cell is then flagellate and able to swim about. No evidence regarding the fusion of such swarm cells is available.

The effect upon the host tissue is to cause the infected cells to become active and to divide rapidly, it is during this division of the host cells that schizonts of the fungus are distributed through the tumour. The tumours are rounded in shape, greenish in their early stage, but becoming whitish brown as they mature. They appear on the stem just above the ground. Young tumours are completely filled with myxamoebae, but in older ones spores appear and in the younger parts of such tumours swarm cells and small myxamoebae may be found shewing that the spores germinate without liberation to the exterior. A similar condition has been recorded in *Sorodiscus radicicolus*. The host cells are not greatly increased in size as a result of the parasite, and the myxamoebae seldom fill the cell. The nucleus of the host cell in time disorganises. Infected cells do not produce many chloroplasts and these gradually disappear during the development of the fungus. Starch grains are present in the host cells during the early part of the life-cycle of the fungus but these disappear before spore formation.

Tetramyxa Triglochinis MOLLIARD.
(Pl. 10 Figs. 27—29.)

MOLLIARD (1909): Bull. Soc. Bot. France Vol. 56 p. 23—25.

This organism was described briefly by MOLLIARD in 1909 from material collected at St. Nectaire, Puy-de-Dome. The material consisted of flower spikes of *Triglochin palustre* which were twisted and had developed small galls. In the same year MAIRE and TISON found similar deformation of the flower spikes of *Triglochin maritimum* attacked by the organism on the salt marshes at the estuary of the Orne at Sallenelles.

The structure of the tumours consists of cells more or less swollen with their nuclei enlarged and deformed; frequently several deformed nuclei occur in the same cell. The tissue attacked is the flower axis and the result is generally the arrest of their growth and finally the development of tumours. The flowers in the infected region are sterile. On only one occasion have the leaves been found attacked and the result was the formation of a tiny gall 1 mm in diameter.

The parasite appears in the host cells in the form of multinucleated myxamoebae which fragment rapidly into uninucleated schizonts which are rounded or crescent shaped. The nuclear division is protomitotic and stages in the division have been seen and figured by MAIRE and TISON. No spores have been found either by MOLLIARD or by MAIRE and TISON and on these grounds the latter authors consider that the parasite should not be included in the genus *Tetramyxa* which is characterised by the arrangement of the spores in groups of four. On the other hand since one of the characteristics by which the genera are distinguished is by the spore system it is obvious that there is no reason to place it in another genus. MAIRE and TISON consider that in this species spores are never formed and therefore they prefer to place the organism in a new genus under the name *Molliardia Triglochinis*. It is difficult to see how distribution is effected in such a life-history.

In 1926 the present author also found this species on the flower axes of *Triglochin maritimum* at Gravesend, Kent. No spores were present but the myxamoebae were similar to those found by MAIRE and TISON. Comparisons made between this material and slides sent by Prof. RÉNÉ MAIRE shewed that the same organism was present in the Gravesend material as had previously been found in France. It is believed that this constitutes the first British record of the organism.

The systematic position of this organism presents difficulties. The structure of the myxamoebae and the nuclear division is similar to that found in the other genera of the Plasmodiophoraceae. In the absence of spores it differs remarkably since in all the other species these are most commonly met with and are far more abundant in collections of material than the earlier stages. It seems very improbable that they could therefore have been missed. On the other hand the present author finds it difficult to recognise as a species of the Plasmodiophoraceae an organism in which spores are not produced. Parasitic amoebae have been recorded in a number of Phanerogams and it may be that eventually this organism will find its position in that group. In the present state of our knowledge there seems no reason for introducing a new genus in the Plasmodiophoraceae, and it is more desirable to retain provisionally the older name *Tetramyxa Triglochinis* until such a time as by further work the true systematic position becomes known.

The following diagnosis, based on that made by MAIRE and TISON from their material is appended, MOLLIARD not having published any diagnosis of his organism.

Myxamoebae forming uninucleated schizonts. Schizonts subglobose or fusiform, straight or curved, produced in very large numbers in the host cells. No spores formed.

In the flower axes, rarely in the leaves, forming little tumours or swelling of the tissue. In *Triglochin palustre* and *T. maritimum*, in France and *T. maritimum* in England.

Genus VI. *Ligniera* MAIRE and TISON.

MAIRE & TISON (1911): Comptes Rendus Acad. Sci. Paris Vol. 152 p. 206.

Spores not aggregated together into a spore-ball, or spore-cake, nor enclosed in a common membrane. Myxamoebae small, completely filling the host cells. When mature myxamoebae producing both spores and zoosporangia. Zoosporangia on germination producing zoospores. Spores on germination producing swarm cells. Conjugation occurring between swarm spores and zoospores respectively. Reduction division taking place prior to spore and zoospore formation.

The organisms cause no hypertrophy of the host tissue.

Two species are considered to belong to this genus.

Key to the species.

I. Spores spherical walls smooth. Zoosporangia producing zoospores occur commonly. *L. Junci* p. 222.

II. Spores spherical, walls warted. Zoosporangia not recorded. *L. verrucosa* p. 227.

This genus differs from *Plasmodiophora* in the presence of zoosporangia, and in the spores being produced in groups of irregular shape, not enclosed in a membrane, but not so scattered as in that genus. It also differs in the occurrence of zoosporangia as a second method of reproduction. *Ligniera* differs from *Sorosphaera* in the arrangement of the spores and in the absence of a common membrane. It differs from the other genera in the same characters as it does from the two mentioned above.

1. *Ligniera Junci* (Schwartz) Cook.
(Pl. 11 Figs. 30—32.)

Schwartz (1910): Annals Botany Vol. 24 p. 511—522.
Cook (1926): Trans. British Mycological Soc. Vol. 11 p. 196—213.
Syn. *Sorosphaera Junci,* Schwartz (1911): Annals Botany Vol. 24 p. 511—522.
Sorosphaera graminis, Schwartz (1911): Annals Botany Vol. 25 p. 791—797.
Ligniera radicalis, Maire and Tison (1911): Comptes Rendus Acad. Sci. Paris Vol. 152 p. 206.
Sorolpidium Betae, Němec (in part) (1911): Bull. Internat. de l'Acad. Sci. Bohême Vol. 16 p. 136—144.
Ligniera Bellidis, Schwartz (1914): Annals Botany Vol. 27 p. 227—240.
Ligniera Menthae, Schwartz (1914): Annals Botany Vol. 27 p. 227—240.
Ligniera Alismatis, Schwartz (1914): Annals Botany Vol. 27 p. 227—240.
Anisomyxa Plantaginis, Němec (in part) (1916): Bull. Internat. de l'Acad. Sci. Bohême Vol. 18 p. 18—32.
Ligniera pilorum, Fron and Gaillat (1925): Bull. Soc. Mycologique France Vol. 41 p. 388—390.

Spores spherical, 4—7 μ diam., with thin hyaline walls. Zoosporangia subglobose, 15—20 μ diam. giving rise to zoospores, 4.5 μ long by 3.5 μ diam. Spores germinating to produce swarm cells. Both zoospores and swarm cells producing amoebae which become myxamoebae. Schizont formation does not occur. Meiosis occurring immediately before spore formation, or after the formation of zoosporangia. The fungus causes no hypertrophy of the host tissue. It has been recorded from various parts of Europe including England.

The historical account of the species is complicated and has resulted in some confusion arising in the minds of some systematic writers. This is particularly true of the recent account by Fitzpatrick, in which he fails to recognise the difference between the genera *Ligniera* and *Sorosphaera.* It will be necessary therefore to consider the matter in detail.

The genus *Ligniera* was made by Maire and Tison in 1911 to include two species which they had found, *L. radicalis* and *L. verrucosa.* In another paper in the same year they proposed to transfer *Sorosphaera Junci* to this new genus. *Sorosphaera Junci* had been described by Schwartz in 1910 and since at that time very little was known about the genera of the Plasmodiophoraceae Schwartz had placed the organism in the same genus as *S. Veronicae* which he had studied, although he recognised at the time that it differed considerably from it. In 1912 WINGE also transferred *Sorosphaera graminis* to the genus *Ligniera.* SCHWARTZ had described this species in 1911 before the work of MAIRE and TISON had reached this country. In 1914 SCHWARTZ in describing three further species very similar to his *Sorosphaera graminis,* recognised MAIRE and TISON's new genus and referred his species to that genus. In 1918 PALM described a further species occurring in the leaves of *Isoetes lacustris.* A critical account of the genus *Ligniera* was made by COOK in 1926 and it was shewn by cross innoculation experiments that *Ligniera Junci* could infect a number of Phanerogams and that all the five species described by SCHWARTZ were really host varieties of one species *Ligniera Junci.* At the same time it was shewn that *Ligniera pilorum* described in 1925 by FRON and GAILLAT was also a variety of *Ligniera Junci.* In 1927 COOK brought forward evidence to shew that the Chytridiaceous fungi *Sorolpidium Betae* and *Anisomyxa plantaginis* were not good species, but consisted of a mixture of *Ligniera Junci* and certain Chytridiaceae, a fact which was supported by GUYOT in the same year.

In 1928 COOK gave a full account of the cytology of *Ligniera Junci* and described the formation of zoosporangia as an additional method of reproduction, a feature which had been indicated briefly in the 1926 paper. In the same year GUYOT suggested that both *L. radicalis* and *L. verrucosa* should be included in the one species *L. Junci.*

The grounds upon which *Sorolpidium Betae* is regarded as partly composed of *Ligniera* is based upon experiments made by both GUYOT and the present author. Beets inoculated with *Ligniera Junci* and *Olpidiaster radicis* developed symptoms entirely similar to those described by NÊMEC as characteristic of his *Sorolpidium betae.* The case of *Anisomyxa Plantaginis* is also discussed and it is considered that the description given by NÊMEC is insufficient to justify that organism being considered as anything but *Ligniera Junci* with possibly another chytrid associated with it. *Ligniera pilorum* was separated from *L. Junci* because it caused hypertrophy of the host root-hairs. It has, however, been shewn that *L. Junci* may under some conditions also cause similar swelling and it is considered that such a small point is not sufficent to justify the erection of a new species. *Ligniera radicalis* was considered as a separate species before the wide variety of hosts attacked by *L. Junci* was realised. MAIRE and TISON considered it very similar to *L. Junci.*

Speaking of the latter species they say "Cette Plasmodiophoracée décrite par Schwartz présent sensiblement les mêmes caractères généraux que le *L. radicalis*, dont elle est extrèmement voisine. It est certain que le développement de cette éspèce est à peu près identique à celui du *L. radicalis*".

The only recorded difference between *L. Junci* and *L. radicalis* is in the size of the spores, which in the latter are 4—5 μ in diameter, whilst in the former they measure 5—7 μ. It seems that this slight difference in spore size is insufficient to separate the two species.

