Recent Researches on the Parasitism of Fungi¹.

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INTRODUCTORY.

THE definition of 'recent' must always be relative, and in the present connexion it refers to very late times indeed: times not only within the period of the lives of all of us, but in the recollection of most of us. For it should not be forgotten that we have not yet reached the jubilee of the germ-theory of disease, or that of modern pathology and mycology.

Even if we take as our starting-point the period of Cohn's classical work (48) on *Empusa Muscae*, 1855, and of A. Braun's monograph (35) on *Chytridium*, 1855; of De Bary's *Untersuchungen ü. d. Brandpilze* (4), 1853, and of Tulasne's splendid *Mémoires sur les Ustilaginées comp. aux Urédinées* (184), 1847 and 1853—a period rich in mycological investigations—we are still only just at the jubilee of the foundation of the modern anatomical school of mycology.

It was not until De Bary's supreme classic, *Recherches sur le développement de quelques champignons parasites* (5), in 1863, followed by his *Morphologie u. Physiologie d. Pilze, &c.* (7), in 1866, that the foundation of the parasitism of Fungi, as now understood, was established, so that I am well within the limits of historical truth in insisting on the fact that we have not yet arrived at the jubilee of the demonstration of parasitism and infection on a scientific basis.

As regards bacteriology, events are even more recent, for I think I am right in dating the whole of the modern germ-theory of disease from 1876, the date of Cohn's publication of Koch's paper on Anthrax (99), though, as we shall see, the way had been paved here also by the indefatigable labours of earlier botanical investigators.

But these were merely the foundations. No consistent doctrine of the pathology of plants, a branch of science which has now grown to enormous

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dimensions, with libraries and laboratories of its own, was possible until they were securely laid, as the following historical sketch will show.

MYCOLOGY.

Prior to the publication, in 1857, of Berkeley's Introduction to Cryptogamic Botany (28), which we may regard as the last important pre-Darwinian work on Fungi, comparatively little had been done with these plants beyond collection and classification—into the service of which figures of extraordinary merit had been pressed—and what system existed was rapidly degenerating into chaos.

But much of the little that had been done was good. Stimulated by the activity in other departments of microscopy, and by the rapid improvements made in optical appliances, as also by the increasing conviction that the history of development alone could save the situation, numerous observations on the mycelia, sclerotia, sporophores, and fructifications of both lower and higher Fungi were being made by workers of the stamp of Corda (50), Henfrey (82), Berkeley (28), Leveille (104), Bonorden (31), and others, including Sachs, in his early paper on *Crucibulum* (148), in 1855.

Then came the immediate and rapid crisis which culminated in the revolution for mycology, as for other branches of cryptogamic botany, in the publication of De Bary's *Morphologie und Physiologie der Pilze, Flechten und Myxomyceten* (7), in 1866.

Among the pre-Darwinian works it is impossible to overlook Tulasne's papers in the *Annales des Sci. nat.* on *Elaphomyces* (177), 1841, *Scleroderma* (179), *Polysaccum* and *Geaster* (181), 1842, on *Onygena* (182), and on *Nidularia* (183), 1844, *Secotium* (178), 1845, various Lichens (180), in 1851–3, and especially the papers on Ergot (176), and on Uredineae, Ustilagineae (184), and Tremellini (174), in 1847, 1853, and 1854; leading to the Fungi Hypogaei (175), in 1851, and culminating, in 1861–5, in the *Selecta Fungorum Carpologia* (173), works of supreme beauty and undying reputation. With some exceptions, chiefly concerned with the germination of spores, the work of the Tulasnes was still anatomical, however, and it must never be forgotten that the methods of anatomy and comparative morphology alone are not sufficient for the elucidation of the life-history of small organisms. Striking as many of Tulasne's conclusions were, and especially in the later works in which much was done to establish the polymorphism of the Fungi, it can never be overlooked that the mere juxtaposition of two forms of Fungi growing together may readily lead to, and often did lead to error.

The clear recognition of this, and the stricter adherence to the method of continuous observation under the microscope, checked by experimental work, are the characteristics by which the three greatest men in this connexion are to be marked—viz. Cohn, Pringsheim, and especially De Bary.

Indeed Cohn's papers on *Pilobolus* (42), 1852, *Chytridium* (43), 1855-6, *Empusa* (48), 1855, and *Über Pilze als Tierkrankheiten* (47), in 1854; Pringsheim's on *Achlya* (137), in 1857; and De Bary's on *Achlya* (13), 1852, *Aspergillus* (14), 1854, and *Myxomycetes* (11), 1858, in the recently founded *Botanische Zeitung*, and above all, his *Untersuchungen ü. d. Brandpilze* (4), 1853, laid a foundation for an edifice of philosophical science which has been building ever since, and becoming statelier and statelier as it grows.

Darwin's *Origin of Species* (54), which appeared in 1859, of course deals in no way especially with Fungi, but we must note that it gave impetus in a marked degree to such work as I have just referred to, because in no branch of investigation had the problems of evolution and of species come more prominently into the foreground; and the fullest acceptance of the developmental method and of the theory of evolution was already evident in De Bary's *Morphologie und Physiologie, &c.* (10), which came out in 1866, i. e. seven years after the *Origin of Species*.

In this classical work De Bary not only brought together the results of his discoveries on the germination of spores and the proofs of direct infection by means of germ tubes in *Peronosporae*, *Uredineae*, &c. (first given (5) in the *Ann. des Sc. Nat.*, 1863), but he also generalized on the real significance of parasites on and in plants and insects, &c., and rendered clear the distinction between saprophytes and parasites.

De Bary also brought together the then recently discovered facts concerning sexual reproduction in the Fungi; and although some of his conclusions have not withstood the test of time, no investigator can afford to overlook the importance of his ideas.

Of equal, or even greater, importance to the development of the subject was his chapter on so-called pleomorphy and alternation of generations in Fungi. Tulasne had (176), in 1851, called attention to the fact (anticipated to some extent by Corda (51)) that one and the same species of Fungus may produce a succession of two or more totally different kinds of spores and of spore-bearing apparatus; and had thus wiped out at one blow, as it were, a number of genera of Fungi which were nothing more than descriptions of a Fungus in one particular stage of its development, which same Fungus in another stage (when bearing one of its other kinds of spore) had hitherto been described as belonging to some other genus. But Tulasne's proofs, as was usual with him, depended chiefly on observation of the contiguity of forms. De Bary, however, proved by direct sowing of the Fungus, and observation of its development, that a particular spore produced a mycelium which then bore the second form of spore; and thus showed how to criticize the numerous reckless statements of careless observers which were rampant then and soon afterwards.

But the most striking of all De Bary's numerous striking discoveries was his proof of heteroecism in *Puccinia graminis*, first recorded in his paper

'Neue Untersuchungen über die Uredineen,' &c. (9), in the Ber. d. Berl. Akad., 1865, and referred to in the present book in a modest paragraph on p. 221.

The germ of yet another discovery, destined like the last-named to have extensive consequences, first saw the light on p. 291 of this remarkable book, namely, the view that Lichens are not autonomous plants, but consist of a Fungus and an Alga associated in a peculiar way and living a life in common. It is true that this idea was only generalized, so as to include all Lichens, two years later, in 1868, by Schwendener (160), and did not emerge triumphantly from the storm of controversy which it evoked until considerably later, after Bornet (32), Famintzin and Baranetzki (68), 1867 and 1868, Treub (171), 1873, and Stahl (166), 1877, and others had isolated and cultivated the gonidia, and synthetically reproduced a Lichen by allowing the Alga and Fungus to come together; and after De Bary in 1879 had himself definitely launched the doctrine of symbiosis (17), and strengthened his argument by numerous other cases.

Enough has now been said to show you how firmly established are the claims of De Bary's classical book to fame, and I pass to a short review of some of the chief fruits of his inspiration.

A rapid development of the new mycology, founded on the rigid application of the study of development of Fungi, at once followed. De Bary himself, and his collaborator Woronin, produced a rich harvest of discoveries published in their *Beiträge zur Morphologie und Physiologie der Pilze* (18), begun in 1864; and in 1884 we had from the hands of the master the *Comparative Morphologie und Biologie der Pilze*, &c. (67), in which he developed his ideas on the great series of Ascomycetes and their allies, on the one hand, and of the Basidiomycetes and certain smaller groups on the other. These were based on his comprehensive account of *Pythium* and the Peronosporae in the *Beiträge* (18) for 1881, and in the *Botanische Zeitung* (21) of the same year, where he established the doctrine of gradual inception and accomplishment of apogamy—the abandonment of the sexual process—in the group. The researches of Pringsheim on *Achlya* (138), 1882; of Van Tieghem (167), Bainier (1), and Le Monnier, in 1873–5 and 1883; and of Nowakowski (122), and Schröter on Chytridiaceae (159), 1876–8, and others also furnished materials for a comprehensive survey of the Phycomycetes as a whole, and from this date onwards the definite establishment of this alliance of Fungi was assured.

In the Ascomycetes proper, De Bary's celebrated contention for sexuality was argued at length, on data derived from his own work (6) on *Eurotium* and *Erysiphe*, &c., in 1870, and from numerous papers by his pupils and others, among which those of Van Tieghem (169), 1875–7, of Kihlmann on *Pyronema* (89), 1883, and of Janczewski on *Ascobolus* (88), 1871, are important. The extraordinary pleomorphism of the group is also set forth in considerable detail.

The Uredineae, a special subject of De Bary's, come in for exhaustive treatment; his further researches on Witches' Brooms (15), 1867, and *Aecidium abietinum* (12), 1879, as well as investigations by Schröter (154), 1869-75, Wolff on *Aecidium* (*Peridermium*) *Pini* (203), 1876, and others, having yielded several other cases of heteroecism as well as materials for more definite lines of classification.

Then follows an excellent discussion of that difficult and enormous group, the Basidiomycetes, the materials for which were still chiefly anatomical. Although Hesse (83) had succeeded in germinating the spores of *Cyathus* in 1876, and Eidam (59) those of other Nidularieae in the same year, and Woronin (207) had traced the whole life history of *Exobasidium* in 1867, and although a considerable amount of developmental work had been done by Brefeld (36) on *Coprinus* in 1879, and on *Agaricus melleus* (78) by Hartig in 1874, nevertheless the materials for full treatment were scanty; and De Bary's comparison of the teleutospores of the tremelloid Uredineae with the basidiospores of the Tremellineae proper—a comparison which bore abundant fruit later at the hands of Brefeld—as well as his able comparative treatment of the Gastromycetes, are evidence of the keen morphological insight he possessed.

BACTERIOLOGY.

Ehrenberg (58) in 1838 described a considerable number of minute motile organisms which he regarded as animalcules and called *Vibrionia*, some of which had been observed as long ago as 1683 by Leeuwenhoek (103), and again by Müller (114), who classified them in 1786 under the names *Vibrio*, *Spirillum*, and *Bacillus*. Further attention was devoted to these apparently unimportant, though interesting living particles by Dujardin (57) in 1841, and by Perty (127) in 1852; and it was about this period that the attention of microscopists was first attracted to the organisms in drinking water as possibly having something to do with an epidemic of cholera; indeed, the suspicion gained ground that the micro-organisms of sewage-contamination, &c., were of vital importance from the sanitary point of view. Hassal (80), in 1850, gave an account of these organisms in London water, and in 1852 and 1866 Cohn (42) made a very thorough and, for the period, wonderfully exhaustive investigation of certain of these organisms, thus starting a subject which soon grew into a special study.

Meanwhile, Pasteur (124) had published the results of his investigations on lactic, butyric, and other fermentations; and in 1866, as we have seen, De Bary's classical *Morphologie und Physiologie der Pilze* (10) appeared, in which he was able to summarize what was then known of the ferment and putrefactive organisms, as well as his own discoveries on the parasitism of Fungi, in which he had definitely demonstrated the fact of infection

by means of spores. We thus see that the period was ripening for great things, though little did the investigators of those days foresee what startling events were ahead of them.

In 1870-6 Cohn (44) brought forward that splendid series of papers which will always establish his fame as the founder of bacteriology. Not only did he describe with marvellous accuracy, considering the technique of his day, a considerable number of Bacteria; but he made observations on their movements, spore-formation, cell-contents and life-history, which put them at once on a definite footing as organisms to be classified and dealt with as were other plants, conclusions by no means so obvious then as now. Not only did Cohn establish the plant-nature of Bacteria, however, but he gave (45), in 1875, a scheme of classification of the various genera which has had to be reckoned with ever since, although the numbers of species or forms now known vastly outnumber the score or so known to Cohn in 1875; as may be seen by comparing Winter's list (139) of sixty-nine species in 1884 with Migula's estimate (111) of nearly 1,000 in 1896. Moreover, the definitions and characters of genera and species have undergone great changes, as is readily seen on comparing the principal schemes of classification proposed by successive authorities, e.g. Winter (139), 1884, Van Tieghem (168), 1884, Zopf (209) in 1885, Flügge (73), De Bary (19), and Hueppe (86) in 1886, De Toni and Trevisan (170) in 1889, Fischer (70) in 1897, and Migula (111) in 1896, each of whom has attempted to include the general results of the various and rapidly following discoveries concerning the general morphology, pigments, cilia, spore-formation and germination, mode of growth and division, and putrefactive, pathogenic, and other physiological properties of these organisms.

In 1876 Cohn was enabled to introduce to a startled and incredulous world a practical result of the patient and faithful study of development introduced so successfully by De Bary, Pringsheim, and himself, which, taken together with De Bary's proof of the infection of plants by the germ-tubes of parasitic Fungi in 1863, may be looked upon as the foundation of the parasitic or germ-theory of disease. This was Robert Koch's paper on *Die Aetiologie der Milzbrandkrankheit* (99), in which he gave the principal phases of the life-history of *Bacillus anthracis* inside and outside the animal body, and thus started that important series of researches which, together with Pasteur's work and the labours of numerous pupils, have brought such maladies as anthrax, tetanus, diphtheria, tubercle, and several other infectious or contagious diseases out of the region of mystery into the clear light of science.

It is of course beyond the scope of this address to enter into the numerous collateral branches of successful research to which these results gave the initial impulse; but I may remind you of the important position in any history of the science of the last thirty years which such subjects as

antisepsis, the theory of toxins and vaccination, and other outcomes of these fundamental researches of Cohn and De Bary—to which should be added those of Lister and Pasteur—must always occupy ; and we shall see that these are by no means the only directions in which exact botanical researches have effected far-reaching results on the well-being of mankind.

It is more germane to my immediate subject to refer to another great question which the work of Cohn, De Bary, and Pasteur, brought to a series of tests which finally rid the world of a bugbear.

The idea of spontaneous generation, although it had lost prop after prop, as the conditions of development of the more minute organisms were carefully and conscientiously examined, had for some time apparently secured a stronghold among the Bacteria, from which it seemed impossible to dislodge it.

