SOME NOTES ON THE HISTORY OF THE CLASSIFICATION OF THE UREDINALES.

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The Uredinales are a group which seem to give rise to more problems that do any other group of fungi. One has only to think of, amongst others, the problems of heteroecism, biological species, polymorphism and the relations with other groups to understand the attraction the group has, even for those botanists who have not otherwise the slightest interest in mycology. The Uredinales were amongst the earliest microscopic fungi to be noticed because of their attacks upon cereals. In the words of Persoon, " Plusieurs sont connues même du vulgare par le dommage qu'elles occasionent." In recent years, some people interested in their study have counted the number of times rusts are mentioned in the Old Testament, the infliction of blight or blasting being regarded as one of the Divine judgments for the sins of the people. The number seems to be at least five, the first occurring in Genesis. The reference in the New Testament to the " corruption " caused by " moth " and " rust " seems to have no phytopathological significance. We know that the Greeks and Romans were familiar with these diseases and it seems certain that any nation which cultivated cereals had at least a nodding acquaintance with what could, in such a mysterious way, cause such a difference in the crops upon which they so much depended. The nature of the disease was of necessity quite unknown to the ancients, but theories and assertions were never lacking.

As an example of what a competent naturalist of the 17th century thought of the subject one may take the case of Robert Plott, LL.D., Keeper of the Ashmolean Museum and " Professor of Chymistry " in the University of Oxford. Writing in 1686 in his book on the Natural History of Staffordshire (a book I have to thank Miss Lorrain Smith for calling my attention to) he mentions that to avoid blasting and smutting, the inhabitants of the county steeped " their grain in brine before they sowe it," and that (to prevent Meldewing, the most pernicious of all the annoyances, that inclosures and rich lands are lyable to, Thomas Cartwright, parish Clerk of Womburn, in this County, either mixes his corn with soot before he sowes it, or sowes soot upon

it after the wheat's in the ground: by which means he has preserv'd the corn from being Meldewed, in lands always observed to have been lyable to it, and this not for one or two, but for ten years together." He therefore looks "into the causes of this annoyance" and also how it comes to pass that this treatment "proves a Medecin for it."

"First then, as to the causes of Meldews some have thought them much occasioned by an unseasonable time of sowing, and therefore have sown very early, as judging corn most subject to this disease when sown late: but this cause is certainly but ill grounded some land meldewing at what time soever they are sown. Others again have placed the origin of meldewing in making small inclosures, corn not being so lyable to this evil in the common open fields: which tho' it must be confest in part, yet this can but be an accidental cause at most: for let the inclosures be never so small, so the land be poore the corn that it bears shall rarely be meldew'd. It remains therefore that the adequat original cause of this malady, must be in the richness of the soile, especially if not naturally, but made such by dung, which fattening it, and sending up a moist viscous steam, that upon congelation in the Air falls down upon the corn again in a dew of the sweetness and consistence of hony, and there sticking to the straw, and further harden'd by the Sun, so binds up the pores of it, that the nourishing juice in great measure is prevented thereby, ascending to the ear: whence the grain becomes shrank as we commonly see it in all corn affected with this distemper. And this I take to be the true origin, and process of Meldewing. Now if this steam when ascended, be anyway hindered, being dispersed by the wind, or shaken off the stalks of the corn, when fallen on them, by the height or narrowness of inclosures, it must be owned that they are thus farr an accidental social cause of Meldews: but for their true original I believe it to be nothing else but that viscous steam rais'd by the heat of the Sun out of the fattness of the dung, which is suck't up, or kept down by any adust matter, that it cannot ascend at all, as I suppose it is by the soot, the annoyance thereby is fully prevented." Where there is not sufficient soot for treatment he suggests "sowing bearded wheat, whose ailes catching the dew, do prevent in great measure its falling on the straw and doeing the mischief above mention'd."

As is well known Jethro Tull, the father of modern agriculture, in his book on "The Horse Hoeing Husbandry," as late as the third edition in 1751, attributes the attack to small insects "brought (some think) by the east wind" which feed upon the wheat leaving their excreta as black spots upon the straw "as is shown by the microscope."

Fontana in 1767 seems to have been the first to establish the

fungoid nature of the wheat rusts. He gives figures of the teleutospore and uredospore stages. He regarded them as rootless plants which exhausted the wheat and stated that no remedy was possible until a careful study of all the phases of the disease had been made.

Ninety years before this, however, Robert Hooke in his famous work *Micrographia* had decided that the rust on damask rose leaves must be a plant and gave an illustration of it.*

The idea that the rusts were parasitic fungi was not generally accepted until well into the 19th Century. This need occasion no surprise when it is considered what strange ideas were prevalent in certain other branches of botany.