Ligniera Isoetes was described by Palm in 1918 from material of *Isoetes lacustris* which had been preserved in 65 per cent alcohol and had been given to the Botanical Institute of the University of Stockholm by M. Vlengel. Since the material had not been cytologically fixed, Palm was unable to make out any nuclear structures, but discovered amoebae in the cells of the leaves which appeared to be multinucleated — at least, there were empty spaces in them which he suggested were comparable with the akaryote stage. It is difficult from his description to determine how the spores were arranged. In one place he states "Les balles de spores mûres occupent dans presque tous les cas l'espace entier de la cellule-hôtesse en se conformant à peu prês à la configuration dans parois des cellules occupées. La fig. 2a donne l'extérieur de deux balles voisines; on remarquera la 'reticulation' externe. La figure 2b montre une balle qui à été coupée en deux. Ici apparaissent distinctement les spores individuelles entroitement serrées les unes contre les autres de sorte qu'il s'est formé une espèce de tonne où de flotteur entièrement fermé. Du reste — comme on le voit — la ressemblance avec les espèces radicicoles de *Ligniera* est complète, sauf que la construction des balles de spores donne l'impression d'être plus solide." In another part of the paper he says: "Ces spores sont encore irregulièrement dispersées dans la cellule; dans la fig. 3c, elles se sont disposées contre les parois de la cellule-hôtesse". It is difficult to reconcile these two descriptions. If there is a spore-ball similar to that in Fig. 2, then it is probable that the organism should have been placed in the genus *Sorosphaera*: if there is no spore-ball, and Fig. 3 represents the normal condition, then the organism may be correctly placed in the genus *Ligniera*. No information as to the presence or absence of a common membrane round the spores is given. It seems impossible to accept as a new species one described solely from preserved material, especially when the fixation is not good enough for the nuclei to be made out. As far as can be seen, the author has not brought forward sufficient evidence to show that this species belongs even to the Plasmodiophoraceae, and certainly not sufficient to assign it to any particular genus. On the other hand, *Isoetes lacustris* might very reasonably be infected by an omnivorous species and it will be necessary to shew precisely in what respects *L. Isoetes* differs from *L. Junci* before this new species can be accepted.

The life history of *Ligniera Junci*, as will have been realised already, has been studied by a large number of workers, and there are few stages which have not been elucidated. The earliest stage generally found consists of a small uninucleate spindleshaped body lying in the epidermal or cortical layers of the root. The nucleus divides, and the body becomes amoeboid. In time, by further nuclear division, a myxamoeba is formed which completely fills the host cell. Nutrition is thought to be mainly achieved by the absorption of elaborated food materials lying in the host tissue. But Maire and Tison record that these myxamoebae have the power of ingesting solid bodies, and they have themselves observed certain myxamoebae ingesting algae which were also present in the host tissue. Schizont formation is apparently entirely absent from the species, or, if it occurs at all, it is only at a very early stage of development.

During the vegetative part of the life cycle, the nuclei divide protomitotically. In this division, the nuclear membrane persists, but is frequently drawn out around the poles of a rather indefinite spindle. No asters or radiation phenomena accompany the division. The chromatin arranges itself in a comparatively thin ring around the equator of the spindle. In the centre is the karyosome which is oval in shape. There is no connection formed between the karyosome and the chromatin ring, as has been suggested, and the chromatin ring is completely homogeneous, not being differentiated into individual chromosomes. The ring splits into two extremely fine rings which thicken and contract as they pass to the poles. Meanwhile, the karyosome has constricted about its centre, and the two halves have passed towards the poles, accompanying, but on the inner side of, the chromatin ring. The spindle fibres gradually become less and less distinct, and disappear before the chromatin reaches the poles. During the division, the nuclear membrane becomes drawn out and frequently becomes crescent-shaped. At length it becomes invaginated at its centre and from this invagination the membranes of the daughter nuclei are completed. After this, the nuclear membranes become spherical, the karyosome a circular mass in the centre of the nucleus and the chromatin a mass of indefinite granules around the periphery. This type of nuclear division continues throughout the growth of the myxamoeba, and all the nuclei in the same myxamoeba divide simultaneously.

With the approach of spore formation, the nuclei pass through an Akaryote stage. This is initiated by the appearance of radiation phenomena around the nuclear membrane, and subsequently the karyosome becomes smaller and smaller and finally disappears. It is followed by the chromatin, which also is extruded into the cytoplasm, which as a result stains up deeply The nuclear membranes, however, do not disappear. The further development depends upon whether the myxamoeba is about to form zoosporangia or spores.

In spore formation, the nuclei are reconstituted by the entrance of chromatin, which assumes the form of a coiled thread lying against the nuclear membrane. This is the spireme thread. A spindle is formed and the nuclear membrane disappears, while the chromatin fragments into a number of separate chromosomes which pass to the equator of the spindle. The number of these chromosomes has not been accurately determined, but it is about eight. The chromosomes pass to the poles, and a second division follows immediately. In this second division, although the chromosome number is unknown, the total mass of chromatin present is exactly half that present in the first division. At the end of this division, furrows appear in the cytoplasm around the nuclei and in them the walls of the spores are deposited. The spores are spherical, with a thin yellow membrane, and contain a single nucleus.

In the formation of zoosporangia, the nuclei behave in exactly the same way as in spore formation, except that prior to the first division a wall is formed around the unreduced nucleus. Within the zoosporangium so formed meiosis occurs, and this may be followed by a third mitotic nuclear division. The walls are then laid down separating the zoospores from one another. These membranes are extremely thin and delicate, and may consist of little more than slightly differentiated cytoplasm.

The germination of the zoosporangia has also been observed; the zoospores which escape being 4.5 μ in length and 3.5 μ in diameter. They are pyriform in shape and possess a single apical flagellum of about the same length as the cell. These zoospores infect root hairs, boring their way in and sometimes continuing to swim actively after entering the hair. After a short while, they become amoeboid, and may either develop immediately into myxamoebae within the root hair or migrate in an amoeboid form to the cells of the cortex. No fusion of zoospores has been observed although it is concluded that this takes place. The germination of the spores has not been observed in detail, although in tubes of sterile water containing the fungus small swarm spores have been seen. Owing to the difficulty of distingulshing these swarm cells from the zoospores, it cannot be stated definitely that these bodies originated from the spores. It is regarded as certain that the swarm cells fuse in pairs at some point before developing into myxamoebae. The precise significance of these two types of reproduction is not understood, but it is thought possible that whilst the zoospores mainly assist in spreading the disease during the summer, the swarm cells reinfect plants in the spring. It must be admitted, however, that both spores and zoosporangia are found during the whole of the growing period of the host plants.

No pathological effect is produced by the fungus on the host tissues and even the infected cells themselves do not become enlarged, nor do their nuclei disintegrate nor become deformed. *Ligniera Junci* has been recorded in the following host plants: *Poa annua*, *Juncus articulatus*, *J. obtusiflorus*, *J. lamprocarpus*, *J. bufonius*, *Callitriche stagnalis*, *Alisma plantago*, *Potamogeton natans*, *Polygonum Hydropiper*, *Iris pseudocorus*, *Ranunculus circinatus*, *R. aquatilis*, *Plantago major*, *Mentha Pulegium*, *Cerastium vulgatum*, *Veronica Beccabunga*, *Bellis perennis*, *Chrysanthemum Leucanthemum* and possibly *Isoetes lacustris*. From such a variety of hosts it seems probable that this fungus is able to infect any vascular plant under suitable environmental conditions.

2. *Ligniera verrucosa* Maire & Tison.
(Pl. 11 Figs. 33—34.)

Maire & Tison (1911): Comptes Rendus Acad. Sci. Paris Vol. 152 p. 206.

Spores spherical, 4—5 μ diam, with thin verrucose walls. Spores on germination producing swarm cells from which myxamoebae arise. Schizont formation does not occur, and zoosporangia have not been found. Meiosis occurs before formation. The fungus causes no hypertrophy of the host tissue. It has only been recorded from France.

This species was found by Maire and Tison in 1910 in the root hairs and cortical cells of the roots of *Veronica arvensis*. In 1926 Guyot found what he considered to be the same species in the roots of various grasses (*Bromus* and *Festuca*) at Montigny-Beauchamps. Later he also found it in the roots of *Chenopodium album* at the same locality and also in *Beta vulgaris* in the garden of the Station de Pathologie vegetale at Paris.

The development of this species has not been so fully studied as the last but MAIRE and TISON have shewn that the myxamoebae increase in size accompanied by protomitotic nuclear division. Prior to spore formation they saw on one occasion the two meiotic nuclear divisions and the formation of the spores. These spores are arranged differently according to where they are developed. If they occur in root hairs they are produced in a single row, more or less free from one another, but if produced in the parenchyma of the cortex they become arranged in balls either spherical or ellipsoidal, and solid. In neither case is any membrane formed around them.

GUYOT considers that probably *L. verrucosa* merges imperceptibly into *L. Junci*, and he finds it difficult to distinguish between them. Thanks to Dr. GUYOT and Prof. MAIRE the present author has examined slides of the material from each and finds no difficulty from distinguishing it from *L. Junci.* In the samples sent by Prof. MAIRE, it was found that the spores were aggregated into balls, whereas those of Dr. GUYOT were mostly in single rows in the root-hairs. In the latter's slides the warting was certainly not so pronounced as those of Prof. MAIRE. GUYOT found that it was possible to inoculate Beetroots with his *Ligniera verrucosa*, and independently considered *Sorolpidium Betae* to be a mixture of that species with *Olpidiaster radicis.* He also pointed out the close similarity between *Rhizomyxa hypogaea* and species of the genus *Ligniera*, a fact which had already been pointed out by MAIRE and TISON. Unfortunately *Rhizomyxa hypogaea* has not been recorded since BORZI first found it and until further confirmation of its life-history is made it seems more reasonable to consider it as a mixture, since the association of Chytridiales with the Plasmodiophorales is known to occur in several other instances. The multispored sporangium which BORZI described may be the zoosporangium of a *Ligniera* and if it is considered that the species of *Ligniera* represented in his description is *L. verrucosa*, it means that here we have the only evidence of zoosporangia formation in this species. This interpretation seems more likely that, that put forward by FITZPATRICK, that it is a species of *Olpidium*. If it is considered that *Rhizomyxa hypogaea* is in part *Ligniera verrucosa* it means that this fungus can attack another host plant namely *Trifolium resupinatum.*

Species no longer recognised as belonging to the genus *Ligniera*.

1. *Ligniera vascularum* (MATZ) COOK (1929): Journ. Dept. Agric. Porto Rico T. 13.

This species was made by M. T. COOK who transferred an organ im attacking sugar canes in Porto Rico from the genus *Plasmodiophora* to *Ligniera* on the grounds that there was no hypertrophy. The present author has shewn that the organism is not a species of the Plasmodiophoraceae. (See *Plasmodiophora vascularum* p. 197).

Genera excluded from the Plasmodiophoraceae.

1. *Sporomyxa* LÉGER.

LÉGER (1908): Archiv. f. Protistenkunde. Bd. 12 p. 109—130.

A single species *Sporomyxa Scauri* was described by LÉGER from the coelomic cavity of the imago of *Scaurus tristis.* At that time, prior to the work of MAIRE and TISON in France and SCHWARTZ in this country, very little was known about the Plasmodiophoraceae other than *Plasmodiophora Brassicae*, and it is not surprising that LÉGER should have placed his organism in what he termed the "Mycétozoaires endoparasitées". In the light of more recent work the habitat, as well as the presence of ellipsoidal spores lying free in the cells of the host, is quite distinct from anything found in the other genera of the family. The cytology was only very imperfectly worked out. No further work has been published upon this organism and as it is at present known, there is wholy insufficent evidence to justify its inclusion as a genus of the Plasmodiophoraceae.