Cohn's work (49) on the Hay Bacillus, in 1876, during the course of which he observed the formation of the endospores, brought forward very clearly the fact of the resistance of spores to extremes of temperature, and his experiments, together with those of Pasteur on the organisms of the atmosphere (125), 1862, and those of Tyndal (186), 1876, on discontinuous sterilization, laid the spectre of abiogenesis, which had repeatedly arisen at intervals since the time of Van Helmont (81), 1745, and Needham (119), and had recently been revived to great activity by Bastian (25) ; and we should observe that Cohn did not merely devise experiments which showed that a something or other got into a putrescible liquid and fermented it or not according to circumstances, but he showed what that something was—the spore of the Bacillus—and followed its development to complete proof of the relation it bore to the phenomenon.

Yet another question of general importance arose in connexion with Bacteria. Several observers had laid stress on the fact that forms of definite shape, to which generic and specific names had been given by Cohn and others, altered their sizes and shapes during development, and assumed morphological characters which had been used to define other genera and species. Billroth (29), 1874, Nägeli (116), 1887, and Zopf (208), 1882, carried their views so far as to deny, more or less categorically, any constancy of form whatever among these organisms, or even to assert that all the forms were derived from one or a few only. It seems strange to us at this distance of time that so much research should have been necessary to prove that the so-called pleomorphism of the Bacteria was merely due to the species in question having been described and named by different observers who saw them in different stages of development. Exactly similar conditions of affairs would arise if an Oak seedling was named by a man who knew not the tree, and the latter by another who did not know it was developed from the former.

PLANT-PATHOLOGY.

Our present extensive knowledge of the pathology of plants has been developed chiefly from the study of two branches of botany, viz. the physiology of nutrition and the parasitism of the Fungi, and dates from that active period of research at the zenith of which appeared Kühn's *Die Krankheiten der Kulturgewächse* (100), 1858, and De Bary's *Morphologie u. Physiologie der Pilze, &c.* (10), 1866, on the one hand, and Sachs's *Experimental Physiology* (149), 1865, on the other.

True, general treatises and papers on the diseases of plants had been written before these dates, of which Berkeley's papers on *Vegetable Pathology* (27), in 1854, and the works of Unger (187), 1833, Wiegmann (200), 1839, Meyen (110), 1841, and Ratzeburg (140), 1839 and 1866, may be especially mentioned; nor would full justice be done to the subject without reference to numerous publications on agriculture and forestry which appeared before 1866. Most of these earlier efforts suffered from two prominent deficiencies, viz. a lack of understanding of the meaning and significance of parasitism, and of comprehension of the fact that pathology is abnormal physiology. De Bary first rendered clear the former, and Sachs was the pioneer who cleared the way to the latter.

During the period intervening between then and now, a considerable number of important treatises have appeared, of which the following may be deemed to have exerted the greatest influence on what is now a very special branch of knowledge:—

Hartig, R., *Wichtige Krankheiten d. Waldbäume* (78), 1874; *Die Zersetzungserscheinungen d. Hölzer* (79), 1878; Frank, *Krankheiten d. Pflanzen* (74), 1882 (and 2nd ed. 1894-6); Hartig, R., *Lehrbuch d. Baumkrankheiten* (77), 1882 (2nd ed. 1889); Sorauer, *Handbuch d. Pflanzenkrankheiten* (164) (2nd ed. 1886); Kirchner, *Die Krankheiten, &c., unserer landwirtschaftlichen Kulturpflanzen* (90), 1890; Prillieux, *Maladies d. plantes agricoles, &c.* (136), 1895; and Tubeuf, *Pflanzenkrankheiten* (172), 1894.

TERMINOLOGY.

Perhaps the most striking summary of the effects of the half-century of work glanced at above is afforded by the number of new terms, or of terms with new connotations, which have been introduced into Botany. Here I have only time to advert to a few, but the following brief list will serve to remind you of a whole dictionary of names of new ideas. Antiseptic. Biologic forms. Toxins and anti-toxins. Form-species. Heteroecism. Infection-tube. Infection. Separation-cultures. Immunity. Spraying. Germ-tube. Adaptive parasites. Specialized parasitism. Bridging species. Pure cultures. Susceptibility. Area of infection.

Wound-parasites. Sub-cultures. Facultative and obligate parasitism. Saprophyte. Incubation-period. Symbiosis. Stomatal infection. Abiogenesis. Cuticular infection. Fermentation. Predisposition. Enzyme. Capacity of infection. Prototrophic, metatrophic, and autotrophic. Haustoria. Appressorium. Pleomorphism. Inoculation. Chemotaxis. Positive and negative chemotropism. Infection vesicle. Adaptability. Intra- and inter-cellular mycelium. Mycoplasma. Pleophagism. Mycorrhiza. Endo- and exo-trophic. Lipoxeny.

UREDINEAE.

It is now time to pay some regard to the practical limits of my subject, imposed alike by the time at command, and by the patience of my hearers. It would be quite impossible in this address to cover the whole of the ground implied in the parasitism of the Fungi, and I therefore propose to deal more especially with the group in which the most important victories in our struggles for new knowledge of parasitism have been won. This group is the Uredineae, a group which has become especially interesting, not only on account of the great tax its ravages have imposed on our corn and other cereal crops, but because it is the focus of the classic work done by De Bary, referred to above, and of the important discoveries since made, matters which I propose to deal with below.

HETEROECISM.

Almost simultaneously with De Bary's classical researches (9) on *Puccinia graminis*, *P.* '*Rubigo-vera*,' and *P.* '*coronata*,' in 1864-5, where he showed that the latter is heteroecious on *Rhamnus*, as is the former on *Berberis*, Oersted (123) proved that the so-called *Roestelia* on Pomaceae is merely the aecidium-form of the *Gymnosporangia* of Junipers.

Thereupon followed a period of busy seeking after alternate hosts, with such success that by 1870 as many as seven, and by 1880 fourteen well-established cases had been accepted, chiefly the results of investigations by Magnus (106), 1874, Schröter (156), 1875, Wolff (205), 1874 and 1877, Rostrup (143), 1874, Winter (202), 1874-5, Nielsen (121), 1877, Reichardt (141), 1877, and De Bary (9): of these the most interesting was probably Wolff's demonstration that *Peridermium Pini* was merely the aecidium of *Coleosporium Senecionis*.

By 1890 the number of cases of heteroecism had amounted to fifty, of which Hartig's (78) work on *Calyptospora* deserves to be especially mentioned: you will remember that the remarkable *Calyptospora Goeppertianum* on *Vaccinium* was here shown to be the puccinia-form of *Aecidium columbare* of the Silver Fir.

The number of demonstrated cases of heteroecism now known is about

150, of which the long and hitherto vain search for the alternate form and host of *Aecidium Elatinum*, the Fungus of the Witches' Broom of the Silver Fir, and which Fischer (69), 1902, has shown to be *Melampsorella Caryophyllacearum*, is surely the most interesting.

But another interesting aspect of this fascinating theme was the discovery that heteroecism is not confined to the Uredineae, for Nawaschin and Woronin (117), 1896, have shown that *Sclerotinia heteroica*, an Ascomycete, alternates between *Ledum* and *Vaccinium*.

Equally interesting is the result that several animal parasites, especially certain Vermes, Arthropoda, and Protozoa, are heteroecious on two or even three hosts. An interesting example is that of the insects producing Galls on the Spruce and Larch; but as Mr. Burdon, who has for some time been working at this subject in our laboratory, will give you an account of these phenomena, I pass them by with this reference.

CYCLE OF LIFE-HISTORY, AND CLASSIFICATION.

Most species of *Uromyces*, *Puccinia*, *Melampsora*, *Pucciniastrum*, &c., form teleutospores which germinate only after resting through the winter, and are heteroecious; but there are many cases—e. g. *Endophyllum*, *Puccinia Asparagi*, *P. malvacearum*, *Uromyces appendiculatus*, &c.—where these spores germinate during the summer or autumn of their development and are autoecious.

Moreover, *Endophyllum* and others only form teleutospores, and have a perennial mycelium. A perennial mycelium also occurs in *Gymnosporangium* and others.

In the cases of *Chrysomyxa Rhododendri* and *C. Ledi*, again, we find that the mycelium remains alive in the leaves throughout the winter, and develops teleutospores in the spring, and these germinate forthwith.

In *Cronartium* and *Coleosporium*, on the other hand, it is the aecidial mycelium which is thus perennial; while in *Melampsorella* both the teleutospore- and the aecidium-mycelia are perennial.

An important step forward, after the discovery of heteroecism, was made by Schröter in 1879 (155), in proposing as a basis of classification within the genera *Puccinia*, *Uromyces*, &c., the sequence of spores and their behaviour. Schröter suggested that the various groups should be put into sections according to the existence of aecidia or not, according as they were heteroecious or autoecious, and according to the behaviour of the teleutospores, &c.

Taking, for example, *Puccinia* as the largest and best worked genus, Schröter denominates the aecidial-form I; the uredo-form II; and the teleutospore-form III; and groups as follows:—

Eupuccinia, I, II, III, all known.

Pucciniopsis, I, III known, but no uredo.

Brachypuccinia, spermogonium, II, III only known, but no aecidium.

Hemipuccinia, II, III only known ; no aecidium or spermogonium.

Micropuccinia, III only, germinating *after* the winter rest.

Leptopuccinia, III only, but germinating at once.

In like manner the genus *Uromyces* falls into *Eu-uromyces*, *Uromycopsis*, *Brachyuromyces*, &c., and so on with the other forms in so far as they form aecidia or not.

Under each we then have subdivisions according as they are autoecious or heteroecious ; and, further, account may be taken of the spring or the autumn germination of the teleutospores, and of perennial mycelia, &c.

The biological groupings are of course provisional, since at any time we may find the aecidium of a supposed hemi-form—as has recently occurred with *Melampsorella Caryophyllacearum* (see p. 10). As another example of like kind I may mention my proof in 1881 of the existence of teleutospores in *Hemileia*, the Fungus of the Coffee leaf-disease.

There can be no doubt that Schröter's ideas, extended by Dietel, Klebahn, and Brefeld, saved the situation, which was rapidly degenerating into chaos.

SEXUALITY.

It is impossible for me to go into the alleged sexuality of the Uredineae, or into the further details of classification based on spore-formation, &c. But reference ought to be made to Mr. Blackman's (33) summary of the matter, and his own interesting and important histological work, 1904 ; however, as he will himself give you his results, I may here pass over the matter with the mere expression of opinion that Sapin-Trouffy and Dangeard have not established a case sufficiently strong to upset Brefeld's contention that the Uredineae like the Basidiomycetes have no recognized sexual process ; whether Blackman has succeeded in doing so is matter for further investigation, and there can be no question of the importance of his results.

SPORE-DISTRIBUTION.

It is astounding how little we actually know of the distribution of the spores of the Uredineae. I refer more particularly to the modes of distribution, and the number of spores conveyed ; and to what distances they may be carried and still remain alive.

I showed clearly enough in 1881 (192) that the uredospores of *Hemileia* are carried by wind, and can be caught on slides smeared with glycerine and exposed in the air ; and the fact that wind is the principal agent of dispersal of such spores cannot be doubted.

That such spores may retain their germinating power for from sixty-

one to ninety-four days at least, has also been shown by Miss Gibson and myself in the case of the Chrysanthemum Rust and of *Puccinia dispersa*.

Klebahn also points out that insects must carry many such spores. The only contribution I can offer here is the fact that flies may have spores attached to their feet, and that a small dipterous larva (*Diplosis*) commonly occurs in large numbers feeding on the uredospores, and itself dusted with them. I found these larvae in abundance on Coffee in Ceylon in 1880-1, yellow with uredospores of *Hemileia*, and have since observed them very commonly on Bromes, and similarly coloured with the uredospores of *Puccinia dispersa*.

Mr. Salmon has shown the same to be true of Erysipheae, the spores of which are eaten with avidity by a *Diplosis* larva, possibly identical with the above, which he has reared and examined in this laboratory.

But there can be little doubt that other insects co-operate in the carrying of spores—e. g. *Aphides*. I commend the subject to any one who will undertake what should be an interesting and definite subject for research.

THE GERMINATION OF UREDOSPORES.

As is now well known uredospores and aecidiospores usually germinate easily in water; but it is a common experience that, of those sown, the percentage of spores which germinate freely varies. In some cases, moreover, very few, or even none at all, will be found to have germinated: and Eriksson refers to these phenomena as 'capricious.'

Now there can be little doubt that such a term only implies that some condition or conditions have not been realized in our experiments: at any rate, we have no warrant for supposing that any spore is not amenable to changes of conditions. Indeed we have now gone some way towards proving this.

I often find, as also did Freeman, that thorough drying—such as would result from passage through the air on a high wind—facilitates germination; and Eriksson showed that chilling to the point of freezing—another way of drying out superfluous water—quickens the germination of such uredospores.

My results also point to the necessity for perfect ripeness of the spores, in order that they may germinate freely: and no doubt water is expelled during maturation.

Klebahn found that spores which germinate badly—as measured by the percentage of germinating spores in those sown, e. g., in a watch glass—may nevertheless infect readily, and Freeman showed something of the same kind.

Uredospores do not germinate freely if plunged under water; and Evans, working in my laboratory, found that it is often better to have the surface of the leaves merely damp, not thoroughly wet, so that Klebahn

is probably right in saying that germination and infection occur better in dew and mist, alternating with sunshine, than in rain—apart from the fact that spores may be washed off during showers.

But I have evidence to support the generally accepted view that external conditions of other kinds affect the germination of uredospores, as they are known to do that of other spores.

That the temperature is an important factor must be conceded ; but it is surprising how little has been done in this connexion as regards Uredineae. I found (190, p. 269) the optimum for *Puccinia dispersa* to be near 20° C. ; the minimum being below 10°–12° C. ; and the maximum about 27° C. These uredospores failed to germinate at 30° C., and were killed at 65°–70° C. ; though their age and ripeness affect the matter.

As regards age, De Bary found that the uredospores of *P. graminis* lost their capacity for germination in from one to two months.

Klebahn (98, p. 26) was able to infect with spores of *Peridermium Pini* after keeping them five weeks ; and with spores of *P. Strobi* after keeping twenty days.

I found the uredospores of *P. dispersa* germinated after being kept dry for sixty-one days, and the experiments were only closed then for lack of material ; while Miss Gibson, working in my laboratory, kept aecidiospores of *Phragmidium* for fifty-four days, and the uredospores of the Chrysanthemum Rust for ninety-four days, when they still germinated. Again the work had to be stopped, and we do not know how much longer they would have continued to live.

Jacky, also, found the uredospores of the Chrysanthemum Rust alive after keeping them from December 1 to February 5, in gauze bags in the open (87).

I can also give you a few other data, bearing out the same point. Barclay (2, p. 234) gives as the limits of germination-capacity for various species, from two to eight months ; and Bolley (30) says that *P. 'Rubigovera'* infected after thirty days' exposure to air and sunshine.

Even in cases where the teleutospores do not germinate until the following spring, it is clear that facts such as the above will have to be reckoned with before any one can deny the possibility of a uredo being carried safely through the winter period.

Further research—and the subject is a good one—will have to decide how far the climate, shelter, lurking in crannies or concealed in dry tufts of herbage, and so forth affect the matter. It is true that perennial mycelia have been sought for in vain in many of the forms here concerned ; nevertheless Magnus states that *P. Caricis* passes the winter in the uredo-stage, and the same is affirmed of others—e.g. by Dietel and Schröter of *Uromyces Funcki* and *Puccinia Luzulae*, and by Barclay of *P. coronata*, the uredo of which he found throughout the winter in sheltered places.

Lagerheim (102) found the uredo of *P. Poarum* just after the melting of the snow about it; and Dietel (56) describes two kinds of uredospores in *P. vexans*, the thicker walled of which he regards as resisting the winter.

I myself found germinable uredospores of *P. dispersa* on Bromes during every month throughout the year 1901-2, even in February and March, the least favourable of times.

Plowright in 1882 also found uredospores on *Agropyrum repens* at the end of December and in March, and says that those of *P. 'Rubigo-vera'* can be got all the year round.

Hitchcock and Carleton (84) found uredo on Wheat all through January, February, and March, and Carleton says that *P. 'Rubigo-vera' Tritici* lives all the year round in the uredo-state as we pass from the Southern to the Northern States; while Bolley confirms this, and asserts, further, that even in the Northern States he finds the germination-capacity preserved through the winter.

Even Eriksson (62, pp. 153-4) admits Nielsen's statement that uredo withstands the winter on green leaves; and other cases given by Kuhn (110), Blomeyer (34), Rostrup (142), McAlpine and Cobb (40), go to swell the evidence that we cannot afford to overlook such facts as the above in discussing the question of the period of infection, or of the limits of germination-capacity of these spores.

SPECIALIZED PARASITISM.

Before proceeding to consider the details of infection and consequent phenomena, it is necessary to break the thread of our story, as it were, in order to render clear a subject which becomes more and more involved in the cycle of phenomena yet to be described. After the period of research in which investigators had been concerned chiefly with the hunt after new cases of heteroecism, and with the unravelling of the species of Uredineae from the threatening chaos to which their rapidly increasing numbers was leading, the next step of fundamental importance was the discovery of specialized parasitism.

Before going into this question I may remind you that the matter has a history behind it. The older observers, e. g. Persoon, of course named each Fungus on a different host as a distinct species, or even genus, as the words *Aecidium*, *Peridermium*, *Roestelia*; *Puccinia*, *Coleosporium*, *Gymnosporangium*; *Uredo*, *Uromyces*, &c., sufficiently attest.

Then came the controversy regarding polymorphism, and the Tulasnes and De Bary especially did yeoman's service in proving that even heteroecious forms passed through such stages as *Uredo*, *Puccinia*, and *Aecidium*. The next stage was the proof that species like *Puccinia graminis* and *Peridermium Pini*, in the old sense, were really composite forms; and that the aecidia of the different cereal forms were developed on plants other

than the Barberry, and the uredo-stage of the *Peridermium* on hosts other than *Senecio*. Here, again, the investigations passed through several stages of discovery and of controversy, but the upshot was that in the first place morphologically different Fungi growing on grasses were extracted from the collective species hitherto named *P. graminis*—e.g. De Candolle's (38) *Uredo Rubigo-vera*, 1815, and Schmidt's (152) *U. glumarum*, 1816, and Corda's (50) *P. coronata*, 1837, began to emerge as definitely morphological species, especially after De Bary (9) in 1866 had shown that *Aecidium Asperifolii* belonged to *P. Rubigo-vera* and *Aecidium Rhamni* to *P. coronata*; and similarly, the various forms of *Gymnosporangium* and *Roestelia* were sifted out, in connexion with various species of *Crataegus*, *Pyrus*, &c. Researches along these lines culminated in the demonstration that, quite apart from the morphologically distinguishable species of rust, there are other forms which, although utterly undistinguishable by the microscope, are nevertheless sharply distinct in respect of their parasitism. Eriksson especially has proved by careful and long-continued experiments that, for instance, the *Puccinia graminis* which grows on Wheat does not attack Rye, Barley, Cocksfoot, *Alopecurus*, *Aira*, *Agrostis*, or *Poa*, if its uredospores are sown on these Grasses. Nevertheless *P. graminis* is common on these hosts. Similarly the uredospores from the *P. graminis* growing on Rye and Barley will not directly infect Wheat or Oats, &c.

Now, since there are no morphological distinctions between these forms of *P. graminis* on different hosts, while there are physiological or biological invisible differences, it is clear they must be distinguished. It should be pointed out that De Bary (5), in 1863, had already insisted on the intimate choice of hosts (*choix rigoureux*) of the Rust Fungi for particular cases; and had insisted that the morphological differences between the aecidium-forms of *Chrysomyxa Rhododendri* and *C. Ledi* were so slight that these are 'rather biological than morphological species.'

Schröter, who first called special attention to this matter in 1879 (153, p. 69) in the case of *P. Caricis*, in 1893 (158, p. 31) proposed to term such forms, sister species (*Species sorores*). Rostrup (144, p. 40) in 1894 called them *biologiske Arter*—i.e. biologic species, using practically the same term as Klebahn, who called them *biologische Spezies*, had proposed in 1892 (93, pp. 258 and 332).

Hitchcock and Carleton in 1894 (84) proposed the term *physiological species*.

Eriksson in 1894 (60, p. 292) suggested the term *specialisierte Formen* or *formae speciales* (specialized forms) and has supported his term with much admirable work.

Rostrup in 1896 (145, p. 37) suggested the term biologic races (*biologische Rassen*); while Magnus in 1894 (107, p. 82) proposed *Gewohnheitsrassen* (adapted races) as the preferable term for such forms.

There is one observer who has done excellent service in this connexion, to whom full justice has hardly been done, and the matter appeals to us especially here because he is almost a local man—I refer to Dr. C. B. Plowright of King's Lynn.

Between 1880 and 1900 Dr. Plowright published a large series of papers on the Uredineae, as well as a monograph (129) on the British Uredineae and Ustilagineae, and it is to be noted that this long-sustained and important work (so far as the Uredineae are concerned) was done in the intervals of a busy practice as a medical man.

Not the least of Dr. Plowright's contributions must be reckoned his clear-sighted recognition of a series of forms which are only distinguishable by their biological, and not by their morphological peculiarities. Among others I may mention the *Gymnosporangia*, *Puccinia Phragmitis*, *P. Phalaridis*, and the various forms of *Puccinia* on *Carex* (129–35).

ERIKSSON'S *FORMAE SPECIALES*.

It is to Eriksson, however, that we owe the clearest exposition of the idea of specialized parasitism, since his paper in 1894 (60) on the breaking up of the old species *P. graminis* into at least two species and a number of special forms; as well as his work on the unravelling of the chaos of special forms in the species *P. glumarum*, *P. dispersa*, *P. coronata*, and *P. coronifera*.

The application of Eriksson's results at once led to the establishment of specialized forms for the species of *Puccinia* on *Phalaris*, *Carex*, &c., and those of *Melampsora* on Willows.

In his paper in 1901 (61, p. 101) Eriksson summarizes the results of infection experiments which led him to break up the older *Puccinia graminis*, *P. Rubigo-vera*, &c., into finer 'species' and races. These results may be put shortly as follows:—

SPECIES I. *P. graminis*, Pers., the Black Rust of cereals, is heteroecious on Barberry, and has at least six specialized forms:

F. sp. 1. *Secalis*, on Rye, Barley, *Triticum repens*, and some other Grasses; but not on Wheat or Oats.

F. sp. 2. *Avenae*, on Oats, *Dactylis*, *Alopecurus*, and some other Grasses; but not on Wheat.

F. sp. 3. *Tritici*, on Wheat, but not on the other cereals or Grasses.

F. sp. 4. *Airae*, on *Aira caespitosa* only.

F. sp. 5. *Agrostis*, on *Agrostis* only.

F. sp. 6. *Poae*, on *Poa* only.

SPECIES II. *P. Phlei-pratensis* (Er. and Henn) is the Black Rust of *Phleum pratense* and *Festuca elatior*, and was formerly regarded as identical with *P. graminis*; its aecidium is as yet not known. It was hitherto included under *P. graminis*, but owing to its inability to infect Barberry or Wheat it must be separated.

SPECIES III. *P. glumarum* (Er. and Henn), the Yellow Rust of Wheat, was formerly

included with the next nine species in *P. Rubigo-vera*, DC., but it has no aecidium form as yet known. There are at least five specialized forms of it, as follows :

F. sp. 1. *Tritici*, on Wheat ; but not on Barley, Oats, or Rye.

F. sp. 2. *Secalis*, on Rye, but not on Wheat, Barley, or Oats.

F. sp. 3. *Hordei*, on Barley, but not on the other cereals.

F. sp. 4. *Elymi*, on *Elymus*.

F. sp. 5. *Agropyri*, on Couch Grass.

SPECIES IV. *P. dispersa*, Er. This is the Brown Rust of Rye, and is heteroecious on *Anchusa*, where it produces the *Aecidium asperifolii* of previous authors.

SPECIES V. *P. triticina*, Er., the Brown Rust of Wheat, has no aecidium as yet known, and is not heteroecious on *Anchusa*.

SPECIES VI. *P. bromina*, Er., is the Brown Rust of the Bromes. Its aecidium is as yet unknown. [Since this was written, F. Müller has shown that the aecidium is formed on *Symphytum* and *Pulmonaria*, &c.]

SPECIES VII. *P. Agropyrina*, Er., is confined to *Agropyrum repens*, and has no known aecidium.

SPECIES VIII. *P. holcina*, Er., is confined to *Holcus*, and no aecidium is known.

SPECIES IX. *P. triseti*, Er., occurs only on *Trisetum flavescens*, and has no known aecidium.

SPECIES X. *P. simplex*, Kcke. Er. and Henn, is a dwarf species, hitherto regarded as a variety of *P. Rubigo-vera*, DC., occurring only on Barley and with no known aecidium.

SPECIES XI. *P. coronifera*, Kleb., was previously confused with *P. coronata*, Corda. It is the Crowned Rust of Oats, &c. It is heteroecious on *Rhamnus catharticus* ; but not on *R. Frangula*. There are at least six specialized forms, as follows :

F. sp. 1. *Avenae*, on Oats.

F. sp. 2. *Alopecuri*, on *Alopecurus*.

F. sp. 3. *Festucæ*, on *Festuca elatior*.

F. sp. 4. *Lolii*, on *Lolium perenne*.

F. sp. 5. *Glyceriæ*, on *Poa aquatica*.

F. sp. 6. *Holci*, on *Holcus*.

SPECIES XII. *P. coronata*, Corda, the Crown Rust proper, produces its aecidium on *Rhamnus Frangula*, and has at least five specialized forms, as follows :

F. sp. 1. *Calamagrostis*, on *Calamagrostis arundinacea*, &c.

F. sp. 2. *Phalaridis*, on *Phalaris arundinacea*.

F. sp. 3. *Agrostis*, on *Agrostis stolonifera*.

F. sp. 4. *Agropyri*, on Couch Grass.

F. sp. 5. *Holci*, on *Holcus*.

SPECIES XIII comprises a third species of the *P. coronata* group ; with two forms, as follows (neither has any known aecidium, and they were previously included with the two preceding species under *P. coronata*) :

F. sp. 1. *Epigeii*, on *Calamagrostis Epigeios*.

F. sp. 2. *Melicæ*, on *Melica nutans*.

That we must accept these data as the experimental results of a good investigator is unquestionable ; but there is room for differences of opinion

as to the validity of Eriksson's 'species,' and as to the exact value of his 'form-species.' My own opinion is that no species can be accepted as valid until it is capable of definition in morphological terms; and we shall see that the results of cross-infections have shown that bridging species (of host-plants) seriously affect the question of autonomy regarding the form-species.

Much remains to be done, however, before we can settle these questions, and I would point out that here, again, a definite line of research exists in the inquiry after the as yet undiscovered aecidia, and the testing of form-species on different hosts.

Eriksson, meanwhile, appears to insist on the rigid specialization of these forms, each to its own hosts; and in one case at least the aecidium form discovered for *P. dispersa*, f. sp. *bromina*, bears out his contention, though other results shake his conclusions, as will appear in the sequel.

The researches of the last few years have brought out the fact, soon suspected and looked for, that specialized parasitism is not confined to the Uredineae.

Magnus (107, p. 81) in 1894 pointed out that *Peronospora parasitica* and *Ustilago violacea* show a, so to speak, choice of hosts which points to the same phenomenon; and Rostrup in 1896 (146, p. 116) called attention to several Ascomycetes, e.g. *Dasyscypha Willkommii*, *D. calycina*, *D. abietis*; species of *Sclerotinia*, *Epichloë*, &c.; *Sphaerotheca pannosa*; as well as certain Ustilagineae, &c., as indicating by their behaviour a similar specialization.

In 1902 (120, p. 342) Neger showed, by means of cultures, that specialized parasitism is probably quite common in the Erysipheae, at any rate as regards the conidial form; and the phenomena have been very exhaustively followed out by Salmon (150), who has proved the question up to the hilt, and has shown that the course of events is similar in all respects to what occurs in the Uredineae. Much of this work was done in my laboratory, and I can testify to the accuracy and thoroughness of Salmon's work.

Giesenhagen (76, p. 319) in 1895, and Ludi (105, p. 1) in 1901, have also discovered similar phenomena in Exoasceae and Chytridiaceae; and Beijerinck's (26) results with the bacillus of the leguminous root-nodules point to the same conclusion, as do many other investigations in Bacteriology.

Stäger in 1903 (165) showed the same to be true for *Claviceps*; see also Ed. Fischer (71, p. 53).

On the other hand, *Cystopus*, *Botrytis*, and others appear to be pleophagous so far.

Nor is specialized parasitism confined to plants. Species of *Chermes*, according to the researches of Cholodkowsky (39), and of Burdon—the latter working in my laboratory—are specialized more or less to certain trees; and similar results obtain for the Pine-beetle, Willow Galls, and even the Hessian Fly and, according to recent work, the root Nematodes.

THE BROMES AND THEIR BROWN RUST.

In 1902 I published the results (191 and 199) of my first experiments with the Bromes and their Rust-Fungus, *P. dispersa*, f. sp. *bromina*, and have continued these during the intervening years.

My point of view involved some generalizations based on previous experience—for I may be allowed to say that the Uredineae and their parasitism is an old study of mine.

In the first place, it has always appeared to me that we are too apt to overlook the behaviour of the host in its relation to the Fungus, whereas the physiological condition of the host is always a factor of prime importance.

Secondly, the real meaning of infection can never be thoroughly understood merely from culture-experiments in the open: it will be necessary to examine not only the behaviour of the Fungus in detail, and the reactions of the host-plant to the Fungus, but also the effects of the environment on both.