2. *Peltomyces* LÉGER.

LÉGER (1909): C. R. Acad. Sci. Paris Vol. 49 p. 239—240.

This genus was made by LÉGER in 1909 to include three species which he had found in the Malpighian tubes of certain insects. The parasites formed schizonts which later gave rise to sporonts which produced binucleated spores, which multiplied exogenously. The spores were oval $9 \times 3\ \mu$ in size.

The advance which has been made is our knowledge of the Plasmodiophoraceae since 1909 shews that it in impossible to include such a genus, and it is therefore considered that the genus *Peltomyces* with the three species *P. Blatellae*, *P. hyalinus* and *P. forfulicae* can no longer be considered to belong to the group.

3. *Cystospora* Elliott.

Elliott (1916): Delaware Agric. Exper. Station Bull. No. 114 p. 1—25.

This monotypic genus is based upon *Cystospora batata*, which was the name given by Elliott to an organism causing a "soil rot" or "pox" of sweet potatoes in the United States. Although the systematic position of the responsible organism is still very doubtful Elliott does not bring forward any points which seem to justify his contention that the organism is a member of the Plasmodiophoraceae. Before this genus is included it would be desirable that a careful systematic examination was made of the fungus by a worker familiar withe the existing species in the group.

4. *Trematophlyctis* Patouillard.

Patouillard (1918): Bull. Soc. Morphol. France Vol. 34 p. 89—91.

This monotypic genus was described by Patouillard in 1918 and is based upon *Trematophlyctis leptodesmiae* which caused pustules on the leaves of *Leptodesmia congesta* in Madagascar. Only dried material was available and only imperfect observations could be made. What is known of the life-history and structure seems to indicate that the organism is in no way related to the Plasmodiophoraceae, though the description is so brief as to prevent any accurate picture of it being formed.

Genera considered as incorporated in the recognised genera.

1. *Ostenfeldiella* Ferdinandsen & Winge.

The single species *O. Diplantherae* is here treated as belonging to the genus *Plasmodiophora* under the name *P. Diplantherae.*

2. *Clathrosorus* Ferdinandsen & Winge.

The single species *C. Campanulae* is considered here as a species of the genus *Spongospora* under the name *S. Campanulae.*

3. *Molliardia* Maire & Tison.

The single species *Molliardia Triglochinis* is considered under its older name *Tetramyxa Triglochinis* since the separation of this species in a special genus is scarcely justified.

4. *Rhizomyxa* Borzi.

The species *Rhizomyxa hypogaea* is considered as being made up partly of a species of *Liginera*, probably *L. verrucosa*, associated with an unidentified species of the Chytridiales.

5. *Sorolpidium* Nemêc.

Sorolpidium Betae has been shewn to consist of a mixture of *Ligniera Junci* and *Olpidiaster radicis*, and is not a separate species.

6. *Anisomyxa* NEMÈC.

The species *Anisomyxa Plantaginis* has been found to consist of a mixture of *Ligniera Junci* associated with a species of the Chytridiales not definitely identified.

The Phylogeny of the Plasmodiophoraceae.

All the earlier accounts of systematic myxology fail to consider the systematic position of the Plasmodiophoraceae in any detail. ZOPF was the first to make a definite statement regarding the position of the group when in 1885 he used the name Plasmodiophoraceae as a family and included it along wlth Pseudosporaceae and Gymnococcaceae in a group the Monadineae zoosporeae. Such a classification was obviously unsatisfactory and was superseded by SCHROETER who using the family name Phytomyxinae placed the group in the Myxomycetes, Mycetozoa or Schleimpilze as one family allied to the Acrasieae and Myxogasteres. The subsequent indiscriminate use of the terms Myxomycetes, Mycetozoa and Myxogasteres to refer to the saprophytic order has led to further confusion. In general the tendency has been to keep the Plasmodiophoraceae somewhere near the Mycetozoa, but unfortunately the systematic position of the latter group has been subject to very great disagreement. SCHROETER considered that they were fungi, a view similarly expressed by SCHINZ in RABENHORST's Kryptogamenflora, but many zoological writers have preferred to place the group in the Protozoa as an order of the Lobosa.

In modern text books on mycology different views are express ed. GAUMANN [1]) and GAUMANN and DODGE [2]) considered then in the Archimycetes, a group equivalent to FISCHER's Myxochytridiales. In this classification they were placed along with the Olpidiaceae, Synchyaceae and Woroninaceae, and sharply separated from the Chytridiales. GWYNNE VAUGHAN and BARNES [3]) consider that they are allied to the Myxomycetes, and following the view put forward by PASCHER [4]) in 1918 do not think that they can be considered as Fungi. COOK considered that they represented a separate group

[1]) GAUMANN, E. A., "Vergleichende Morphologie der Pilze". Jena 1926.

[2]) GAUMANN, E. A. and DODGE, C. W., "Comparation morphology of Fungi". New York 1928.

[3]) GWYNNE VAUGHAN, H. I. C. and BARNES, B., "The structure and development of the Fungi". Cambridge 1927.

[4]) PASCHER, A., Ber. d. deutsch. bot. Ges. Vol. 36 p. 359. 1918.

more closely related to the Mycetozoa than the Chytridiales but included them in an all embracing conception of the term Archimycetes or simplest fungi. Fitzpatrick in the most recent treatment included the Plasmodiophoraceae in the Chytridiales, while he places the Mycetozoa in a group the Myxothallophyta, a subdivision of the Protista.

From such a wide diversity of views it will be realised that scarcely any workers agree regarding the systematic position of the group. Unfortunately many who have been responsible for altering the systematic position appear to have very little personal acquaintance with the organism. It may be, however, that by a critical comparison of the group with all other groups which are in any possible way related, that some idea of their position may be seen.

Unfortunately our knowledge of many of the other lower fungi is extremely scanty, and detailed comparison cannot be made. At the same time the Lobosa, among the Rhizopoda, the Mycetozoa and certain of the Chytridiales are fairly fully known and with them critical comparison is possible.

The relationship of the Plasmodiophoraceae, will, therefore be considered under the following heads:

Protozoa
Mycetozoa
Chytridiales.

Relationships of the Plasmodiophoraceae of the Protozoa.

A relationships of the Plasmodiophoraceae to the Protozoa is based largely upon the views expressed by zoologists, most of whom have a very imperfect knowledge of the members of the group. Parker and Haswell [1]) in 1910 include the Mycetozoa as a part of the Protozoa of equal rank with the Rhizopoda but point out that the Mycetozoa differ from all the other protozoa in the or terrestrial habit. They suggest that they should be considered as animals on account of their structure and physiology of the flagellate, amoeboid and myxamoeboid stages, also in exhibiting movement and in being able of ingest solid food. The Plasmodiophoraceae are not mentioned, nor are any of the species included, but it will be seen that from the definition which these writers consider justifies their

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1) Parker, T. G. and Haswell, W. A. "Text book of Zoology". London 1910.

placing the Mycetozoa in the Protozoa, the Plasmodiophoraceae should with equal reason be placed with them in the same group.

HARTOG [1]) in his volume on the Protozoa in the Cambridge Natural History, separates the Plasmodiophoraceae from the Mycetozoa. The latter group he places in the Sarcodina as a group of equal rank with the Rhizopoda, Sporozoa and Proteomyxa. He places *Plasmodiophora*, the only member which he considers, in the Proteomyxa, referring it to the division Myxoidia, and section Azosporae, and included with *Plasmodiophora*, *Vampyrella* and *Serumsporidium*. HARTOG considers that these forms shew relationships with the Sporozoa, he says "for the absence of cytogamy, and of sickle-germs and of the complex spores and cysts of the Neosporidia, are the only absolute distinctions".

WENYON [2]) in 1926 classified the Mycetozoa as an order of the Class Rhizopoda, but did not make any mention of the Plasmodiophoraceae.

It will be seen therefore that there are two possible groups of the Protozoa which have been considered related to the Plasmodiophoraceae, the Rhizopoda and the Sporozoa. The similarity to the Rhizopoda is based largely upon cytological questions while the relation to the Sporozoa is concerned with the life-cycle. We will consider the claims of the Sporozoa first.

In the simpler members of the Sporozoa the parasite alternates between two hosts. They are typical parasites of cold blooded vertebrates, and a large number attack fishes. In a typical example amoeboid bodies escape from spores and penetrate into the host tissue where they become multinucleated and form a plasmodium which corresponds exactly to the myxamoeba of the Plasmodiophoraceae. The plasmodium, at any rate in some species, is said to have the power of cutting off uninucleated schizonts. When the plasmodium is mature the host cell is caused to swell and sometimes to form small galls by proliferation of neighbouring cells. It has been observed that the nuclei of the host cells degenerate as a result of infection. The plasmodium then becomes converted into spores which are dispersed by the breakdown of the gall and the liberation of the spores into the body cavity. On germination the spore produces a binucleated amoeboid body in which syngamy is

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[1]) HARTOG, O. M., "Cambridge Natural History Vol. 1. Protozoa." Cambridge 1909.

[2]) WENYON, C. M., "Protozoology. "A manual for medical men, veterinarians and zoologists." London 1926.

said to take place. This amoeba makes its way to the tissue subject to attack by the parasite and infection occurs.

In the more advanced members complications occur in which an advanced method of sexual reproduction with morphologically distinct gametes are formed. Little is known about the cytology.

It will be realised, however, that such a life-history is remarkably similar to that of the Plasmodiophoraceae, in fact the differences are more a matter of habitat, and details of spore germination that of fundamental questions. In the Plasmodiophoraceae it is known that under certain conditions the swarm cell is amoeboid from the time it emerges from the spore, which corresponds to the description given of the simpler Sporozoa, the method of infection is roughly similar to that recorded in such a form as Tetramyxa parasitica, and the formation of the plasmodium with a process of budding is equivalent to the development of the myxamoeba and the production of schizonts. In some of the more complex Sporozoa there appears to be a tendency to introduce a stage of multiplication between the germination of the spore and the re-infection of the host by the amoeba, which recalls the multiplication stage found in *Plasmodiophora Brassicae*. Unfortunately little is known about the type of nuclear division in these Myxosporidiae, but should it eventually be found to be of a simple type the comparison between the two groups would be remarkably similar.

The idea of relationship to the Rhizopoda, using that term in its restrict ed sense to refer to these Protozoa in whose life cycle the amoeboid phase is dominant, we find is based chiefly upon cytological evidence rather than detail of life-cycle.

In 1910 Chatton [1]) described in *Amoeba mucicola* a type of nuclear division which was remarkably similar to that found in the Plasmodiophoraceae. In it the karyosome is large and the initial stage in the division is the elongation of this karyosome. A spindle if formed about the centre of the karyosome, and upon it chromatin is deposited in a solid ring, no chromosomes being differentiated. The ring splits and along with the divided karyosome passes to the poles of the spindle. The spindle disappears and the nuclear membrane forms around the daughter nuclei in a complete sphere. Such a nuclear division is remarkably similar to what is found in all the species of the Plasmodiophoraceae. Bělař in a recent paper has shewn that all stages in nuclear division from what at first

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[1]) Chatton, E., Arch. Zool. Expér. et Génév. Vol. 5 p. 239—266. 1910.

sight seems to be amitosis to perfect mitotic division can be found among the amoebae and suggests that these can be arranged in a series of increasing complexity parallel with the evolution of the amoebae themselves.