It was an obvious idea that in order to attack a task of this kind properly, care must be taken that both the Fungus employed and the hosts to be infected by it must be definite as regards species, and pure as regards origin. Consequently, my first object was to work with one species of *Puccinia* only, and to confine the infections to one genus of plants. I chose *Puccinia dispersa*, the Brown Rust of Grasses, and the genus *Bromus*, on which one form of this rust is common, viz. the specialized form, f. sp. *bromina*.

There is still some doubt among authorities as to whether this Fungus, growing on the Bromes, and, as we shall see, very closely specialized in that group, should or should not be accorded specific rank. Eriksson has sharply criticized me for continuing to name it *P. dispersa*, and his contention that it should be regarded as a species (*P. bromina*) is perhaps strengthened by F. Müller's discovery that it is heteroecious on *Symphytum*.

But, while according all due respect to Eriksson's opinion, I maintain that a species must be capable of morphological distinction before it can be accepted as good.

Meanwhile this *Puccinia* (formerly included in *P. striaeformis*, Westend.; *P. straminis*, Fuck; *P. Rubigo-vera*, DC.) was first included in *P. dispersa*, Erikss., and then separated as *P. dispersa*, f. sp. *Bromi*, and, later, separated still further as a species, *P. bromina*, Erikss.; while Klebahn, accepting Müller's name, has it as *P. Symphyti-Bromorum*, F. Müll.

Such are the complexities daily being perpetrated in synonymy; and I hold them to be unnecessary until we discover morphological differences in this form sufficient to distinguish it from *P. dispersa*.

Having selected this Fungus for the work, the next thing was to become so familiar with its characters that it could always be distinguished from other morphologically distinct species.

But on extending my collection of Bromes—I have now obtained and grown every species that could be got from all parts of the world—it soon became evident that nothing short of a revision of that genus would suffice to reduce the chaos inflicted on them by well-meaning authorities and amateurs, and I had carefully to work out each species and variety as occasion demanded. Only those who have acquaintance with the forms of *Bromus erectus*, *B. secalinus* and its allies, and such species as the South American *B. unioides* and the North American *B. ciliatus*, will be able to appreciate the labour here involved; but it was clearly useless to attempt any strict delimitation of the experiments without attempting this.

One of the first general results was the demonstration that uredospores taken from *B. mollis*, of the group *Serrafalcus*, will not infect *B. sterilis* or *B. erectus*, species of the groups *Festucoides* and *Stenobromus*, or do so very rarely; whereas they readily infect *B. secalinus* and its allies of the same group. Again, spores from *B. sterilis* (*Stenobromus*) refused to infect *B. erectus* (*Festucoides*) and *B. mollis* (*Serrafalcus*), but readily infect others of its own group.

In short, the uredo on the species of Brome belonging to any one group are remarkably closely specialized to species of that group; and this was borne out by Freeman, who repeated and extended these experiments.

It was interesting to notice that we both found a few exceptions to the rule, of which more later on.

IMMUNITY AND SUSCEPTIBILITY.

Obviously the results above referred to on specialization of parasitism raise in a new form the old question of immunity and susceptibility, and the problem resolves itself into this:—Why is it that, of two closely allied species, or varieties, both equally exposed to infection, one will prove immune and the other susceptible?

The suggestion that the immunity depended on structure, and that immune varieties would be found to have thicker cell-walls, fewer or smaller stomata, more or longer hairs, waxy cuticles, &c., had been made from several sides, but I believe it was Cobb, in Australia, who first put this question to the test in 1890–3 (41), and he thought that a thicker cuticle, more stomata, and absence of waxy bloom, made for immunity.

Eriksson was unable to confirm this (62, pp. 355–63).

My researches, published in 1902 (190, p. 302), for which I claim greater exactness in measurement, counting, &c., than had hitherto been attempted, showed that the curves of infectibility and of numbers, sizes, &c., of stomata, hairs, and so forth, not only do not correspond, but they show no relations whatever; and clearly led to the conclusion that the matter has nothing to do with anatomy, but depends entirely on physiological reactions of the protoplasm of the Fungus and of the cells of the host.

In other words, infection, and resistance to infection, depend on the power of the Fungus-protoplasm to overcome the resistance of the cells of the host by means of enzymes or toxins; and, reciprocally, on that of the protoplasm of the cells of the host to form anti-bodies which destroy such enzymes or toxins, or to excrete chemotactic substances which repel or attract the Fungus-protoplasm.

The histological examination of the host naturally led to the investigation of the microscopic characters and behaviour of the Fungus in the tissues of the host.

This was done, and the results published in a paper on the Histology of *P. dispersa* (195) in 1903, in which I demonstrated the whole course of normal infection, the development of the haustoria, the behaviour of the nuclei, and the growth of the Fungus in the leaf of the Brome.

ERIKSSON'S HYPOTHESIS.

The necessity for this thorough examination of the host and parasite, and their mutual behaviour one towards the other, had become the more imperative in view of the extraordinary position which had been taken up by Eriksson, than whom no man had earned a better right to speculate, be it said, with regard to epidemics of rust.

Eriksson, it will be remembered, had been driven by the results of experience in the field to conclude that the enormous epidemics of rust which break out so suddenly, at certain seasons, cannot be explained by the incidence of normal infection by wind-blown uredospores.

He therefore framed the hypothesis that the Fungus is able to so combine some of its living protoplasm with the living protoplasm of the host, that a condition of symbiosis is established, both remaining alive and capable of passing from cell to cell of the host-plant.

This symbiotic union Eriksson termed *Mycoplasma*—a word we translate *Mycoplasma*. This mycoplasma was assumed to be capable of remaining dormant in the leaf, or even in the seed into which it had passed, for many weeks or months; and then, under favourable circumstances of the environment, the fungal element—hitherto unrecognizable by any method known to us—would suddenly sort itself out, assume morphological autonomy, and

grow out of the cell into a mycelial form, which in due time extended and developed uredo-patches on the leaf.

The first assertion of this extraordinary hypothesis by Eriksson appears to have been made (63 and 64) in 1897, and the principal grounds on which he based it were, so far as I can discover, the following:—

(1) Certain forms—i. e. cultivated varieties—of Wheat always show rust in a short interval after sowing, e. g. 4–5 weeks, no matter what time of year the seed is put into the ground. But it should be noted that, in Sweden, the rust appears in summer earlier on winter-sown than on spring-sown crops.

(2) The Barberry, which carries the aecidial form of *P. graminis*; the two species of *Rhamnus* which carry the aecidia of *P. coronata* and *P. coronifera* respectively; and the Boragineae which bear the aecidia of *P. dispersa*, are by no means always present in the neighbourhood of these sudden outbreaks of rust, and cannot possibly be credited with the infection. Similar statements have been made by others—e. g. Barclay (3) in 1892 pointed out that *P. graminis* appeared in India at a distance of 300 miles from any Barberry; Cobb (40) in 1891 had assumed that the uredo-form must be perennial in Australia, and so on.

We may safely accept the fact that outbreaks of rust frequently occur at distances so remote from any plant known to carry the aecidial form, that it is almost impossible to believe that spores blown from such plants are responsible.

(3) Dismissing the probability of wind-blown aecidiospores as explaining the outbreaks, Eriksson proceeds to demolish the idea that lurking uredospores, which have passed the winter in the died-down stocks of grasses, may be responsible for the outbreaks.

Here we may note that De Bary in 1865 (20, p. 23) had sought in vain for a perennial mycelium of *P. graminis*, persisting through the winter, in *Agropyrum repens* and *Poa pratensis*; and Eriksson confirmed this in 1896 (62, p. 40), and also failed to find any such wintering uredo on *Dactylis glomerata* or *Agrostis vulgaris*.

On the other hand, Blomeyer in 1876 (34, p. 405); Rostrup in 1884 (147); Plowright in 1882 (132, p. 234); Kühn in 1875 (101, p. 401); Hitchcock and Carleton in 1893 (85, p. 11); and Bolley in 1898 (30, p. 894), specifically demonstrated that the uredospores can live through the winter on Wheat.

(4) But the principal evidence on which Eriksson relies is, perhaps, that obtained by growing Wheat, &c., in glass cases in his experimental fields.

Herewith I append a summary and analysis of these experiments, compiled from Eriksson's account:—

TOTAL EXPERIMENTS.

	Year.	No. of Plants.	Successes.	Failures.
(a)	1892	15	0	15
(b)	1892-3	126 at least	0	126
(c)	1893	35	0	35
(d)	1893 ¹ (<i>tubes</i>)	10	0	10
(e)	1893	90 at least	0	90
(f)	1894-9 ² (<i>tubes</i>)	32 at least	7	25
(g)	1894 ³	14	2	12
(h)	1894	20	0	20
(i)	1895	20	1	19
(j)	1897 ⁴	14	9	5
(k)	1898	15	0	15
Total . .		391	19	372

(a) Oats in cases, summer 1892. To see if they can be cultivated in cases, and what importance may be attached to the presence of spores in soil. Three cases. *One* = 5 seeds Oats covered with *T. repens* + Black Rust. *Two* = 5 seeds in sterile soil. Sowed June 5. No trace of rust to August. Eriksson says all grew too abnormal to develop the mycoplasma germ out. Yet inoculations on Aug. 23 and 24 gave + results in 10-20 days!

i. e. 15 seeds sown and all proved failures.

(b) Autumn Wheat in cases in autumn 1892 and through winter to 1893. Michigan Bronze and Yellow Rust, to which it is susceptible. 14 cases. Questions: (1) Can seed or seedling be contaminated by *Uredo glumarum*? (2) Or by *Pucc. glumarum*? (3) Can disease proceed from diseased seed? (4) Can disinfection (heat dry, or Jensen's hot water) of seed destroy the Fungus?

Case.	Began.	Soil.	Seed.
1	Sept. 12	Not sterilized	9 seeds with <i>Pucc. glumarum</i> .
2	"	Sterilized 5 h.	" "
3	"	Not sterilized	" no teleutospores.
4	"	Sterilized 5 h.	" "
5	"	"	" no teleutospores, and disinfected by Jensen.
6	Sept. 13	"	" with teleutospores and disinfection dry, 4 h. at 40-43° C.
7	"	"	Whole spike with <i>Pucc. glumarum</i> .
8	"	Not sterilized	9 seeds quite free of rust.
9	Sept. 14	Sterilized 5 h.	" "
10	Sept. 15	"	" " but <i>Uredo glumarum</i> added.
11	"	"	" " but added <i>Puccinia</i> .
12	Sept. 16	"	9 seedlings devoid of Fungus, but added uredospores.
13	"	"	9 seedlings and added teleutospores.
14	Sept. 17	"	9 seedlings and no addition.

¹ No rust but abundance of *Erysiphe*!

³ Cases appear to be openly ventilated.

² In midst of badly infected rusted Wheat.

⁴ Aphides in one of the successful cases.

All gave negative results, although in the fourteenth case further infections were made with *teleutospores* on Sept. 22 and 24. On Mar. 29, 1893 = plants still growing, but died soon after. *No rust.*

i. e. at least 126 sown and 126 failures.

(c) Spring Cereals in cases in summer, 1893. Used 7 cases. All began May 15.

Case.	Soil.	Seed.
1	Not sterilized	5 Barley, showing <i>Pucc. glumarum</i> .
2	Sterilized 3 h.	" "
3	Not sterilized	5 Barley, free of Fungus.
4	Sterilized 3 h.	" "
5	Not sterilized	5 Oats, free of Fungus, but added <i>Puccinia</i> .
6	Sterilized 3 h.	" "
7	"	5 Oats, free of Fungus, and nothing added.

Results totally negative to Aug. 9.

i. e. 35 sown and 35 failed.

(d) Autumn Wheat in long tubes in spring of 1893.

Used 10 seedlings, each in a tube, but although they got *Mildew* (*Erysiphe*) they had no rust. N.B. Eriksson points out that there was very little rust anywhere, as it was a poor year for the Fungus!

i. e. 10 seedlings and 10 failures.

(e) Autumn Wheat in ventilated boxes, autumn, 1893. Ten cases used.

Case.	Sown.	Soil.	Seed.
1	Aug. 29	Not sterilized	9 seeds showing <i>Puccinia</i> .
2	"	Sterilized 3 h.	" "
3	"	Not sterilized	9 seeds, free of Fungus.
4	"	Sterilized 3 h.	" "
5	"	"	Whole spike <i>rusted</i> .
6	"	"	9 seeds showing <i>Puccinia</i> and sterilized 3 h. at 48° dry.
7	"	"	9 grains. These were inoculated on Sept. 8 on roots or leaves with <i>uredospores</i> .
8	Sept. 4	"	9 grains, free of Fungus, also inoculated on Sept. 10-11 with <i>teleutospores</i> .
9	"	"	9 grains, Fungus free.
10	"	"	" "

Here, although the cultures in the cases were in every respect excellent, yet none showed rust. In *no case* were positive results obtained. The only remarkable point here is that of case 7, where the after-inoculation with *uredospores* also failed.

i. e. at least 90 sowings and 90 failed.

(f) Autumn Wheat in tubes in 1894 to 1899 and in case in the spring of 1894.

In spring, 1894, put 10 seedlings in tubes:—

In 4 tubes = plants died in 3-4 weeks.

In 2 tubes = cotton carried away by wind.

In 2 tubes = plant died in 3 months.

In 2 tubes = *pustules* showed in about 40 days.

These tubes were in the midst of badly rusted Wheat of the same plot, &c. Another tube, started May 11, showed *pustules* in about 40 days. A large case, covering a tuft, showed *pustules* in 2 months after covering, and soon after rust appeared outside! In 1895 = 5 tubes of Horsford on April 23 and 5 tubes Rye May 20, and in 1896 on May 8 = 5 tubes of the same Wheat.

All gave negative results, and Eriksson says because it was a poor rust year.

But 1897 was a favourable rust year. Here we have 5 tubes on May 5, of which 2 soon died, 3 bore *pustules*.

Yet Eriksson says these cases prove non-infection from outside, because

(1) Where could infective spores come from?

(2) Uredospores could not survive the winter!

(3) Even if they could they would need but 10, not 40-41 days for incubation!

Yet Eriksson admits that *Erysiphe* appeared in such tubes, and, later, that *Aphides* appeared. Does he intend to argue that *these* were carried in the seed?

He argues that the *pustules* were (1) either due to *teleutospores*, which is absurd; or (2) to *mycoplasma*!

The results of (f) may therefore be summarized as follows:—

$$10 + 1 + 15 + 5 = 31 \text{ tubes.}$$

$$1 \text{ case} = 1$$

$$\text{Total } 32$$

i. e. = at least 32 plants were used, of which $2 + 1 + 3 = 6$ tubes and 1 case gave *positive results*, while 25 tubes resulted in failure.

(g) Barley in cases during the summer of 1894.

In each case = 7 seeds sown on May 11 and continued to Aug. 7, i. e. 88 days.

Results = 1 case totally free.

1 case had 2 plants infected.

i. e. of 14 plants 2 yielded positive results.

(h) Autumn Wheat in cases in the autumn of 1894.

There were 4 cases, each with 5 grains.

Case.	Sown.	Soil.	Seed.
1	July 7	Sterilized 3 h.	5 seeds, badly attacked with <i>Puccinia</i> .
2	"	"	5 seeds, free of Fungus.
3	"	"	"
4	Sept. 6-13	"	5 seedlings, infected with teleuto-spores.

No results to Nov. 14.

i. e. 20 seeds, &c., and 20 failures.

(i) Barley, Oats, and Twitch in cases in the summer of 1895. Began May 15 in 4 cases.

Case.	Sown.	Soil.	Seed.
1	May 13–June 1	Sterilized 3 h.	5 seeds Barley, attacked with <i>Puccinia</i> .
2	May 14	„	5 seeds, free of <i>Puccinia</i> .
3	„	„	5 seeds Oat, free of Fungus.
4	May 15	„	5 rhizomes of Twitch, washed and ? free.

On July 4 case 1 showed *one* plant with *pustules*. No others in this or other case.

i. e. 20 seeds and plant with 19 failures and *one success*.

(j) Barley in cases in the summer of 1897.

Three cases used, sterile soil and 5 seeds each.

Case.	Sown.	Results.
1	May 31	1 <i>pustuled</i> in 26 days and others followed till <i>all</i> 5 were <i>pustuled</i> .
2	June 1	No rust at all on any plant.
3	June 3	4 seeds only germinated. <i>Pustules</i> visible on July 25, and next day discovered the presence of <i>Aphis</i> , and <i>aphides</i> rapidly increased till numerous.

This insect was 'traced' *via* a crack and *pustules increased daily*.

Results = 14 plants, of which 9 *rusted* and 5 *failed*.

(k) Spring Wheat and Barley in cases in the summer of 1898. Began May 26 and used 3 cases, with 5 seeds each. On September 6 = all free of rust.

i. e. 15 seedlings and 15 failures.

(1) Experiments in 1896–9. But resulted in no further success.

(5) It was noteworthy that although Eriksson had called attention to certain 'corpuscules spéciaux' (*eigenthümlichen Körperchen*) in the cells of the host, in the neighbourhood of young rust pustules, and had declared that these peculiar bodies were the incipient mycoplasma growing out into the inter-cellular spaces as mycelium, we were anxiously awaiting figures of these bodies for some time. Eriksson's first enunciation of the mycoplasma-hypothesis was in 1897 (63 and 64) be it remembered; but no figures appeared until 1901–2 (65), when the author gave a plate of outline drawings of these peculiar bodies.

Those of us most familiar with the haustoria of the Uredineae were at once reminded of these bodies. I had made a very special study of these haustoria in the case of *Hemileia*, the Fungus of the Ceylon coffee-disease, in 1880–2 (192), and was convinced of the identity of the bodies in *Puccinia dispersa*; but in order that there should be no jumping to conclusion I worked out the histology of that Fungus from spore to spore, and in 1903 placed the matter beyond cavil (195).

Klebahn and others upheld the same view, and indeed the former seems to have suggested the resemblance already. However, the details are now of the less importance since Eriksson (66 and 67) has practically admitted the validity of my proof.

(6) Eriksson relies to a certain extent on the analogy alleged to exist between his mycoplasma and certain cases of intra-cellular parasites, such as Woronin's *Plasmodiophora* (206), Viala and Sauvageau's *Pseudocommis* in Vines, &c. (188) and others, and claims resemblances between them to which I shall have to refer later on.

Taking these six points one by one, I would point out:—

(1) The rusting of winter-sown Wheat at an earlier period in spring than spring-sown Wheat may obviously be due to the former having been longer exposed to the few spores which have survived the winter: it takes time for the year's crop to become epidemic, and we know how easy it is to overlook the first pustules of the season.

Moreover, the undoubted differences of susceptibility and immunity of various races complicate this question: nor can we overlook the weight of the evidence summed up in the references on pp. 13 and 14.

(2) The absence of the Barberry and other aecidial hosts is conceded in many cases, and would be a real difficulty if the uredospores were found to be so short-lived as has been assumed; but the mere fact that such spores will keep their capacity for germination for from sixty-one to ninety-four days (see pp. 11 and 12), and the evidence that we do not yet know the limits, should make us cautious here, to say nothing of the fact that germinable spores of *P. dispersa* have been found all the year round. See also p. 14.

(3) Here again the reply is partly the facts just referred to, and partly that we are only at the beginning of knowledge as to the transmissibility of spores from Twitch and other weed Grasses, either direct or by means of 'bridging species.' Moreover, the results given in Blomeyer (34), Rostrup (147), Plowright (132), Kühn (101), Hitchcock and Carleton (85), and Bolley (30) are, so far as they apply, dead against Eriksson's conclusions: they all declare for the persistence of uredospores and their retention of the capacity of germination through the winter.

(4) An analysis of Eriksson's experiments in large glass cases and tubes in the open is not easy; but the tubes (d) of 1893, a poor rust year, showed the presence of *Erysiphe* on the plants. Does Eriksson deny that this *Erysiphe* reached his plants by means of spores; or does he also intend us to assume an internal origin for that Fungus also? In the cases where he does get uredo he asks us to believe that it is due to mycoplasma; but if *Erysiphe* spores reached his specimens, surely the uredospores may have done so.

Again, in the tubes (f) of 1894-9, where, of thirty-five plants, seven were rusted, I find there was abundance of rust around the experiment.

Yet Eriksson asks us, Whence came the infection? He argues that uredospores cannot survive the winter; and that even if they could ten and not forty days are necessary for incubation. But here again, both *Erysiphe* and *Aphides* appear in such tubes. Are the *Aphides* derived also from an internal source, like 'mycoplasma'?

In series (g) again, where two cases were used and seven seeds employed, during the eighty-eight days of the experiment one case remained free from rust, while two plants in the other were rusted.

Further, in series (i), where four cases of Barley, Oats, and Twitch were tried, five seeds or rhizomes in each case, of the twenty plants only one was rusted, and this had *Puccinia* on it at the start.

Surely there is something wrong in the distribution of the parasite here, if Eriksson's idea is correct.

With regard to series (j), where three cases of sterile soil were sown with Barley, five grains each, case No. 2 showed no rust; case 1 showed rust in twenty-six days; and case 3 was rusted in fifty-two days and had *Aphides* in it.

Now, apart from the question, Does Eriksson imagine that the *Aphides* arose from within? is it not suggestive that *Aphides* can carry the spores of Uredineae about on their bodies?

(5) Since Eriksson has admitted (67) that his 'corpuscules spéciaux' figured in 1901-2 (65) are haustoria, in accordance with my explanation of them (195), I need say no more on this subject here. Further details regarding histological points will be dealt with later.

(6) With regard to analogies afforded by other parasites, Eriksson has in my opinion fallen on somewhat unfortunate examples.

Nawaschin (118) has shown that the amoebae of *Plasmodiophora* are perfectly distinct, and remain so, from the cytoplasm of the cells they invade, and modern staining methods make it impossible to believe that where the nuclei of the host-cells and of the parasite stain so distinctly as they do in Uredineae no better traces of them could be obtained than Eriksson supposes.

In support of his hypothesis, Eriksson might have used the then mysterious seed Fungus of *Lolium temulentum*; but Freeman has now shown, in my laboratory (75 a), that the Fungus is perfectly traceable in the developing seed. It is interesting to note by the way that Lindau has since found this in Egyptian seeds buried for about 4,000 years (104 a).

With the question of *Pseudocommis* I have dealt on p. 34.

INFECTION.

When the sporidia (*basidiospores*), developed from the promycelium (*basidium*) of the germinating teleutospore of *P. graminis*, are sown on the Barberry, the germ-tube put forth pierces the cuticle; and we now know that

many parasitic spores, only capable of attacking young organs, adopt this mode of cuticular infection.

In the case of uredospores and aecidiospores the process is different, as De Bary first showed ; their germ-tubes enter the stomata, and it is with this stomatal infection only that we have here to do.

But further research shows that two events must be sharply distinguished, in addition to the preliminary act of germination of the spore itself

First, we have the entry of the germ-tube *via* the stoma, preceded by a swelling of the tip into the so-called *appressorium* over the external orifice of the stoma. The tip then sends a slender offset through the orifice into the respiratory cavity, and there it swells into the *sub-stomatal vesicle*, and the entry of the Fungus is assured.

Secondly, we find this sub-stomatal vesicle puts forth one hypha (or more) which grows towards the cells bounding the inter-cellular spaces, attacks them by sending in haustoria, and thus the act of *infection* is completed.

It will be evident that we have in the process of *entry* or *inoculation*, a phenomenon quite distinct from and independent of that of *infection*.

We cannot assume that either the stomatal or the mesophyll-cells of the host are passive or inert in this matter. As regards the former it is suggestive that inoculation is best effected by sowing in the evening ; it often fails in bright daylight, and apparently always does so if the temperature is high, or the plant in darkness.

In 1882, at Owens College, I observed the following phenomenon. A slice of bean-stem in a hanging drop, to which some zoospores of a *Pythium* were added, was under observation. A zoospore was seen to gyrate rapidly in smaller and smaller circles, and suddenly dart on to the exposed cut surface of the bean section, where it remained stationary, and in half an hour had begun to germinate. In a couple of hours its tip was boring through the cell-wall.

My attention at the time was directed to other matters ; and it is to this fact and to my lack of that particular form of insight which is called genius that must be ascribed the stupid failure to see that here was a case of what we now know as chemotaxis.

In 1883 (128, p. 524) Pfeffer published his first paper on the directive actions of chemical stimuli, which he subsequently named chemotaxis, and which he showed to be so potent a factor in attracting the tips of hyphae to enter plants ; a theme worked out more in detail in this connexion by his pupil Miyoshi (113), 1894, and (112), 1895.

I have always maintained that in parasitism we must consider not only the power of the parasitic Fungus to attack a given host-plant, but also the reaction of the host on the parasite (198), 1890, and (197), and also (190), and it is characteristic of modern work that this view is spreading.

Massee (109), in an interesting summary of experiments on chemotaxis with certain Fungi, in which he confirms previous results, goes so far as to say that 'infection is due to positive chemotaxis,' and that immunity is due to the fact that the plant, 'owing to the absence of the chemotactic substance in its tissues necessary to enable the germ-tubes of the Fungus to penetrate, remains unattacked' (p. 23).

But, apart from the fact that chemotaxis is also a factor in saprophytic life, and that the entrance of a hypha into a stoma is only a preliminary act, not necessarily indicative of parasitism, there are other objections to the title of Massee's paper, 'On the Origin of Parasitism in Fungi.'

Miss Gibson, in my laboratory, has shown that the germ-tubes of almost every Uredine she tried will enter quite the wrong host by the stomata, as the annexed table shows:—

<i>Spores.</i>	<i>Species of Fungus.</i>	<i>from</i>	<i>Host.</i>	<i>Result.</i>
Uredospores	<i>Uredo chrysanthemi</i>	<i>Chrysanthemum sinense</i>	<i>R. Ficaria</i>	Enter freely.
Aecidiospores	<i>Phragmidium rosae-alpinae</i>	<i>Rosa</i>	"	" "
"	<i>Uromyces poae</i>	<i>Ranunculus repens</i>	"	" "
"	<i>Aecidium bunii</i>	<i>Bunium</i>	"	Negative.
"	<i>Puccinia poarum</i>	<i>Tussilago</i>	<i>Caltha</i>	Enter freely.
Uredospores	<i>Uromyces geranii</i>	<i>Geranium</i>	"	" "
Aecidiospores	<i>Puccinia Menthae</i>	<i>Mentha</i>	"	Enter not very freely.
Uredospores	<i>Puccinia</i>	<i>Carduus</i>	"	Enter freely.
Aecidiospores	<i>Phragmidium Sanguisorbae</i>	<i>Poterium</i>	"	2 or 3 doubtful entries.
Uredospores	<i>Puccinia glumarum</i>	<i>Triticum vulgare</i>	"	1 certain entry.
"	<i>Puccinia graminis</i>	<i>Poa aspera</i>	"	Enter freely.
"	<i>Uromyces poae</i>	<i>Poa pratensis</i>	"	" "
"	<i>Puccinia taraxaci</i>	<i>Taraxacum</i>	<i>Tropaeolum</i>	" "
"	<i>Coleosporium Sonchi</i>	<i>Tussilago</i>	"	" "
"	" "	" "	<i>Valeriana</i>	" "
"	<i>Puccinia pulverulenta</i>	<i>Epilobium</i>	"	1 entry.
"	" <i>Centaureae</i>	<i>Centaurea nigra</i>	"	Enter freely.
"	" <i>Menthae</i>	<i>Mentha</i>	"	" "

It cannot be too clearly understood that the entry *via* a stoma is not infection. Over and over again I have found leaves which are immune, penetrated at hundreds of stomata without effect. This is why I have taken to speaking of the *germ-tube* and *appressorium*, formed outside the stomata, as distinct from the *sub-stomatal* or *infection-vesicle* and *-tube* developed later, in successful cases, in the respiratory cavity beneath the stoma.

Infection proper depends on two sets of factors. On the one hand the relations between host and parasite, involving the power of attack by means of enzymes and toxins of the latter, and the power of resistance, by means of anti-bodies, &c., of the host. On the other hand, the effects of the environment on both parasite and host.

External influences undoubtedly exert important effects. I have given evidence (190, p. 291) to show that too high a temperature during incubation may ruin the Fungus. Internal influences may result in the death of both hypha and host-cell, and then comes ruin to the former.

Klebahn (92, p. 262) shows that sporidia of *P. Convallaria-digraphidis* if sown on *Polygonatum*, and that the sporidia of *Gymnosporangium clavariaeforme* if sown on *Pyrus Aucuparia* (91, p. 150), form poor spots, &c. Also Bolley (30, p. 893) got mere specks on cereals with uredospores; and I have given similar examples (191, p. 298).

Here we have several cases possible: (1) It is possible that the environment stops the growth of the Fungus; (2) too many competing infections may be present; (3) the Fungus may be too weak to overcome the host-cells; (4) the host-plant may be too rich in antitoxins; (5) the Fungus may be too strong, and so kills the cells destructively; or (6) the host is too weak and succumbs too rapidly at the spot attacked.

In this connexion it is instructive to find that Mr. Evans and myself have satisfied ourselves (1) that so-called immune plants furnished us by the agriculturists may be really badly inoculated, bearing innumerable minute yellow and brown spots, each of which is an abortive infection area; (2) that experimental inoculation results in just such spots: the germ-tube goes in, but the walls of the cells in contact with it turn brown and die, and the hyphae are starved; and (3) we can stop the infection-tube, even when well in the leaf, by various modes of interference with nutrition, especially by starving the leaf of carbon dioxide: also by floating the leaf on water and starving it of salts, or by heating or cooling the roots.