It is argued that from a comparison between the nuclear division in such amoebae as *Amoeba mucicola* it is reasonable to consider that there must be a phylogenetic connection between these Amoebae and the Plasmodiophoraceae, and that the development of spores is a specialisation evolved by the latter after they had become adapted to their particular environment. On the other hand it has been pointed out that our knowledge of the method of nuclear division of so many of the primitive groups of animals and plants does not justify our basing phylogeny between such a pair of types without being able to contrast other groups which may subsequently be shewn also to exhibit protomitotic nuclear division.

The relation between the Plasmodiophoraceae and the Protozoa is not generally accepted by botanists, largely because they prefer to include the group within the Fungi chiefly on sentimental grounds and because of the habitat in which they are found. As will be realised, however, from what has been said, there are some very remarkable similarities both in life-cycle and cytology between the two groups and the possibility of such a relationship cannot be entirely ignored.

Relationships of the Plasmodiophoraceae with the Mycetozoa.

Our knowledge of the life-history of the Mycetozoa has been increased within recent years by the work of Jahn [1], Skupienski [2], Wilson and Cadman [3] and Cadman [4]. From these researches we are now able to contrast the condition in that group with the Plasmodiophoraceae.

The first division of the nucleus of the spore takes place either while within the spore coat, as in *Didymium nigripes* and *Ceratiomyxa fruticulosa* or shortly after germination as in *Reticularia Lycoperdon*. In *Didymium nigripes* three or four nuclear divisions

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1) Jahn, E., Ber. d. deutsch. bot. Ges. Vol. 26 A p. 342—352. 1908.

2) Skupienski, F., "Recherches sur le cycle evolute de certains Myxomycetes". Paris 1920.

3) Wilson, M. and Cadman, E. J., Trans. Roy. Soc. Edinburgh Vol. 55 p. 555—608. 1928.

4) Cadman, E. J., Trans. Roy. Soc. Edinburgh Vol. 57 p. 93—142. 1931.

follow after which the swarm cell becomes amoeboid. To this structure the term myxamoeba has been applied. The myxamoebae fuse in pairs. In *Reticularia Lycoperdon* there is no myxamoeba stage and the swarm cells fuse together in a flagellate condition by their posterior ends. This zygote is considered as a plasmodium, it is amoeboid and can ingest both swarm cells and unconjugated myxamoebae, it can also coalesce with other small plasmodia. In *Reticularia Lycoperdon* the young plasmodium only ingests flagellate swarm cells. The plasmodium increases in size accompanied by mitotic nuclear division, and more small plasmodia are drawn into the single large plasmodium which eventually forms a structure visible to the naked eye. This plasmodium is saprophytic though Gilbert has shewn that the plasmodia of many species could ingest the spores of fungi, though they shewed a variation in their desire to do so. *Didymium nigripes* shewed a far greater readiness in this respect than *Reticularia Lycoperdon.* When the plasmodium is mature sporangia are formed and within them the nuclei undergo a reduction division. In *Didymium nigripes* cleavage and meiosis go on simultaneously while in *Reticularia Lycoperdon* meiosis precedes cleavage. Finally spores are produced each possessing a single haploid nucleus. Cadman considers that of the two species she has studied that *Didymium nigripes* is a more advanced type than *Reticularia Lycoperdon* because of the presence of myxamoebae and the fusion of amoeboid gametes.

The comparason between the Mycetozoa and the Plasmodiophoraceae is based upon the development of the plasmodium (myxamoeba in the Plasmodiophoraceae) and the formation of spores. It is considered that the production of specialised sporangia in the Mycetozoa is associated with its free living condition and that such structures would not be advantageous to the Plasmodiophoraceae and therefore have not been evolved. In this connection it may be suggested that the membrane around the spore-ball may be looked upon as roughly equivalent to the sporangium of the Mycetozoa. The chief difference between the two groups lies in the behaviour of the germinated spores. In the Mycetozoa there is clear evidence that there is a division of the spore content into several swarm cells so that the gametes, whether flagellate or amoeboid are not the entire product of a single spore. On the other hand the fact that either flagellate or amoeboid cells can function as gametes is in agreement with what is found in the Plasmodiophorales. It is important to note, however, that the flagellate swarm cells of the Mycetozoa fuse by their posterior ends, while those of the Plasmodiophoraceae fuse by their anterior ends, both, however, are uniflagellate.

From this comparison it will be seen that there are important differences between the two groups, which in the opinion of some authorities, preclude the view that there is any close relationship between them. The most important of these is the fact that in the Mycetozoa the gamete is not the direct product of the spore, whereas in the Plasmodiophoraceae it is, though it must be admitted that this stage has only been followed in detail in a few species. It is considered, however, that these are sufficent to justify a definite statement that division of the swarm cells does not take place in the Plasmodiophoraceae prior to fusion.

Relationships of the Plasmodiophoraceae with the Chytridiales.

This view is upheld chiefly by Gaumann, Gaumann and Dodge and Fitzpatrick. Gaumann and Gaumann and Dodge place in a Class Archimycetes four families, Olpidiaceae, Synchytriaceae, Woroninaceae and Plasmodiophoraceae. This class is considered to be separated from the rest of the Chytridiales which are included in the Phycomycetes. They consider that these families stand very close to the Mycetozoa and the Flagellata, but differ from them chiefly in their parasitism. They admit however that the four families are to be regarded as four different lines "which have developed independently of each other from the Sporozoa — Flagellata — Myxomycete line". Unfortunately their reasons for this treatment of the family breaks down largely owing to the fact that they quote work which has been shewn to be untrue in support of their view, suggesting that caryogamy occurs just prior to spore formation. They bring forward very little constructive evidence to explain the introduction of the family in this group, which they appear to regard as a dumping ground for a group of families, probably not related, but which they do not regard, as they do the Mycetozoa, as lying outside the Fungi.

Fitzpatrick, on the other hand definitely included the Plasmodiophoraceae within the Chytridiales and places it as his first family. He admits that this treatment is new and justifies it by the following contention.

"In attempting to indicate the bases on which it seems desirable to incorporate the Plasmodiophoraceae in the fungi rather than in the Myxomycetes it is necessary to deal in generalisations on account of inadequate data. Enough is known concerning the group, nevertheless, to warrant the attempt. In the character of the zoospores and in the unusual type of the vegetative mitosis, the Plasmodiophoraceae are unlike other known fungi. The zoospore seems to resemble that of the Myxogastres, the nuclear division to some extent that of certain Protozoa. In the absence of capillitium and so-called 'sporangial walls', in the absence of a true plasmodium, and in the presence of parasitism, the group differs strikingly from the Myxogastres and corresponds with the Woroninaceae and Synchytriaceae of the Chytridiales. In the small and apparently rather definite number (1—8) of zoospores [1]) freed in the germination of the sporangium ("spore") the Plasmodiophoraceae resemble the Myxogastres more than they do the Woroninaceae and Synchitriaceae where the number is usually much larger. . . .

In summarising the available facts, it would seem that the Plasmodiophoraceae resemble the Myxogastres less than they do the Woroninaceae and Synchytriaceae. Their failure to form a true plasmodium is regarded in this connection as an essential feature. However, in placing the family in the Chytridiales, it should not be assumed that the relationship to members of this order is necessarily close. . . . A correctly drawn phylogenetic tree would probably completely disrupt the group. These forms have been treated together in one order merely because they constitute the most primitive fungi, not because they are regarded as a coherent group of closely related genera. A more natural arrangement is much to be desired, but cannot as yet be attempted. This situation makes much easier the inclusion of the Plasmodiophoraceae in the group, and taking into consideration the striking differences in the morphology of the swarm spores in the three families, it does not seem unreasonable to assume that the Woroninaceae and Synchytriaceae

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[1]) This statement appears to be based upon the observations made by Johnson in 1908 that eight zoospores are freed from the spore in *Spongospora subterranea*. This however was corrected by Kunkel in 1915, who found that only one was formed. The author also seems to have confused the statement made by Cook that in *Ligniera Junci* both spores and zoosporangia develop from the myxamoeba. It is only in the zoosporangium that a number (4 to 8 zoospores) are formed. In this connection it may be pointed out that the use of the term "zoospore" by Fitzpatrick in the sense of "swarm-cell" or "swarm-spore" is confusing.

are as closely related to the Plasmodiophoraceae as to each other. To the writer it seems likely that these several groups have arisen more or less in parallel from yet more primitive Protozoa, and wholly independent of the Myxogastres which have arisen from the same or different Protozoa along another line. The existence in a limited section of the Protozoa of a type of nuclear division resembling the cruciform division of the Plasmodiophoraceae indicates perhaps the origin of this family, but it does not of necessity preclude the possibility that other families, which now possess a higher type of mitosis, have arisen from the same or closely related group."

It is unfortunate that some of the features which have been used in this presentation of the relationships have been found to be untrue in the light of more recent investigations. It will, however be convenient to consider these three families separately since they are the ones generally selected as being most like the Plasmodiophorales. Of the three the Woroninaceae is considered most comparable.

Our knowledge of the Woroninaceae and in particular the genus *Woronina* is by no means extensive. In the vegetative part of the life-history the production of a multinucleated mass of protoplasm of variable shape suggested at first the myxamoeba of the Plasmodiophoraceae. Material examined by the writer, which had unfortunately been previously preserved in formalin, failed to shew any detail of nuclear structure, and until this is more accurately studied it is difficult to draw a sharp comparison between them. No record of schizont formation is recorded, though since frequently consecutive cells are found with plasmodia of the same stage of development it may be that some such process does occur. The protoplast when mature divides up into a number of zoosporangia, which superficially resemble spores of the Plasmodiophoraceae, but which on germination, frequently *in situ*, produce a number of zoospores each of which is spindle shaped and provided with a pair of laterally borne flagella [1]). An additional stage in which the protoplast fragments to form resting spores which fuse up to form a single thick walled body termed a cystosorus, is also described in

[1]) Since the above was written a study has been made of living material of *Woronina polycystis* which will shortly be published. From this work no evidence has been found to support a relationship between the Plasmodiophoraceae and *Woronina*, and several points have been discovered which suggest that the relationship is, even more distant that was previously thought.

this species. The spores so formed germinate to produce zoospores similar to those formed in the sporangia.

To compare such an organism with the Plasmodiophorales seems difficult, since the only really close similarity is the development of a naked protoplasmic vegetative stage which culminates in a reproductive phase. This reproductive stage, however, is in no way similar to the Plasmodiophoraceae, the sporangia formed in the Plasmodiophoraceae not being comparable with the zoosporangia of *Woronina*, and, even if it be argued that the spores of the Plasmodiophoraceae are sporangia in which the zoospores are reduced to one, the swarm cells of that group cannot be compared with the zoospores of *Woronina* with its two flagella, not does it seem very reasonable to compare them with those of the Olpidiaceae and Synchytriaceae.

Winge attaches considerable importance to the discovery by Juel [1]) in 1901 of *Pyrrhosorus marinus* which occurs as a saprophyte, Winge thinks partly as a parasite, on the branches of *Cystoclonium purpurescens*. The formation of a plasmodium is described by the aggregation together of uninucleated masses of protoplasm. It is stated that there is a change in size of the nuclei during the development and it is suggested that after division the nuclei are small and that they increase in size before the next division can take place. Schizonts are also described as occurring in this species. When mature the myxoplasms, as they are called, surround themselves with a wall and within uninucleated spore mother cells are formed. A kind of Akaryote stage is described before this and three nuclear divisions occur within the spore mother cells. Eventually eight naked zoospores are formed, each containing nuclei in which 2—5 chromosomes are said to be present. The zoospores escape in a mass from the mother cell, they are pyriform and provided with two lateral flagella.