That chemotactic actions are factors in the complex fight which results from the antagonism between the Fungus—with its attacking weapons such as enzymes and toxins—on the one hand; and the cells of the host—with their defending armoury of anti-toxins and other enzymes—on the other, cannot be denied. But that it is only one of several sets of factors in an extremely complex phenomenon, seems clear when we see that inoculation—the process of entry of the germ-tube and development of the sub-stomatal vesicle—and infection—the attack of the cells by the infecting tube and haustoria—are two distinct events; that external influences such as temperature, and internal factors such as the age and ripeness of the spore, and the condition of nutrition, starvation, &c., of the host-cells, affect the matter; and that a certain species of host A, though perfectly capable of being infected with, say, *Puccinia dispersa*, will refuse to be infected by spores of that Fungus taken from a host B, while it *will* take it from a host C, and will even take it from C when the latter has received it from B.

It seems justifiable, therefore, to speak of predisposition and immunity in the light of the above facts.

ERIKSSON'S CRITICISMS.

In 1903 Eriksson made reply (66) to my paper in an article entitled 'The Researches of Professor H. Marshall Ward on the Brown Rust of the Bromes and the Mycoplasm Hypothesis,' in which he courteously appreciates the work, but at the same time maintains his previous position, insisting that my cultural and histological results have little or nothing to do with the matter.

Of my pure cultures in test-tubes (193, 1902, p. 451) he says:—'The pure cultures in test-tubes, described in 1902, where the results were negative in the cases when no infective substance was introduced, prove no more against the theory in question than do the numerous experiments with cultures, equally negative in their results, which I myself had carried out in isolated glass houses during the years 1892-8.'

This I concede: in both cases the absence of positive results is, so far as it goes, dead against the existence of 'mycoplasm' in the seedlings or plants.

Eriksson then proceeds to state that he ventures to regard the existence of mycoplasm 'as proved, at least until sufficiently comprehensive proofs to the contrary have been produced from some other quarter.' Surely this is a travesty of the kind of logic demanded by science! We have given proofs over and over again of the course of normal infection; these proofs are in accordance with the experience of others and in other parasitic Fungi. It may be quite true that certain possibilities can be conceived. Eriksson states (66, p. 143) that 'if we try to make clear to ourselves the origin of the outbreak of an uredo-pustule fleck of an heteroecious species of rust (e.g. *Puccinia graminis*) we have to suppose several different possibilities. The fleck can arise (1) from an infection by uredospores (e.g. *Uredo graminis*); or (2) from an infection by aecidiospores (e.g. *Aecidium Berberidis*). Numerous experiments have fully proved that both of these modes of origin occur. . . . It is possible that an uredo-pustule can also arise: (3) from a direct infection by teleutospores (e.g. *Puccinia graminis*) without the intervention of an aecidium-stage; or (4) from a latent germ of disease inherited from the parent plant. . . .'

Surely it does not need my emphasis of one of the fundamental rules in scientific reasoning—viz. that the mere assertion that such and such an idea or hypothesis is possible in no way supports its probability, and still less does reiteration of a hypothesis prove it! Surely Eriksson must see that the *onus* of proof lies with him: not with us! Until we know all about the infection by means of uredospores and aecidiospores—and recent work shows how much we have yet to learn as to the limits of germinating power, infective capacity, and so forth of the uredospores—we have no right

to call in another hypothesis, totally subversive of all the laboriously won doctrine of parasitism founded by De Bary. We may admit the *possibility* of other hypotheses—I would be the last to deny honour to him who proposes and tests such—but we cannot accept such on negative foundations only.

I venture to assert that Eriksson has omitted a precaution which might have saved him much trouble, viz. he has not compared the course of normal infection with the phenomena he describes.

We had already worked out the chief points in the histology of *Puccinia glumarum* when Eriksson's second paper (67) since my investigation of the histology of *P. dispersa* was published in January, 1904, entitled 'Ueber d. vegetative Leben d. Getreiderostpilze.' This work was conjoint with Georg. Tischler, and deals with *P. glumarum* in Wheat.

After a short and luminous introduction, showing how De Bary's proof that *Aecidium Berberidis* belonged to *P. graminis*, *Ae. Asperifolii* on *Anchusa* belonged to *P. Rubigo vera* (*P. straminis*), and *Ae. Rhamni* on *R. catharticus* and *R. Frangula* belonged to *P. coronata*, Eriksson states that this by no means ended the Wheat Rust controversy.

True, De Bary's results were in the main confirmed, especially as regards *P. graminis*. But all three Wheat Rusts have now yielded several other species, and have been shown to be each a multiple species.

P. graminis is found to include two, *P. Rubigo vera* eight, and *P. coronata* two new forms which Eriksson regards as species. Of these only four species—*P. graminis* proper, *P. dispersa*, *P. coronifera*, and *P. coronata*—are known to be heteroecious, and of these only three form teleutospores which pass the winter before germinating, the teleutospores of *P. dispersa* germinating in the autumn of their ripening. Eriksson then goes on to repeat his opinion that it is impossible to explain the outbreaks of Rust in certain seasons by means of aecidiospores or of uredospores which have persisted through the winter; and especially insists on his culture-experiments in the open, as driving to the conclusion that some internal source of infection exists. In other words, Eriksson holds fast to his mycoplasm hypothesis.

But under what a different guise does the hypothesis now appear! Hitherto we were asked to assume that the protoplasm of the Fungus and of the cell were amalgamated in an intracellular symbiosis, and that at certain periods this could be seen to be separating out the Fungus-mycelium as 'corpuscules spéciaux,' now shown to be the haustoria.

Now we are told (67, Pl. I, Fig. 2) that the vacuolated and granular contents of certain cells are probably the 'mycoplasm.' Neither the figures nor the description give us any sufficient evidence for this assumption, however, and I see no reason for altering my opinion that Eriksson had here before him simply the intact protoplasmic contents of normal cells

which had taken up the stain, and so showed up these cells, distinguished of course from cells which had been cut into.

The references to the obscure *Pseudocommis* of Viala and Sauvageau (188) and to *Plasmodiophora* (206) appear to me particularly unfortunate, for Prillieux (136, p. 47), writing in 1895, was quite unable to accept the views of Viala and Sauvageau; and Tubeuf, writing in the same year (72, p. 545), also points out that there is no proof forthcoming of the existence of such a parasite. Indeed, the autonomy of *Pseudocommis* has been accepted by no authority.

Moreover, I have myself observed, especially in tropical plants, appearances and alterations in the protoplasm of cells quite like Viala's, but which are due to physiological changes; and I may refer you to Miss Dale's work, in this laboratory, on intumescences (52) for some interesting results suggesting how such phenomena may be artificially induced.

The reference to *Plasmodiophora*, so beautifully worked out by Woronin in 1877-8 (206), is still more unfortunate; for not only did Woronin obtain the spores and germinate them, but Nawashin has shown (118) that it is perfectly easy to distinguish the amoebae in the cells throughout their life.

Eriksson, however, not only accepts all the dubious cases of *Pseudocommis*, &c., described by various authors, but suggests that even where hyphae coexist probably the so-called plasmodia 'nichts anders sind als Mycoplastmastadien verschiedener Hyphenpilze' (66, p. 12).

After making the most of this very questionable evidence, Eriksson then proceeds to a curious shifting of his position.

Hitherto, as we have seen, the mycoplastm was intracellular. He now passes to the consideration of a stage (66, Taf. II, Fig. 10) where it is intercellular, but concludes that this position was accidentally attained owing to manipulation during the preparation.

Eriksson then devotes his attention to certain phenomena observed at the edges of incipient pustules.

The first point to notice is that very young hyphae, which he terms *protomycelium*, are figured as partly creeping filaments, and partly as irregular masses filling up the intercellular spaces.

These are described by the author as follows: 'Keine Scheidewände sind vorhanden, auch keine erkennbare Kerne, nur zerstreute etwas stärker färbbare Körnchen, oft mehrere dicht bei einander. Deutliche Membranen heben sich auch nicht von dem Plasma ab; ob solche in der Tat vorkommen oder nicht, muss fortgesetzten Untersuchungen vorbehalten sein zu entscheiden.'

Owing to their 'almost plasmodium-like nature,' and the complete lack of septa, these structures are alleged to differ essentially from the normal mycelium, and are called 'protomycelia.'

We then read: 'Nach den bis jetzt vorliegenden Auseinandersetzungen

und Untersuchungen unterliegt es für uns keinem Zweifel, dass das intracellulare Mycoplasma und das intercellulare Protomycelium genetisch zusammengehören. Nur sind die Einzelheiten im Übergang von jenem zu diesem Stadium noch nicht so vollständig und genügend aufgeklärt worden, dass wir jetzt auf diese Übergangsfrage näher eingehen können oder wollen.'

Eriksson then describes (66, Taf. II, Fig. 11 *a* and *b*) what he regards as swollen nuclei of the host-cells.

Before proceeding further, I may again remark on the one curious omission in all Eriksson's work. Nowhere, so far as I can discover, does he trace his Fungus from the infection-spot, and in no case has he given a figure of the germ-tube entering the stoma, and compared the phenomena with what he finds elsewhere. True, he denies that the investigation of infection by means of spores is the right way to go to work; but one would have thought that it was at least necessary to compare and contrast what happens in normal infection with what is alleged to take place independently of it. Moreover, as was clearly shown in my paper on the histology of *P. dispersa*, Eriksson would have avoided some important errors had a strict comparative investigation been made; and the application of this to the histology of *P. glumarum* leads us to the same conclusion.

THE HISTOLOGY OF *PUCCINIA GLUMARUM*.

Assisted by Mr. Evans, I have for some time been occupied with the histology of *P. glumarum* in Wheat, under various conditions of growth, normal as well as abnormal; and I would take this opportunity of saying that Mr. Evans has independently worked out the normal life-history and histology in the most thorough manner, as well as helped my part of the work to such an extent that we may regard it as practically conjoint.

The results may be briefly summarized as follows:—

The uredospore of *P. glumarum* germinates on Wheat, and infects it by means of a germ-tube which enters the stoma and puts forth an infection-tube from a vesicle, exactly as in the case of *P. dispersa* on the Bromes.

The sub-stomatal vesicle and the infecting hypha sent out from it are, however, very different in detail from those of *P. glumarum*, the vesicle having a firmer cell-wall and more numerous nuclei, and the infecting hypha being of far greater diameter and containing very many brightly staining nuclei.

Soon after entering the stoma, and having formed the sub-stomatal vesicle, the infection-tube put out from the latter forms its first haustorium, and the further growth takes place much as in *P. dispersa*.

The most remarkable points in these young hyphae are their great diameter (from 3-4 up to 18 μ and more), the rarity of septa, the abundance

of nuclei (often amounting to scores or even hundreds in a short length), and the shortness and stoutness of the branches.

Klebahn (94, p. 255) has this year called attention to the rarity of septa and the abundance of nucleus-like bodies in the hyphae of this Fungus, and has drawn one of the haustoria.

Now it is a noteworthy point that Eriksson figures and describes his 'protomycelium'—i. e. according to him the youngest stage developed from his alleged mycoplasm—as devoid of distinct nuclei.

We find that the nuclei become more and more indistinct, and for the most part diminish in size, as the mycelium ages, or if we *starve it by cutting off carbohydrate food-supplies*; and, without further information, we should certainly have interpreted Eriksson's (66) Fig. 11, on Pl. II, as either older hyphae or starved ones.

In no case have we been able to confirm Eriksson's statement as to the absence of a membrane to the hyphae. It appears very unlikely that among the thousands of preparations, in all stages, examined by us, the so-called 'protomycelium' has been overlooked. Indeed, as already said, we identify it with some of our stages of older or starved hyphae; but these have always a distinct clothing membrane.

It is impossible to avoid the suspicion that, had Eriksson cut serial sections through the patches at the margins of which he finds his 'protomycelia' and 'mycoplasm,' he would have discovered the sub-stomatal vesicle and entering germ-tube, for it should be mentioned that *in the very Wheat he has recommended as so susceptible*—viz. Michigan Bronze—we have seen excellent cases of entry on the *eighth day*, i. e. two days before spore formation may be expected; and in another susceptible Wheat (Red King) we have found the entering hyphae at the stoma on the ninth day. The fact is, the whole of Eriksson's work demands repetition from this point of view: we want not only the preparations from the margins of the young pustular-patches, but from every part of the infected area to its centre. At that centre the presumption is that he will find some of the cases of entry described, and will then see that he is reading the phenomena backwards, as I have all along contended he is doing.

With regard to the haustoria, it is the less necessary to say much, since Eriksson has now accepted my explanation, and withdrawn his erroneous interpretation of the 'corpuscules spéciaux' (66, p. 17). Klebahn had also noticed the similarity of these 'corpuscules' to haustoria (95, p. 89) in 1900.

We are, however, unable to confirm several of Eriksson's statements respecting the mutual behaviour of the haustorium and cell-nucleus, and are quite unable to explain his identification of the 'swollen nuclei' in his Fig. 11 *a* and *b* (66, Taf. II). The criticism of these and other details may be reserved for the full paper.

SUSCEPTIBLE AND IMMUNE VARIETIES, AND THEIR HYBRIDS.

A question of fundamental importance for our purposes is that of the immunity of certain forms of Wheat, and arising from this is the question, Can immunity be induced or propagated?

Mr. Biffen, working at our Experimental Farm, has done excellent service in recording the behaviour of certain races of Wheat, and in hybridizing and selecting them with great care and with an industry and perseverance not easily appreciated by those unacquainted with the kind of work involved. Much of his work has been directed to the testing of Mendel's law, a question into which I do not however propose to enter here; and this is the less necessary since he will himself bring this matter to your notice.

Some time ago I asked Mr. Biffen to select for me grains of a susceptible Wheat, of an immune Wheat, and of a cross between the two, and Mr. Evans and myself undertook to test them according to our own methods.

The races Mr. Biffen was good enough to supply were A, Rivet Wheat, a form found to be almost immune, even when growing in the midst of Rusted Corn; B, Red King, a very susceptible race, covered with Yellow Rust in the season; and C, a crossed Wheat obtained by pollinating Rivet with Red King.

This crossed form, on sowing and cropping, was found to be highly rusted the first year; but in the second year yielded some plants which showed Rust and others which appeared to be practically immune, in the proportion of practically 3:1, whence Mr. Biffen concluded that susceptibility to Rust is a dominant and transferable character. This question does not, however, concern us.

We sowed these several grains in separate pots of similar soil, similarly treated, and infected them in the ordinary way with spores from the same source.

The susceptible form B (Red King) showed signs of pustules on the tenth day, and by the twelfth day was covered with pustules of Yellow Rust.

The 'immune' form A on the tenth day showed what looked like very early stages of pustules, but these as a rule did not pass beyond the stage of pale flecks, and on the twelfth day showed a few spore-bearing pustules only.

On this twelfth day the proportions of pustules on A and B respectively were as follows, counted on three leaves each:—

A. Leaf 1 = 94 pustules.

„ 2 = 7 pustules.

„ 3 = 2 pustules.

B. Leaf 1 =

„ 2 =

„ 3 =

} Many hundreds of pustules:

} far too numerous to count.

As regards the crossed Wheat C, one or two incipient pustules only could be detected on the tenth day, and on the twelfth it was as badly infested as the susceptible form, the numbers of spore-bearing pustules being far too many to count.

We then fixed the infected areas of leaves of each at intervals on the third, fourth, fifth to the eleventh days respectively, cut, stained, &c., and examined the serial sections. Several of each were left growing to determine their behaviour as regards producing spores.

We have made a prolonged series of preparations of all three Wheats, and find that inoculation and infection occur very readily in the susceptible form, the sections showing scores of entries of the germ-tubes: the hyphae then pursue the normal course, are typically stout, branched, and contain hundreds of nuclei. They also form numerous haustoria, and the attacked cells show no evident signs of injury to the chlorophyll-corpuscles or nuclei until a late stage of growth. It was particularly evident that the hyphae show no signs of degeneration until the period when spore-formation begins; but a tendency of the smaller nuclei to become massed together may be observed from about the sixth day onwards.

The microscopic examination of the 'immune' form yielded some very curious results.

It was evident, from the number of entries we found, that the uredospores germinate and send tubes into the stomata as frequently, or nearly so, as they do into the susceptible Wheat. Moreover, the course of events is at first similar: so much so that I thought at first that we were either mistaken in the information received as to the behaviour of these plants in the open, or that the so-called immunity was a mere delusion.

The behaviour of these hyphae after the fourth to sixth day, however, gave us the clue to the mystery.

In the first place the hyphae do not extend far from the point of infection, and they diminish in diameter; moreover, the contents become granulated or almost fibrous and present a starved appearance, while the nuclei not only diminish in size and number, but especially in distinctness and staining capacity, so that it often appears as if they were absent.

In short, these hyphae show evident signs of degeneration in all respects, and we conclude, from comparison with experimentally starved hyphae, that they are undergoing death-changes owing to one of two events, viz. they are either starving for want of food-supplies, or they are being poisoned.

Even more striking are the changes observed in the cells of the host in the immediate neighbourhood of these degenerating hyphae.

In the susceptible Wheat, even where the hyphae are particularly large and abundant, and full of nuclei and deep-staining protoplasm, the adjacent cells, including those into which haustoria have been sent, are still turgid

with well-staining nuclei and chlorophyll-corpuscles, and the cell-walls do not take up the fuchsin.

Here, on the contrary, the cells in the immediate neighbourhood of the hyphae are often collapsed, their nuclei and chlorophyll-corpuscles disintegrated and flowing together into shapeless masses, and deeply stained red, as are also the collapsed cell-walls.

That this is a purely local phenomenon, confined to the immediate neighbourhood of the hyphae—which rarely send haustoria into the cells—is seen by the normal appearance and staining of cells further away.

It is therefore impossible to accept the view that this collapse and abnormal behaviour of these nests of cells are due to the effects of preparation.

The only conclusion we can come to is that the hyphae attack the cells too vigorously at the outset. Instead of capturing them, as it were, by putting in haustoria which delicately tap the cell-contents and make them serve as sources of food-supplies, the Fungus clumsily kills these cells, and is in consequence subjected to all the exigencies of starvation, or worse.

STARVATION PHENOMENA.

Our reasons for this conclusion are not based only on the histological evidence afforded by these so-called 'immune' Wheats.

We have induced starvation phenomena of substantially the same kind, even in susceptible Wheats, in which infection and the growth of the Fungus proceed normally under normal conditions; and this in several ways.

If infected leaves are cut off on the third day or so after infection, and floated on water, the Fungus may continue to grow, but it soon shows signs of starvation; for although the leaves are exposed to light and go on forming carbohydrates, the mineral and soluble carbohydrate supplies soon run short, from being washed out, and other changes occur which bring the normal functions to a stop.

The effects of mere mineral starvation have already been demonstrated by me (194, 1902), but it is clear from our experiments that although they do not kill off the Fungus forthwith, they have their effect on the structure of the mycelium.

Another way by means of which we have induced starvation phenomena is to keep the roots of the infected plants too hot or too cold for normal growth. This was effected by placing three pots of infected plants in reservoirs, plunged in water, in tin boxes. One, the control, was kept at the ordinary temperature; the other was kept heated to temperatures about 30°–35° C. day and night by means of a lamp below; and the third was kept chilled, by ice round the pot day and night, to near 5° C. and below. This treatment refers to the roots only: the foliage was freely exposed to

the light and air of the Eastern greenhouse. Not only did we trace starvation effects on the hyphae, but in the heated pots we found corroded nests of cells as in the immune plants. Since our work is not yet finished, however—we have yet to examine thousands of sections of these leaves—I defer discussion of the details for further communications.

There is one other series of experiments to which I must refer, however.

We have been much occupied with infections on leaves deprived of carbohydrates by keeping them in the dark, or in light from which the red-orange end is filtered off, &c. But especially important are the attempts to grow the Fungus in leaves from which all atmospheric carbon dioxide is cut off by potash, but which are normally supplied with water and light, and in some of the experiments with minerals in normal culture solutions.

I select one series for illustration.

EXPERIMENT 15.

On May 18 three pots were prepared, and in each were sown fourteen grains of Michigan Bronze, a variety selected because it was known to be very susceptible to *Puccinia glumarum*, and was used by Eriksson.

On June 15 the plants were strong and vigorous, each showing the fourth leaf. On June 15, 5 p.m., uredospores obtained from Michigan Bronze were sown on eleven of the first leaves, all over the upper surface, and the inoculated plants were placed under damp bell-jars. The whole growth, and subsequent operations, took place in the Eastern greenhouse.

The inoculated plants were then left for twenty-four hours, to initiate infection; and at 5 p.m. on June 16 were treated as follows:—

Six of the inoculated leaves were cut off close to the base, and each placed in a separate tower-tube, the tubes labelled A, B, to F. The base of this tube contained distilled water, over which was a light plug of wet cotton-wool, on which the cut surface of the leaf rested. Into this basal water plunges the exit end of a tube which carries the air to be drawn through the tower, which air, after passing over the leaf, escapes at the top of the tube.

The tower-tube described above is linked up to a second tower, arranged in exactly the same manner, except that it contains no leaf on a cotton-wool plug, but merely acts as a receptacle of water to wash the air coming through the tube.

This latter is linked to a triad of bulbs charged with a strong solution of potassium hydrate, the proximal end of which is open to the air. In some cases Pettenkofer tubes were employed.

Of the six leaves selected, four were placed as above in tubes thus

linked up to potash-bulbs. The other two were arranged in an exactly similar manner, except that their tower-tubes were not connected with potash-bulbs, and the air passing over their contained leaves passed through distilled water only. Clamps at various points enabled me to regulate the rate of ingress of air.

All six tower-tubes containing leaves were now joined up to a central large flask, by means of tubes linked together, and the flask communicated with a vacuum-pump. On joining up the system, and starting the pump, a little regulation of the clamps easily enabled me to set up a current of air through the towers at uniform rate, and at a low pressure, viz. 20–50 mm. of mercury—and this was done so that about one bubble per second escaped from the afferent tubes and passed over the leaf above.

The histological examination of these infected leaves showed that as soon as the leaf feels the deprivation of carbon supplies the Fungus-hyphae begin to degenerate and starve; and in some of the cases we find corrosions of the tissues beneath the spores on the epidermis. We have made out numerous interesting details regarding the degeneration of the nuclei, breaking up of the chlorophyll-corpuscles, thinning of the cell-walls, and so forth; but since there is still much to be done before all the facts can be linked together I do not propose to go further into the matter here.

The case of the plants with roots kept at high temperatures also promises to be interesting in several directions.

I pointed out some time ago (190, p. 291) that infections are difficult to carry out in hot weather, and gave evidence which goes to show that the mycelium suffers when the temperatures inside the leaf pass beyond certain limits. I also gave some experimental data showing that the temperatures in grass leaves exposed to a summer sun may rise far higher than is usually supposed.

It is interesting to note that Dr. Blackman, working in our laboratory at assimilation and respiration, and using thermo-electric measurements and methods of greater accuracy than were at my disposal, has confirmed and extended these data; as he will himself bring the matter before you in detail, I need say no more now.

These failures of infection in hot weather are so common—we have experienced them several times this summer—and the phenomena are so similar to what occurs in our heated plants, that I am disposed to urge that both cases stand in the same category.

But that is not all. The phenomena—starvation of hyphae in a nest of dead cells, or the corrosion of cells beneath the spores sown on the leaf—are similar in all these cases to what occurs on the so-called immune plants we have dealt with.

BRIDGING SPECIES AND THEIR SIGNIFICANCE.

In 1903 (191, p. 145) I summarized the results of a long account of experimental work, as follows:—

‘The table gives the results of nearly five thousand experimental infections made with the uredospores from eleven species of *Bromus* belonging to the three sections *Stenobromus* (*B. sterilis*, *B. diandrus*, and *B. crinitus*), *Libertia* (*B. Arduennensis*), and *Serrafalcus* (*B. arvensis*, *B. secalinus*, *B. mollis*, *B. intermedius*, *B. japonicus*, *B. patulus*, and *B. brizaeformis*), on sixty-four species and varieties representing all the five sections into which the genus *Bromus* is sub-divided.’ I then gave the tabular results showing that in the vast majority of cases the uredospores from a given species of *Bromus* only infect the same species or, usually in diminishing proportions, species closely allied to it and in the same group.

In the same paper (191, p. 139) I referred to some exceptional cases, which had occurred during the three years over which the experiments had extended, and on which I was at first inclined to lay no stress, regarding them as possibly errors; but since they were found to recur, in certain species, so frequently, I was forced to conclude they had an important significance.

Bromus erectus of the group *Festucoides* was once in thirty-seven trials found to take the infection from spores derived from *B. mollis* of the group *Serrafalcus*; *B. sterilis* (*Stenobromus*) four times out of ninety trials by spores from *B. mollis* (*Serrafalcus*); *B. Madritensis* (*Stenobromus*) once out of thirteen trials by spores from *B. secalinus* (*Serrafalcus*); and *B. maximus* (*Stenobromus*) once out of seventy-four trials with spores from *B. mollis* (*Serrafalcus*); and I raised the question, ‘Is this a case of species raised on *B. mollis* adapting themselves to *B. sterilis* and *B. erectus*, &c., or of the latter proving individually less resistant than their species generally do to the infection?’

I then showed that the phenomenon turned out to be commoner than was suspected.

Freeman (75), working in my laboratory, confirmed my previous results, and showed that in the case of five species infections occurred with spores both from *B. sterilis* and *B. mollis* as follows:—

B. Gussonii (*Stenobromus*) was infected successfully thirty-seven times out of sixty with spores from *B. sterilis*, and six times out of fifty-three with spores from *B. mollis*; *B. Krausei* (*Serrafalcus*) succeeded fourteen times out of twenty-nine with spores from *B. sterilis*, and twenty-seven times out of twenty-seven with spores from *B. mollis*; *B. pendulinus* (*Serrafalcus*) twelve times out of fifty-three with spores from *B. sterilis*, and twice out of twenty-six with those from *B. mollis*.

I then showed (191, p. 150) that *B. Arduennensis* of the group *Libertia* is not only particularly susceptible to spores from its own species, but

also to those from *B. mollis* and *B. patulus* (*Serrafalcus*), and, in the case of its variety *villosus* at any rate, also to spores from *B. sterilis* (*Stenobromus*) as well.

So that *B. Arduennensis* is a 'bridging species' by means of which *P. dispersa* can pass into three of the five groups of Bromes.

I therefore concluded (191, p. 150):—'It seems to me that we have in these cases of "bridging species" the clue to an explanation of a phenomenon which must be assumed to occur in nature, whatever hypothesis we accept regarding the origin and signification of adaptive parasitism, viz. the passage of the Fungus from species of one circle of alliance to those of another, in spite of the fact that it is usually closely adapted to species of one section of the genus only. . . . We may suppose a uredospore from *B. sterilis* to infect *B. Arduennensis* var. *villosus*, and the crop of spores produced on this to further infect *B. Arduennensis*: thence the Fungus could pass to *B. secalinus*, and, further, to *B. brizaeformis*. According to Table III it would appear possible that an odd spore from the latter could infect *B. carinatus*, and if so, this would have for result the passage of the Fungus to four out of the five sections of the genus.'

Further experience only confirms the above, and convinces me that in these 'bridging' forms we have the clue to the phenomenon of the ever-widening cycle of adaptation.

In nine hundred and ninety-nine times out of the thousand the spores educated by, or adapted to, a given small circle of host-plants cannot successfully break through the defences of another circle; but in the thousandth case a single spore just manages to infect the alien host, and, once established, its progeny can go on infecting the new host. Or, it may be, that in nine hundred and ninety-nine times out of the thousand the spores from all kinds of alien sources fall on a given host, and it successfully resists any infection even though the germ-tubes enter the stomata; but the thousandth individual, weak in resisting power—whether machinery, or substance, or physiological activity—lets the enemy in, and it is then established.

The evidence compels us to believe that the host reacts upon and affects the physiological powers of the Fungus: these effects are invisible, and have no distinguishable morphological impress on the spores.

But is this always the case? De Bary's results with *Aecidium abietinum* (12) point the other way: they suggest that very slight morphological results follow according as the Fungus has passed its alternate phase (*Chrysomyxa*) on *Rhododendron* or on *Ledum*, and many similar cases can be quoted.

If this is once established, then we have the clue to the graduations of morphological differences sufficiently distinct for the determination of species.

PHYLOGENY.

It now remains to consider the bearing of some of the above phenomena on the phylogeny of the Uredineae.

In 1881 (192, p. 28) I recorded the fact that when uredospores of *Hemileia vastatrix* from *Coffea* are sown on *Canthium campanulatum*, another rubiaceous plant of Ceylon, the germ-tubes 'blocked up the stomata, sent their branches into the leaf, and commenced to form a normal mycelium in the intercellular passages of the leaf, as in coffee.' I also put forward the view that the origin of leaf-disease on Coffee was due to the spores of *Hemileia* having passed from the native plant, *Canthium*, to the introduced one, Coffee.

Although the words 'specialized parasitism,' 'adaptive races,' or 'biologic species' were not used, it will, I think, be conceded that here was expressed the idea that a native jungle Fungus-parasite had adapted itself successfully to an alien host.

But the idea of specialization of the parasite to the host was also present in De Bary's mind, when he wrote (7, p. 358, Engl. ed.): 'We encounter on the other hand in these Fungi [parasites] a very long and varied series of phenomena of one-sided or reciprocal adaptation between the parasite and the living organism on which it feeds. . . . Every parasite species lives on certain host-species, and the limits within which it can choose its host are different in different species.'