In this species the same difficulty arises in comparing it with the Plasmodiophoraceae, namely that the eight zoospores are produced in each sporangium and that the zoospores when liberated possess two lateral flagella instead of a single apical one. In the occurrence of a chromatin extrusion stage before the nuclear divisions associated with spore formation, we have an interesting, but probably not very significant comparison.

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[1]) Juel, H. O., Bihang t. k. Svenska Vet.-Akud. Handlingar Vol. 26 p. 1—14. 1901.

A comparison with either the Olpidiaceae or the Synchytriaceae seems to the writer to be even more obscure. It is unnecessary to consider them in detail, but the presence of a membrane (which in the Olpidiaceae is thin and in the Synchytriaceae thicker) during the greater part of the life-cycle seems to separate them from the Plasmodiophoraceae. The whole body then functions as a sporangium in which zoospores are produced and not walled spores. These zoospores on escaping are more or less spherical and have a single posterior flagellum, they do not become amoeboid but fuse and develop while still flagellate. In the presence of a membrane around the sporoplast, in the character of the zoosporangium, and the zoospores, neither of these families seem to be closely allied to the Plasmodiophoraceae, nor incidentally to the Woroninaceae.

The use of *Sorolpidium Betae*, *Anisomyxa Plantaginis* and *Rhizomyxa hypogaea* as evidence of a relationship between the Plasmodiophoraceae is considered to be unsatisfactory since it has been shewn that there is very strong evidence that none of them are good species but a mixture of a species of the Plasmodiophoraceae and a member of the Chytridiales. Such an association is known to occur and the writer has found it on several occasions, e. g. *Cystochytrium radicale* with *Ligniera Junci*, *Olpidiaster radicis* with *Ligniera Junci*, *Olpidium radicale* with *Ligniera Junci*, *Synchytrium endobioticum* with *Spongospora subterranea*, *Olpidium Brassicae* with *Plasmodiophora Brassicae* etc.

From the foregoing consideration it will be seen that a close comparison between the Plasmodiophoraceae and either the Protozoa, or the Mycetozoa, or the Chytridiales cannot be made. Of the three the Chytridiales seems to be the most unsatisfactory and to shew the least grounds for comparison, but it must be admitted that close affinity with either of the other groups cannot be considered as probable. No mention has so far been made of the Acrasiales. These curious saprophytes have been but little studied, and our knowledge of them is scanty. The organism exists during the vegetative part of the life-cycle as a naked myxamoeba which crawls about and ingests solid material. Later when mature, or through lack of food, they aggregate together forming a pseudoplasmodium. In this condition the myxamoebae are said to maintain their individuality so that the pseudoplasmodium is really more of the nature of a colony. After migration into a suitable shape, which may be either sessile or stalked, the myxamoebae become differentiated into those which form a more solid protective matrix, corresponding to the wall of a sporangium, and those inside which develop a cellulose wall and function as pseudospores [1]).

Olive in his research into the life-history of the Acrasiales found that two types of nuclear division occurred, the one which takes place shortly after germination, and a second which occurs during the active vegetative condition. From a study of these divisions he was lead to the conclusion that the nuclear division of the Acrasiales did not closely resemble that of either the Amoebae or the Mycetozoa. It will be seen therefore that both from the cytological and morphological aspect there is little reason to regard the Acrasiales as in any way closely related to the Plasmodiophorales.

In 1915 Cavers [2]) commenced a serial account of the Interrelationships of the Protista and Primitive fungi which unfortunately was never completed. In that he suggested that the term Archimycetes should be extended to embrace a considerably larger section of the fungi than had been previously done. He says "Since, as we shall see later, there is much to be said for the view that the so-called 'algal fungi' (Phycomycetes) are far more probably derived from the Chytridiales than from the green algae, it would appear reasonable to extend the name Archimycetes, sometimes used as a synonym for Chytridiales, to include the whole of the lower fungi, which would then fall into the six divisions Chytridiales, Myxomycetes, Plasmodiophorales, Acrasiales, Zygomycetes and Oomycetes". This view was adopted and expanded by the present writer in 1928. In that paper it was suggested that the Plasmodiophoraceae stood apart from all the other groups of lower fungi and could not be closely grouped with any of them. It was therefore suggested that they should be placed in a separate order, the Plasmodiophorales, which at present only contains the single family Plasmodiophoraceae. This order it was suggested shewed some relationship with the Mycetozoa, Rhizopoda, Sporozoa and Chytridiales but not a close relationship with any one of them.

Attention was called to a group, the Proteomyxa, in which were placed a number of simple organisms which shewed little similarity with any of the main groups of either plants, animals or fungi and it was suggested that this group might be looked upon as a common ancestral nucleus of types which formed the basis from which the higher organisms originated. It is argued that in

1) Olive, E. W., Proc. Boston Nat. Hist. Soc. Vol. 30 p. 451—513. 1902.

2) Cavers, F., New. Phyt. Vol. 14 p. 94—104, 164—168, 223—227, 275—280, 302—304. 1915.

the beginning life originated in the form of an amoeboid mass from which there arose two distinct types, the one in which motion was obtained by blunt pseudopodia and the other in which the pseudopodia became fine and whip-like and from which the flagellum was evolved. It is pointed out that a sharp distinction should be made between this flagellum and ciliation characteristic of the Ciliata. It is further suggested that from the Proteomyxa there emerged three kinds of organisms which differed in the method of nutrition which they adopted. The first were the plants which adopted the flagellate structure and evolved chlorophyll, the second were the animals which became holozoic, feeding upon the plants, and the third were the fungi which became parasitic or saprophytic and lived either upon the carbon compounds direct or upon the dead and living remains of other forms of life.

As would therefore be expected, a number of phylogenetic lines have passed out from this complex, some of which have, from an evolutionary standpoint, been more successful than others. The three most successful lines have been the Protozoa, giving the higher animals, the Phytomastigophora, giving the Flagellata (possessing chlorophyll) from which the algae and thus the higher plants have been evolved, and thirdly the Chytridiales, from which the higher fungi have sprung. There remained, however, a number of side lines which also came out from this complex and which did not give rise to any further groups, but which remain to this day without shewing any great advance. Such lines are represented today by the Mycetozoa, the Plasmodiophorales, the Acrasiales and possibly the Sporozoa, to mention only those with which we are immediately concerned. All these groups would therefore resemble one another, since they had a common ancestry in the Proteomyxa, but they are each of them independent lines and therefore this resemblance is not close and precludes their being combined in a single order. It is this latter fact which does not seem to have been sufficiently appreciated by systematic writers who have therefore attempted to fit the groups into a phylogenetic classification dealing either with the fungi or the Protozoa. Such a course does not seem advisable. It cannot be considered that the Plasmodiopnoraceae shew close affinity with any of the groups we have considered; either they are separated by the structure of the spores, or they differ in the type of flagellation of the swarm cells or in their behaviour, whether flagellate and pyriform or amoeboid. Atkinson in 1907 suggested that the number and position of flagella in zoospores was probably an important point is classification, a view which has been amply supported by more recent work. If, therefore the position and number of flagella is significant, the ability of the zoospore or swarm cell to become and sometimes to remain amoeboid must also be looked upon as an important character in classification.

Fitzpatrick and others have mistaken the idea intended to be conveyed in some of the present author's papers regarding the relationships of the Plasmodiophoraceae. Fitzpatrick says "Maire and Tison feel that they have originated from the Chytridiales, while Cook thinks that they shew relationships with the Protozoa". This statement might be construed to mean that an origin from the Protozoa is postulated. This, however, was not intended, all that it was desired to point out was that in certain phases of their life-history the Plasmodiophoraceae resembled the Protozoa rather more closely than they did the Fungi. In the opinion set out here no close relationship with either the Fungi or the Protozoa is considered probable. It is maintained that they represent an independent group having their origin in the Proteomyxa, and that it is that group alone to which they are related. In making this statement the Proteomyxa are regarded as belonging neither to the plant or animal kingdoms but as representing a collection of primitive types from which the two kingdoms originated.

It has been suggested within recent years that the fungi may have had an entirely independent origin from either plants or animals and that they should be regarded as an entirely independent group springing from the Proteomyxa complex. With this idea the present writer is in agreement. He thinks it likely that the Plasmodiophoraceae, Mycetozoa and Acrasiales represent evolutionary series which did not proceed further in their evolutionary development and remained, as it were, at the base of this fungal line of evolution, but this does not imply that they have any greater relationship with that group than with those which gave rise to the two great kingdoms of living organisms.

The following diagram may help to summarise the idea of the relationships of the Plasmodiophoraceae as set out in this account. Since it is maintained that they have no close relationships, the single family is elevated to the rank of an order, the Plasmodiophorales, which is regarded as having the single family Plasmodiophoraceae.

The close uniformity between the six genera during the greater

[1]) Atkinson, G. F., Ann. Mycologici Vol. 7 p. 441—472. 1909.

part of their life-cycles makes their arrangement in a phylogenetic series very difficult. As will have been realised from the description of the species the vegetative phase only differs in very minor points, most of which do not give any indication of an evolutionary series. In the formation of spores or other means of reproduction the species shew a marked difference and this has permitted them to be separated into a number of sharply distinguished genera. It seems reasonable to postulate that the simplest condition occurs when the spores are scattered freely in the host cell and are not arranged in a special system. Hence it is considered probable that the genus *Plasmodiophora* is the least advanced member of the family. In the germination of these spores, however, the introduction of a secondary method of zoospore distribution described in

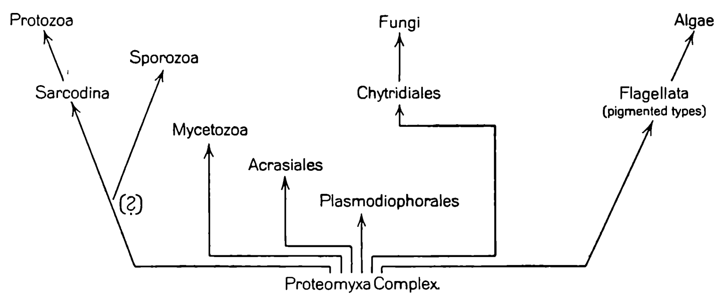

Fig. 13. Possible phylogeny of the main groups of Primitive Organisms.

Plasmodiophora Brassicae seems to indicate that that species is in some respects specialised, and when these stages are more fully understood in the other species it may become necessary to separate them from the genus *Plasmodiophora*. *Tetramyxa* with its spores arranged in fours probably comes next though the reduction into these groups may be regarded as a specialisation. It is desirable here to correct a suggestion which was previously put forward that *Tetramyxa* was specialised, this arose from an imperfect understanding of the spore system. It was thought that the four spores were enclosed within a common membrane, but a reinvestigation of this point has proved it to be incorrect, the spores in that genus shewing only a slight tendency to remain attached together and more frequently to become separated from one another in scattered masses. It seems therefore that the genus *Tetramyxa* comes next to the genus *Plasmodiophora* is a series of increasing complexity. In the genus *Spongospora* where this tendency for the spores to remain together is more marked, we probably have a more advanced type, although it might be argued that *Spongospora* represented a genus in which an enclosing membrane had disappeared though the spores still retained a strong tendency to remain together, a feature which became finally completely lost in the genus *Plasmodiophora*.

The genus *Sorosphaera*, with its very regular sporospheres each enclosed in a delicate membrane, and in which a uniform hollow space is retained so that all the spores are equally exposed to the exterior of the ball, is probably the most advanced type. The genus *Sorodiscus* is then to be regarded is slightly less highly specialised, the spores being arranged in two closely applied plates still allowing all the spores to abut the exterior, but in which the regular hollow centre is collapsed and the two layers of spores have come to touch one another.

The genus *Ligniera*, in having an additional type of reproductive organ — a zoosporangium — stands apart from the other genera. In the arrangement of the spores, however, it seems to lie nearer to the genus *Plasmodiophora*, though even in it there seems to be a tendency under suitable conditions to form the spores into a ball, though the shape of the ball is variable, and it is never enclosed in a common membrane.

The following diagram represents the conception of the phylogeny of the genera of the Plasmodiophoraceae described in this monograph:

Sorosphaera
↑
Sorodiscus
↑
Ligniera *Spongospora*
↖ ↑
Tetramyxa
↑
Plasmodiophora.

Fig. 14. Phylogeny of the genera of the Plasmodiophoraceae.

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Glossary.

The following are a list of the technical terms applied to the Plasmodiophoraceae with the particular sense in which they are used in that group.

Akaryote stage. A condition in which the stainable chromatin is extruded through the nuclear membrane into the cytoplasm, sometimes associated with darkly staining radiations (*Sorodiscus*). The extent to which the chromatin disappears varies in different species.

Amoeboid. Resembling an amoeba, irregular in shape and devoid of a cell membrane. Capable of motion by means of pseudopodia.

Cruciform division. A name given to the metaphase in protomitotic nuclear division owing to the resemblance of the arrangement of the chromatin to a cross, when seen in side view.

Double anchor stage. A name given to the anaphase in protomitotic nuclear division. The shank of the anchor is compared to the drawn out karyosome, while the blade are compared to the chromatin which at this stage is contiguous to the karyosome.

Dumb-bell stage. See "Double anchor stage".

Flagellum. A fine protoplasmic process capable of being actively lashed like a whip by the organism to which it is attached. It is thought that it may have arisen as a specialised pseudopodium.

Gall. A outgrowth from a root or branch caused by proliferation of the cells. It is usually spherical, frequently covered by a layer of cork, and may be hard and woody in texture.

Hyaline. Transparent or glassy; applied to the spore-coat.

Karyogamy. The fusion of the content of two haploid nuclei to form a single diploid nucleus. Directly associated with the fusion of two gametes to form a zygote.

Karyosome. A mass of chromatic material generally spherical in shape which does not contribute chromatin to the chromosomes during nuclear division, but remains intact and divides into two parts during the division.

Myxamoeba. A multinucleated amoeboid body rarely having active movement, tending to fragment into schizonts, the product of the fusion of two gametes.

Plasmodium. A multinucleated amoeboid body formed by the fusion of myxamoebae, swarm cells and amoebae. Exhibits rhythmic circulation.

Protomitosis. A primitive or simple type of nuclear division in which separate chromosomes are not differentiated, the karyosome persists and divides and the nuclear membrane remains, invaginating at the close of the division to form the membranes of the daughter nuclei.

Pseudoplasmodium. A aggregation of amoeboid bodies to form a single body in which the component parts retain their individuality and subsequently separate without change.

Pseudopodium. A process sent out from an amoeba when moving. It may be blunt (Amoebae), fine rigid and tapering (Foraminifera), fine and whip-like (as a flagellum).

Pyriform. Pear-shaped.

Saturn stage. A name given to the metaphase in protomitotic nuclear division. The karyosome is compared to the planet, and its ring to the chromatin ring surrounding it as seen in polar view.

Schizont. A uninucleated body, usually spindle-shaped, occasionally sickle-shaped, which is cut off from a myxamoeba.

Spore. A mass of protoplasm possessing one haploid nucleus enclosed in a relatively thick wall or spore-coat. Generally a resting body, giving rise on germination to a swarm-cell.

Spore-ball. An aggregation of spores together when arranged in a single layer around the surface of a sphere, the centre remaining empty (*Sorosphaera*), also an arrangement of spores in an irregular chambered mass of fairly regular external shape (*Spongospora*).

Spore-cake. An aggregation of spores together which are arranged in two closely applied layers, not separated from one another by a central cavity (*Sorodiscus*).

Swarm-cell. The protoplasmic body that emerges from a spore on germination, containing a single haploid nucleus. It is able to change from a flagellate to an amoeboid condition and later to become flagellate again. Behaves as a gamete.

Swarm-spore. See “Swarm-cell”.

Zoosporangium. A mass of protoplasm containing at first one diploid nucleus which later divided into a number (4—8), enclosed in a relatively thin wall Generally a body of short duration.

Zoospore. A small uninucleated body produced in a zoosporangium, surrounded by a very delicate membrane.

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Description of Plates.

Plates 5—11.

Plate 5.

Plasmodiophora Brassicae.

Fig. 1. Habit, the fungus causing hypertrophy of the roots of a Cabbage. × 1/2.
Fig. 2. Transverse section of the host shewing the plasmodia. × 320.
Fig. 3. Photomicrograph of the spores. × 320.

Plasmodiophora Fici-repentis.

Fig. 4. Habit of the fungus on the host tissues.

Plate 6.

Plasmodiophora Diplantherae.

Fig. 5. Photomicrograph of the plasmodia. × 320.
Fig. 6. Photomicrograph of the spores. × 320.

Sorosphaera Veronicae.

Fig. 7. Habit of the fungus on the host. × 0.
Fig. 8. Photomicrograph of the plasmodia. × 320.
Fig. 9. Photomicrograph of the spores. × 320.

Plate 7.

Sorosphaera radicalis.

Fig. 10. Photomicrograph of the plasmodia. × 320.
Fig. 11. Photomicrograph of the spore-balls. × 320.

Sorodiscus Callitrichis.

Fig. 12. Photomicrograph of the plasmodia. × 320.
Fig. 13. Photomicrograph of the spore-cakes. × 320.

Plate 8.

Sorodiscus radicicolus.

Fig. 14. Habit of the fungus on the host. × $^1/_2$.
Fig. 15. Photomicrograph of the plasmodia. × 320.
Fig. 16. Photomicrograph of the spore-cakes. × 320.

Spongospora subterranea.

Fig. 17. Habit of the fungus on the potato tuber. × $^1/_2$.
Fig. 18. Warts caused by the fungus after storage in a potato clamp (after Pethybridge). × $^1/_2$.
Fig. 19. Habit of the fungus on the roots (after Pethybridge). × 0.

Plate 9.

Spongospora subterranea.

Fig. 20. Photomicrograph of the plasmodia. × 320.
Fig. 21. Photomicrograph of the spore-balls. × 320.

Spongospora Campanulae.

Fig. 22. Photomicrograph of the plasmodia. × 320.
Fig. 23. Photomicrograph of the spore-balls. × 320.

Plate 10.

Tetramyxa parasitica.

Fig. 24. Habit of the fungus on the host. × 0.
Fig. 25. Photomicrograph of the plasmodia. × 320.
Fig. 26. Photomicrograph of the spores. × 320.

Tetramyxa triglochinis.

Fig. 27. Habit of the fungus on the host. × $^1/_2$.
Fig. 28. Photomicrograph of the plasmodia. × 320.
Fig. 29. Photomicrograph of the schizonts. × 320.

Plate 11.

Ligniera Junci.

Fig. 30. Photomicrograph of the plasmodia. × 320.
Fig. 31. Photomicrograph of the spores. × 320.
Fig. 32. Photomicrograph of the zoospores. × 320.

Ligniera verrucosa.

Fig. 33. Photomicrograph of the spores in root-hairs. × 320.
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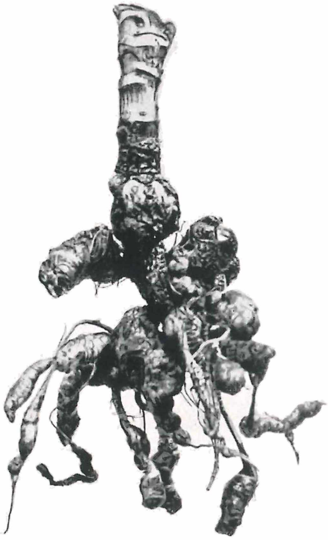

Fig. 1

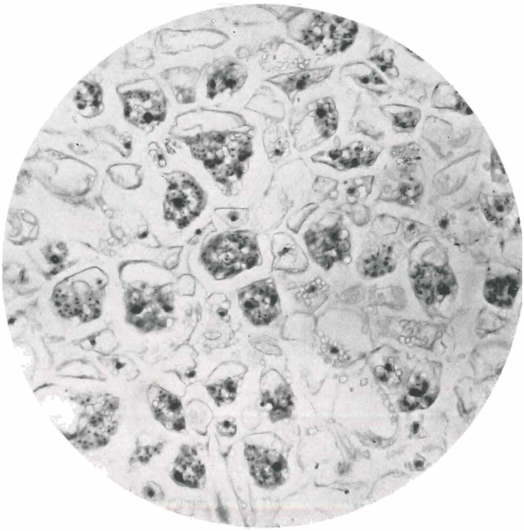

Fig. 2

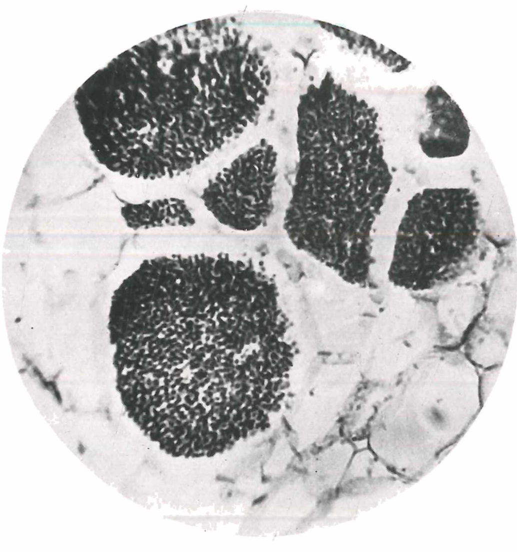

Fig. 3

Plasmodiophora Brassicae.

Ivimey-Cook. photo.

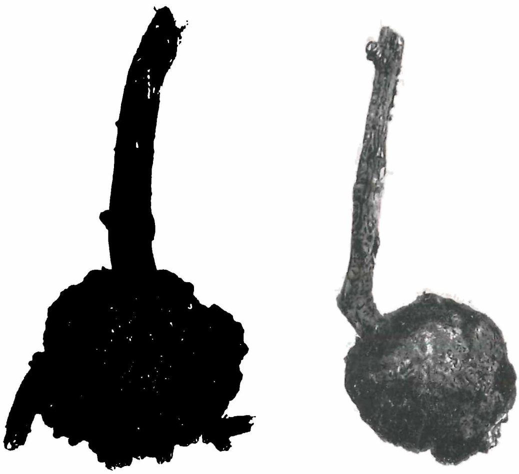

Fig. 4

Plasmodiophora Fici-repentis.