And again (7, p. 359): 'These facts and gradations would lead us to expect that there must also be differences in the aggressive behaviour of a parasite to the different varieties and individuals of a host; or, to express the matter in the converse way, in the *predisposition* of the individuals for the attacks of the parasite. In this direction also there are all possible gradations.'

Again (7, p. 386), De Bary wrote: 'The Fungi which are parasitic on plants naturally exhibit, within the limits of the chief phenomena of parasitic vegetation and its effects, . . . a variety of special adaptations in respect of their choice of a host and their spreading in, upon, or along with it.'

But probably the clearest example illustrating De Bary's attitude is the following:—

In 1879 De Bary (12) worked out the heteroecism of *Aecidium abietinum*, and proved that *Chrysomyxa Rhododendri* is its alternate form; but he found that at lower altitudes, although no *Rhododendrons* were present, the aecidium-form occurs, and showed that here the uredo-stage was *Chrysomyxa Ledi*. Although certain extremely fine distinctions exist between the two forms, which led De Bary to maintain them as species

provisionally, he asks 'ob beide Pilze durch Aenderung der Wirthpflanzen in einander überführbare Formen *einer Species* zu nennen sind oder *zwei* distincte, wenn auch sehr nahe verwandte Species.' It is almost certain that De Bary would, in the light of our present knowledge, have agreed with Klebahn (98, p. 131) that they are 'mehr biologische als morphologische Arten.'

Caecoma Laricis is the aecidium-form of an Uredine on the Larch, the connexion of which with an uredo-form has only lately been demonstrated; it is now known to be the aecidium of a *Melampsora* found on willows (98, p. 149). Klebahn's investigations have shown that spores from some of the aecidia (*Caecoma*) on the Larch readily infect *Salix viminalis*, *S. cinerea*, *S. aurita*, &c.; less readily *S. Caprea*, *S. fragilis*, *S. daphnoides*, &c., *S. acutifolia*. Other spores from aecidia, quite indistinguishable morphologically, readily infect *S. daphnoides*, and especially *S. acutifolia*, but have so far obstinately refused to infect *S. aurita* or *S. Caprea*; while *S. viminalis* and *S. cinerea* seem to be immune or very nearly so.

Klebahn concludes that we have here two Fungi on the Larch which, though biologically distinct, have not yet become sharply differentiated one from the other (98, p. 150). In other words, the Larch *Caecoma* is in process of splitting up into two as yet incipient species.

Puccinia Pringsheimiana, Kleb., and *P. Ribis nigrae-acutae*, Kleb. (I am not concerned in defending the bad nomenclature), both grow on *Carex acuta*, L., and form their aecidia on species of Ribes: this aecidium was long known as *Ae. Grossulariae*. Klebahn (98, p. 150) found that although *P. Pringsheimiana* and *P. Ribis nigrae-acutae* are practically indistinguishable by any morphological characters, the former develops its aecidia with ease on the Gooseberry and some other species of Ribes, except on the Black Currant: occasionally the latter host may be very feebly infected, but out of all comparison with the virulent infection of the Gooseberry. *P. Ribis nigrae-acutae*, on the other hand, infects *R. nigrum* easily and virulently: it also infects some other species of Ribes, but on *R. Grossularia* the infection is poor and uncertain, and rarely proceeds further than the development of *spermogonia*.

Here we have, according to Klebahn, a case similar to the last, but the separation has proceeded further, and the biologically incipient species are more differentiated.

The Fungus previously known as *Puccinia Bistortae*, Strauss, may be cited as a third case.

Infection experiments appear to show that at least two forms of *Puccinia* are comprised under this name on *Polygonum Bistorta*. One of these forms its aecidium-stage on *Conopodium*, as Soppitt showed (161, 1893, p. 4, and 162, 1895, p. 773), and was the first instance known

of a heteroecious *Puccinia* which develops its teleutospores on a Dicotyledon. It is now known as *P. Conopodii-Bistortae*, Kleb.

Another, known as *P. Angelicae-Bistortae*, Kleb., was found by Klebahn to develop the aecidium-form not on *Conopodium*—which does not grow in that part of Germany—but on *Carum*, and also, and still better, on *Angelica*. Ed. Fischer in 1902 (72, p. 12) confirmed the infection of *Carum*. But it appears that yet a third *Puccinia*, forming its teleutospores on *Polygonum viviparum*, is here comprised. It is known as *P. Polygoni-vivipari*, Karsten, and it also infects *Angelica* and forms aecidia on that plant, which again infect *P. viviparum*, but can also, though feebly, infect *P. Bistorta*, and there can be little doubt that there are other cases.

Whether Klebahn's conclusion that *P. Conopodii-Bistortae* and *P. Angelicae* are representative (or geographical) species is correct or no, there seems little room for disagreeing with his view that we have in the case of *P. Angelicae-Bistortae* and *P. Polygoni-vivipari* two forms adapted in different degrees to their mutual hosts.

A series of puccinias on *Digraphis*, formerly comprised as *Puccinia sessilis*, Schneid., offer a still more complex case.

Aecidia on *Allium ursinum*, *Arum maculatum* and certain Orchids, &c., have been proved to belong to this set. Soppitt showed that one of them—now called *P. Convallariae-Digraphidis*, Sopp.—develops its aecidium only on *Convallaria* (163, p. 213); on *Polygonatum* it gets no further than the formation of brown flecks—i. e. it appears to infect this plant, but the infecting tubes cannot grow to maturity, but die in the tissues. Klebahn showed and Soppitt confirmed (161, 1896, pp. 257 and 324, and 1897, p. 8) that *Majanthemum* remains immune.

Another was shown by Plowright (131, 1893, p. 43) to form aecidia on *Paris* but not on *Convallaria*.

Again, Magnus, Wagner, and Klebahn have found the *Puccinia* from *Digraphis* successfully infecting *Convallaria*, *Polygonatum*, *Majanthemum*, and *Paris*, and this form is now described as *P. Smilacearum Digraphidis*, Kleb.

But Klebahn has since found that, whereas *Polygonatum* is richly and easily infected, and *Convallaria* nearly as well; *Majanthemum* and *Paris* are but feebly attacked, and although more work is required, it certainly does look as if we had a *Puccinia* on *Digraphis* here accommodating itself in various degrees to a number of other hosts on which to form its aecidia. Nor is this all. Klebahn (98, p. 151) mentions a form, practically indistinguishable from *P. Convallariae-Digraphidis*, but distinguished by its feeble capacity for infecting *Paris* and perhaps *Majanthemum*.

Moreover, infection experiments have now separated *P. Ari-Phalaridis*, Plowr., forming aecidia on *Arum* but not on *Allium* (135, 1888, p. 88),

and Dietel (55, p. 43) confirmed Plowright's results ; though Klebahn found it infect both *Arum* and *Allium*, but not *Convallaria*, *Polygonatum*, *Majanthemum*, *Orchis*, or *Listera*. However, teleutospores obtained from *Arum* the following year refused to infect any but *Arum*. Now the question before us is, Are the forms now known as *P. Allii-Phalaridis*, Kleb., *P. Ari-Phalaridis*, Plowr., *P. Convallariae-Phalaridis*, Sopp., *P. Smilacearum-Phalaridis*, Kleb., *P. Paridi-Digraphidis*, Plowr., *P. Orchidearum-Phalaridis*, Kleb., &c., all with their puccinia-form on *Digraphis* and their aecidium-form on the host referred to, to be accepted as species ?

To me it is impossible. Until morphological characters can be found which separate it satisfactorily into specific forms, the *Puccinia* on *Digraphis* must be regarded as one and the same morphological species. But it does appear as if this species was adapting itself more and more closely to different alternate hosts, on which to develop its aecidia. Whether this adaptation will ultimately result in the breaking up of the various races into species is another question.

There are several possibilities, suggested by experiment but by no means as yet decided, to be kept in view in future investigations.

It is, for instance, quite possible that these adaptations are local, in the geographical sense ; that a *Puccinia* which in one geographical area is in the habit of infecting one alternate host, in another, where that host is rare or absent, has to adapt itself to another. Klebahn's results with *P. Conopodii-Bistortae* and *P. Angelicae-Bistortae* (*P. Cari-Bistortae*) may well be quoted in support of such a view.

Another possibility, in support of which Klebahn's results with *P. Convallariae-Digraphidis* and *P. Smilacearum-Digraphidis* might be quoted, is that the age of the plant, or the complex of events we term weather, may decide which of a number of potential host-plants shall be chiefly infected during a particular season.

Yet again, we may find that different conditions of culture of the teleutospores may impress on them differences in infective capacity for different alternate hosts, as Klebahn (98, p. 152) has suggested for certain cases. Whichever view comes to be most accepted in the future, however, it seems impossible to escape from the conclusion that specific susceptibility on the part of the host will also have to be taken into account. So far our speculations have concerned the adaptation of the parasite in the alternating phases of its existence—e. g. of the *Puccinia* to a second host on which it can form its aecidium.

But the peculiarity of specialized parasitism, in the more modern sense of the phrase, and due chiefly to Eriksson's work, is that each phase of the Fungus—e. g. the uredo-form—also adapts itself to various species, races, or varieties, and I now propose to inquire into the meaning of this. Eriksson's experiments resulted in not only an extension of the above

results to the heteroecism of the Rusts of Wheat, but also in the proof that the uredo-stage is by itself capable of specialization on particular species and races of Wheat, &c. My experiments with the Bromes showed the same thing for various well-recognized species and varieties within this genus with the uredo of a particular form-species of *Puccinia dispersa*.

Returning to the bearing of these matters on the relatively immune wheat described on p. 37 (A. Rivet Wheat), we see that it is in no degree immune in the sense of being able to prevent the germ-tubes from entering the stomata, or even to keep the infection-tubes from attacking the mesophyll-cells. What seems to occur is that the cells attacked, usually—but not always—succumb at once to some influence, poisonous or otherwise, exerted by the hyphae, and the latter find themselves involved in the ruined débris of these cells. This is an inimical environment for such hyphae, and they die off. Sometimes, indeed, the poisonous action of the Fungus seems to be exerted at the very surface of the leaf.

Unfortunately, although we are justified in assuming the existence of poisons or enzymes in the Fungus, no one has as yet established the fact of their presence in these Uredineae.

De Bary (24) and I myself showed long ago (196) very convincingly that such poisons and enzymes occur in other parasites—e.g. *Botrytis*—and numerous observers have proved the existence of about a dozen different kinds of enzymes in various other Fungi, but I failed to extract any such body from *P. dispersa* (190), and Dr. Green, who at my suggestion has undertaken the investigation of spores and mycelia of *Puccinia glumarum*, has also as yet failed to obtain results beyond the probability that diastase occurs, and possibly cytase also. However, since Dr. Green is continuing this work, we may hope that he will eventually be able to throw more light on the matter.

Now it is interesting to observe in this connexion that we frequently, and indeed usually, find 'immune' plants flecked with small yellow or orange spots. Miss Gibson has recently observed the same kind of thing on leaves of an 'immune' form of Chrysanthemum she was trying to infect with Chrysanthemum Rust during the recent hot weather.

That these flecks are due to the dead tissues shining through appears certain from our examination of a number of cases, and I find that such flecks of corroded tissue in which infection has failed have been observed in the open by other observers. My remarks on p. 298 of the paper 'On the Relations between Host and Parasite in the Bromes and their Brown Rust' (190) refers to the same phenomena.

Moreover, Klebahn states (98, p. 36): 'Keimschläuche und Nährzellen sterben ab, und in Folge der Braun- oder Rotfärbung des Inhalts der Nährzellen erscheinen braune oder rote Flecken an den Impfstellen.' So

beobachtete ich es an *Polygonatum*-Pflanzen, die mit den Sporidien von *Puccinia Convallariae-Digraphidis* besät worden waren.'

I have facts which go to show that infection-hyphae thus arrested in development—whether owing to the high temperature prevailing at the time or to reactions of the host-cells and independent of temperature—are not killed, but may lie dormant, and *may later on resume their growth*. If we can show that such inhibition and arrest of growth can be prolonged for more than a few days, the persistence of such dormant mycelia might explain a good deal. But it would not go to strengthen the mycoplasma hypothesis. But there is another point.

I have already stated (p. 13) that several observers agree that uredospores can live and remain capable of germination for long periods. I found those of *P. dispersa* retained their germinating power for sixty-one days (191, 1903, p. 138), and only brought the experiments to a close from lack of material. Miss Gibson has found uredospores of *Chrysanthemum Rust* germinate after keeping for ninety-four days, and has not yet reached the limit. Magnus (108, p. 18) found the uredo of *P. Caricis* persisted through the winter on the plant; Schröter found (156, p. 3) the same thing with a *Puccinia* on *Luzula*; and Barclay (2, p. 227) states that the uredo of *P. coronata* was found in winter; while Lagerheim found that of *P. Poarum* on *Poa* after the melting of the snow (102, p. 124). I myself found germinable uredospores of *P. dispersa* during every month of the year 1901–2, even in February and March (191, p. 132), and other cases are cited on pp. 13 and 14.

CONCLUSION.

Seeing that uredospores can be found nearly or quite all the year round; that they can be developed on odd tufts of grass here and there during the winter; and that they will retain their germinating power for two to three months—perhaps longer; that, further, specialized forms are not absolutely adapted to their hosts, but can occasionally infect races of Wheat, &c., which normally prove immune, or can pass from one hitherto excluded variety to another by means of 'bridging' species, where is the necessity of the mycoplasma hypothesis?

Moreover, it has been clearly shown—and is now conceded—that the so-called 'special corpuscles' supposed to be the 'mycoplasma' were merely haustoria; and I have traced all the phases of infection by means of sections at all stages shown in the field, and by means of similar sections at intervals of one, two, three to eight, or ten days after inoculation.

It has been shown that pure cultures of the Uredine give no evidence which lends the slightest support to the mycoplasma hypothesis; and all the evidence obtained from the study of starvation phenomena is equally non-supporting.

In fine, no trace of the alleged mycoplasm can be discovered, and all the facts point to the necessity of a thorough revision of the hypothesis in the light of comparison with the normal course of infection, and with what we now know of the behaviour of the spores.

Eriksson claims that the mycoplasm hypothesis is 'proved, at least until sufficiently comprehensive proofs to the contrary have been produced from some other quarter.' But this kind of argument cannot be accepted: the *onus* of proof is with him. I think that if the infecting spores are sought for, by means of serial sections through the flecks which yield the 'protomycelium' and 'mycoplasm' at their edges, they may be found, because we often find the entry even on the eighth or ninth day after inoculation, and are generally able to detect *the place of entry of the germ-tube in pustules on Wheat in the open*. Until this is done, I can only maintain that the mycoplasm hypothesis depends on the reading backwards of the course of events, on the part of an able and eminent observer, for whose work in other departments, and especially in the field, we must all have the greatest respect.

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