STAV FISCHER IN JENA

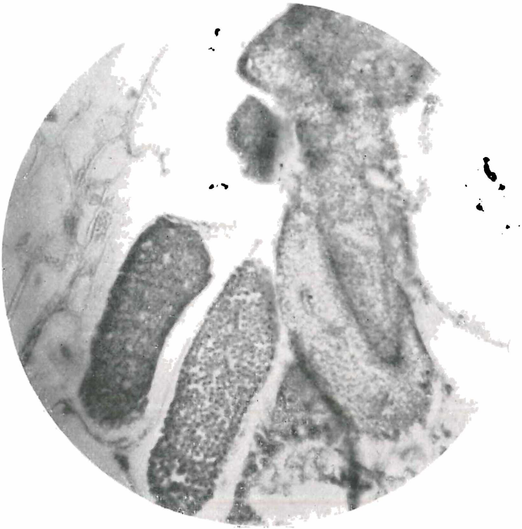

Fig. 5

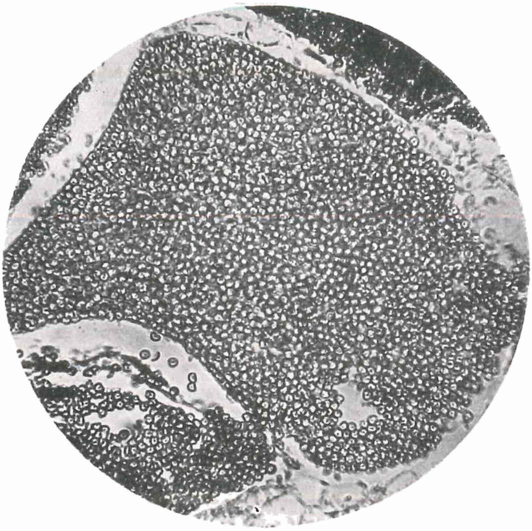

Fig. 6

Plasmodiophora Diplantherae.

Ivimey Cook. photo.

Fig. 7

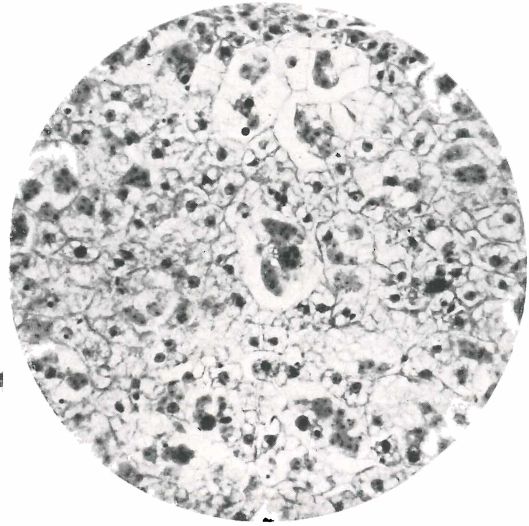

Fig. 8

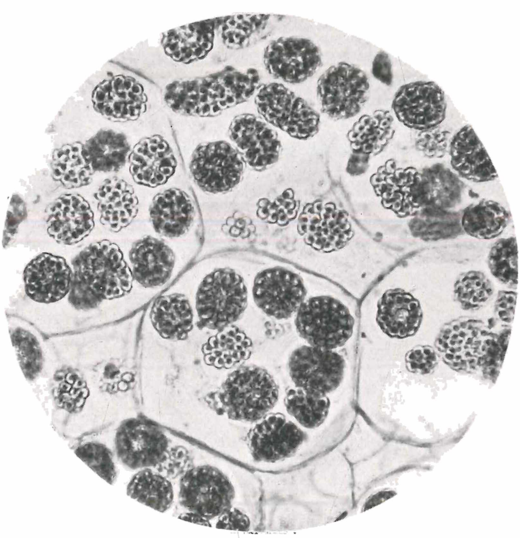

Fig. 9

Sorosphaera Veronicae.

VON GUSTAV FISCHER IN JENA.

Fig. 10

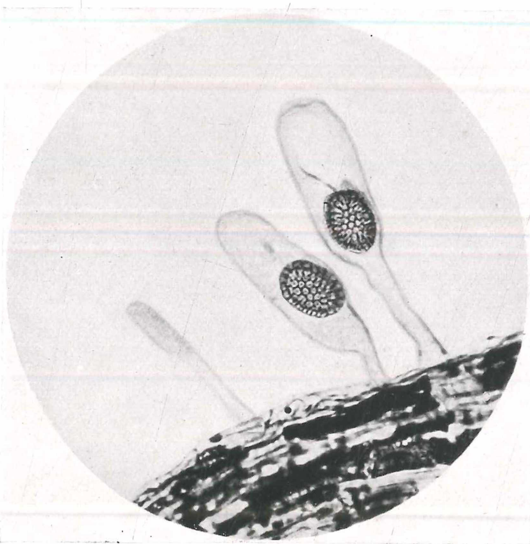

Fig. 11

Sorosphaera radicalis.

Ivimey-Cook. photo.

Ivimey-Cook.

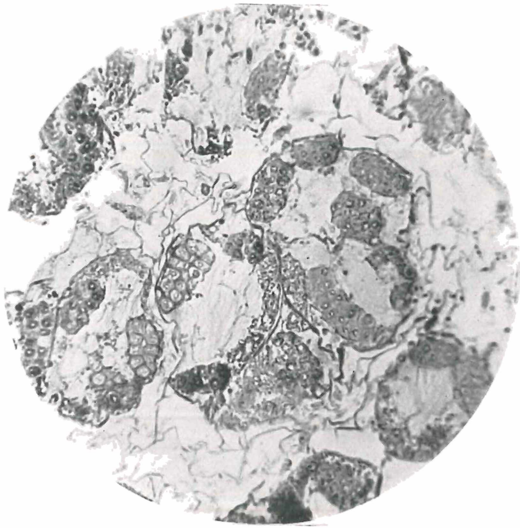

Fig. 12

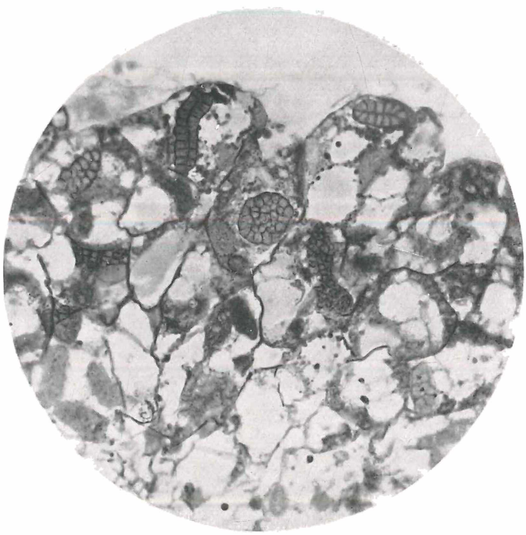

Fig. 13

Sorodiscus Callitichis.

GUSTAV FISCHER IN JENA.

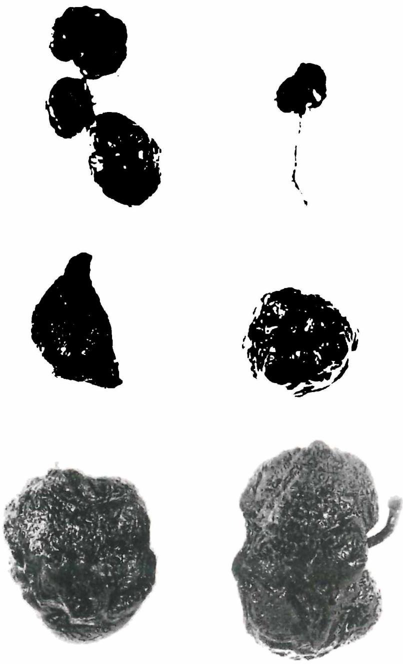

Fig. 14

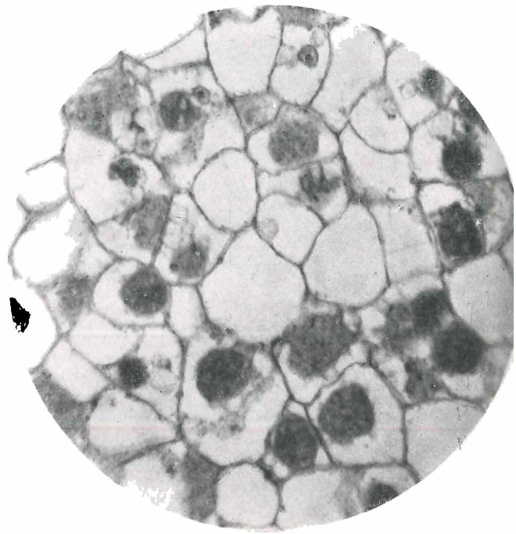

Fig. 15

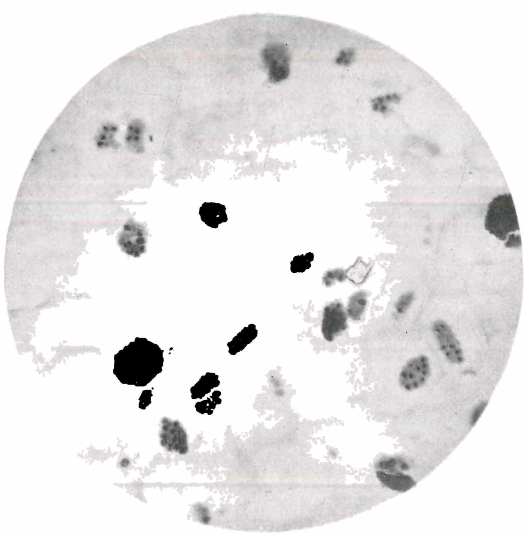

Fig. 16

Sorodiscus radicicolus.

Ivimey-Cook. photo.

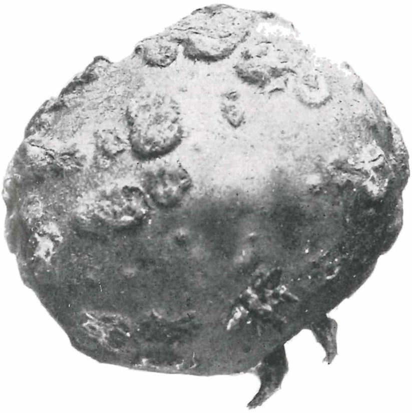

Fig. 17

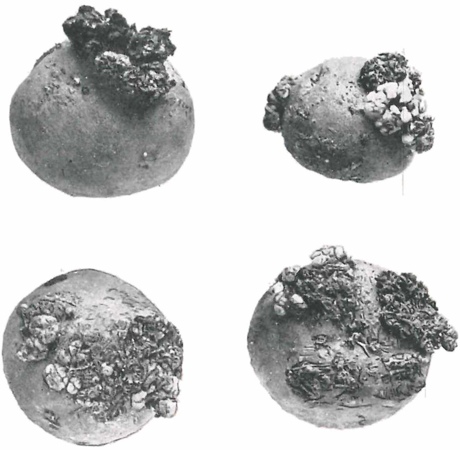

Fig. 18

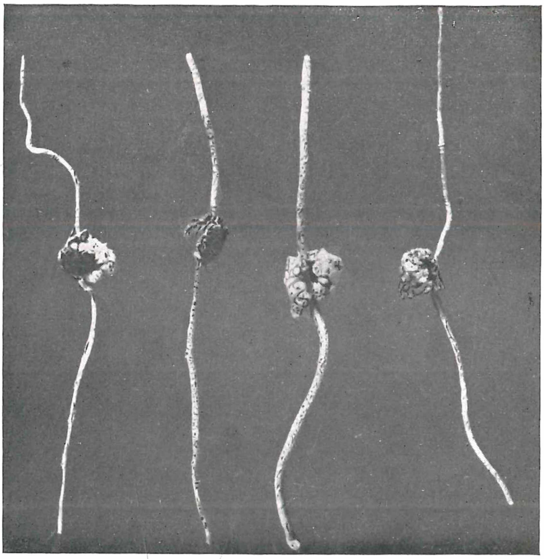

Fig. 19

Spongospora subterranea.

VON GUSTAV FISCHER IN JENA

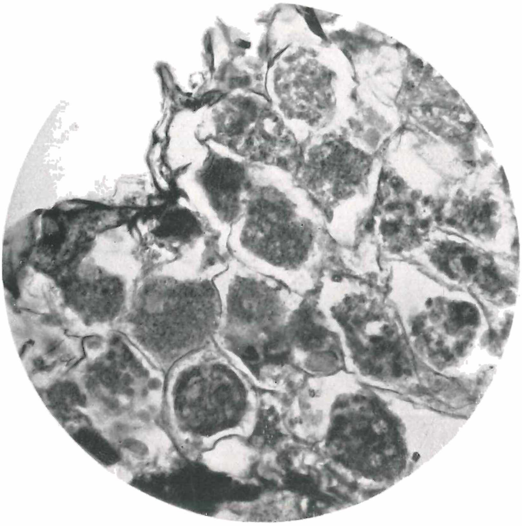

Fig. 20

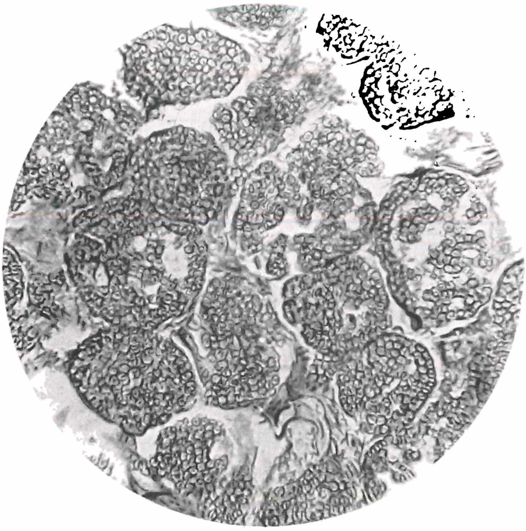

Fig. 21

Spongospora subterranea (con).

Ivimey-Cook. photo.

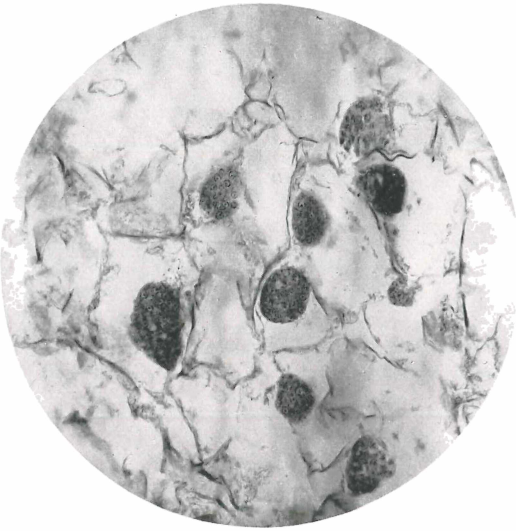

Fig. 22

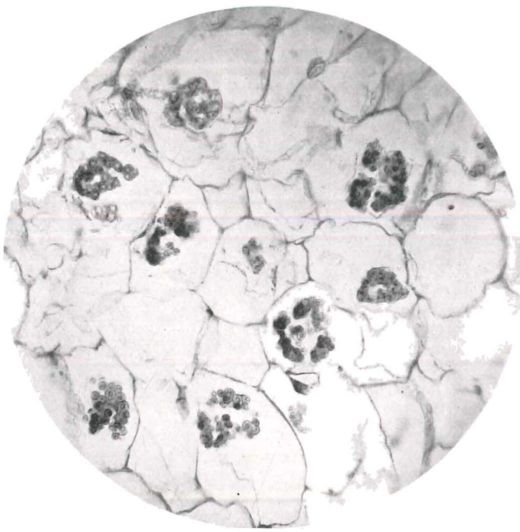

Fig. 23

Spongospora Campanulae.

STAV FISCHER IN JENA

Fig. 24

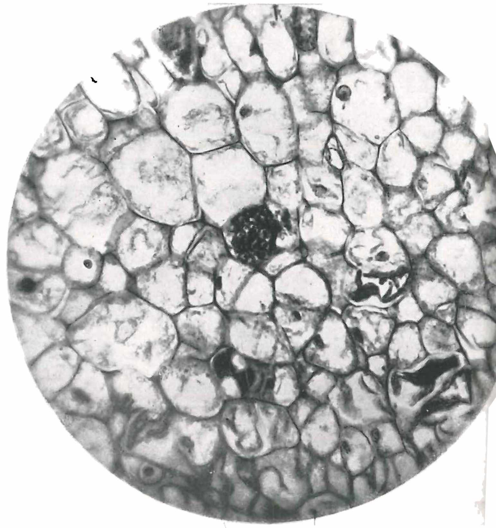

Fig. 25

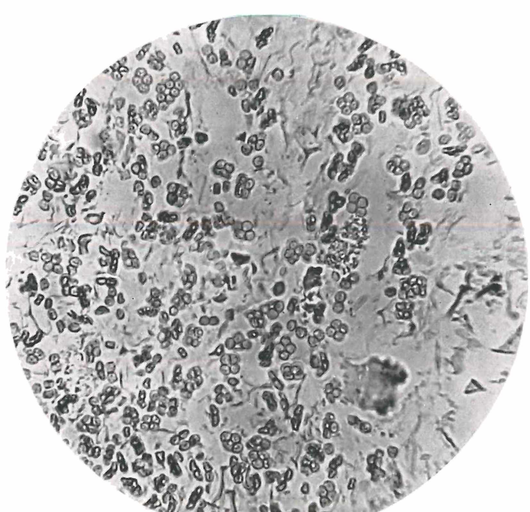

Fig. 26

Tetramyxa parasitica.

Ivimey-Cook. photo.

Fig. 27

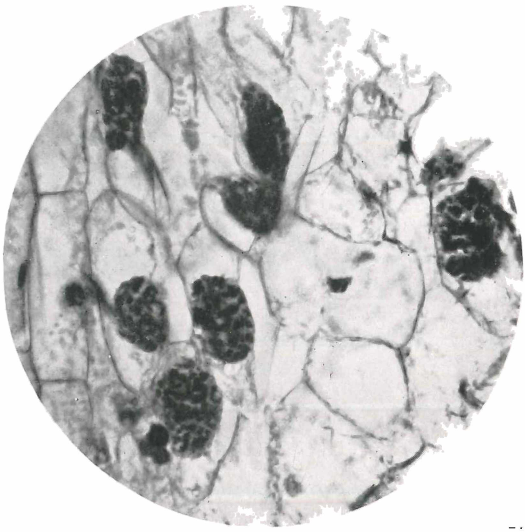

Fig. 28

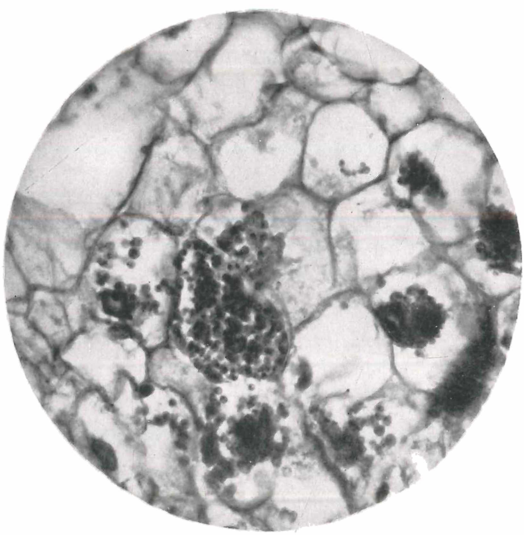

Fig. 29

Tetramyxa Triglochinis.

VON GUSTAV FISCHER IN JENA.

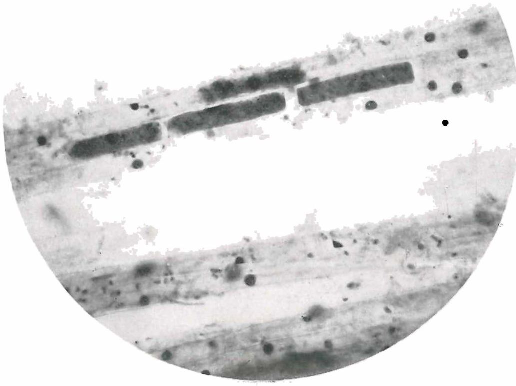

Fig. 30

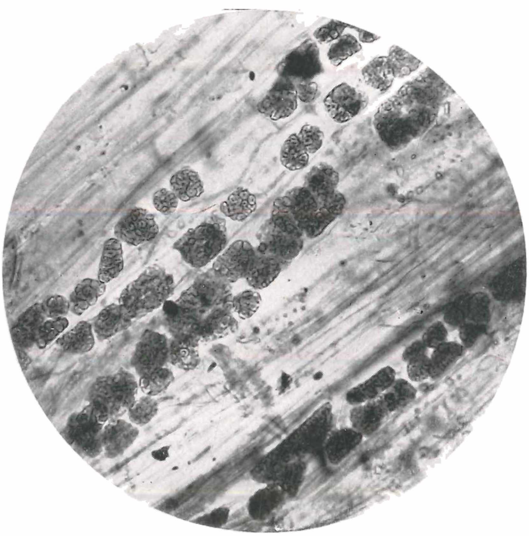

Fig. 31

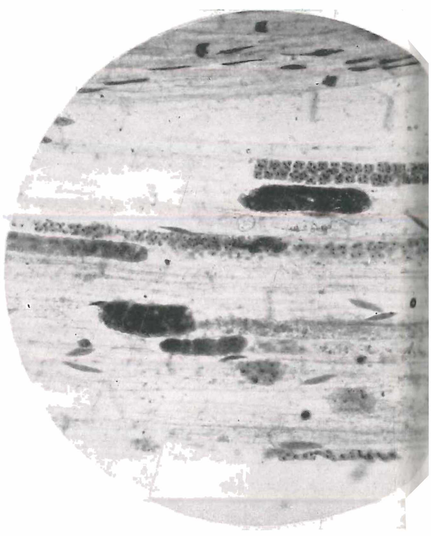

Fig. 32

Ligniera Junci.

Ivimey-Cook. photo.

Fig. 33

Fig. 34

Ligniera verrucosa.

VON GUSTAV FISCHER IN JENA.