The earliest British Floras contain very few references which can be interpreted as referring to Uredineae. Probably the first occurs in the 3rd Edition of Ray's Synopsis, 1724. This edition, which was published over twenty years after Ray's death, was edited by Dillenius, who was afterwards the first Sherardian professor of botany at Oxford. The editor's name did not, however, appear on the title page, as there was (in the words of Dillenius) " some apprehension (my being a foreigner) of making natives uneasy." The additions are, however, marked. Amongst these additions is given " Filix lobata, globularis pulverulentis undique aspera," and the remark that this singular fern was observed in the herbarium of Bobart, where the latter had himself written " This Capillary was gathered by the conjurer of Chalgrave." There is a figure given of the plant which is the leaf of *Anemone nemorosa* attacked by an aecidium. The plant even now is sometimes called " the conjurer of Chalgrave's fern." Who the conjuror was I have been unable to find out, but his place of residence was Chalgrove, the scene of John Hampden's death, and not Chalgrave, if Dillenius' statement that the village is situated seven miles from Oxford is correct. In Druce's Flora of Oxfordshire the name is spelled Chalgrove and it is stated that the original plant is in the Morisonian Herbarium at Oxford. Mr. Druce, however, now informs me that the specimen has been lost, probably during the removal of the collection from the old Sherardian rooms to the present Fielding Herbarium. The Bobart " imposed upon " and given the plant " either ignorantly or in wantonness " is Jacob Bobart the younger, who was the collaborator of Morison (the first Regius professor of Botany at Oxford), and afterwards his successor, who gained fame by transforming a dead rat into the feigned figure of a dragon, which imposed upon the learned so much that " several fine

*Trans. Brit. Mycol. Soc., Vol. iii., pp. 19-20 (1908).

copies of verse were wrote on so rare a subject:" and not Jacob Bobart the elder, who was superintendent of the Oxford botanic garden and who, on rejoicing days, used to have his beard "tagged with silver."

John Hill, in his British Herbal of 1756, under *Anemone nemorosa*, points out Dillenius' error stating that "a small winged insect is apt to deposit its eggs on the underpart of the leaves of this species, and they somewhat resemble the round dots in which the seeds of ferns are lodged. A leaf of it thus decorated is unluckily represented in a figure in the last edition of Ray's Synopsis. The form, substance and disposition of these dots ought to have informed the botanist they were not seeds."

Richard Pulteney, in a paper read before the Linnaean Society in 1792, traces the history of the knowledge of this diseased *Anemone*. He had known the plant for many years but had never troubled about it, having rested in the opinion which he "had met with in several modern authors that the Tubercula or Puncta, as they have been most commonly styled, on the leaves of *Anemone nemorosa*, were the eggs of an insect." He found on examination, however, that the tubercles were themselves a vegetable production of a parasitical kind of the order of fungi," and considered the cause of the disease to be a *Lycoperdon—L. anemones*. He found he could trace the knowledge of such a diseased plant back to the Sylva Hercynia of Thalius, 1585, where it is considered as a distinct species of *Ranunculus*, the infected plants always being sterile: and that Maurice Hoffmann as early as 1662 had ascribed the appearance to the work of insects. It is probable that Pulteney was describing *Aecidium leucospermum*, whereas the Conjurer of Chalgrave's Fern was *Aecidium fuscum*, according to Baxter, "on the authority of the original specimen in Bobart's Herbarium." Pulteney states that the then professor of Botany at Oxford had informed him that he had seen among Dillenius' papers a correction of the mistake by Dillenius himself.

The aecidium on *Tussilago* early attracted attention and was given the name *Lycoperdon epiphyllum* in Linnaeus' Species Plantarum 1753. In the same work *Gymnosporangium juniperinum* appeared under the name *Tremella juniperina*.

Lycoperdon epiphyllum was an extremely convenient species. Any aecidium for a time was placed here, but what more could be expected when the examination was conducted, say, "with one of Mr. Adams's pocket lenses of three glasses united."

In British Floras we first find the name occurring in Lightfoot's Flora Scotica published in 1777. It is given as occurring on dead leaves, moss and rotten wood, and is a species of *Trichia*.

The rusts are mentioned incidentally in the 1st edition of Withering's Botanical Arrangement, 1776, where, in speaking of *Berberis* he states:—"This shrub should never be permitted to grow in corn lands, for the ears of wheat that grow near it never fill, and its influence in this respect has been known to extend as far as 300 or 400 yards across a field." In the 2nd edition, 1792, we find *Lycoperdon epiphyllum* in its proper sense and a statement to the effect that it is not Lightfoot's *L. epiphyllum* which is *Trichia turbinata.*

In the 3rd edition of this work, 1796, the number is increased by the addition of *Lycoperdon innatum* growing on *Anemone nemorosa, Adoxa, Carduus arvensis,* and *Betonica officinialis.* These hosts are copied from Relhan's Flora of Cambridge: the description is really that of *Aecidium leucospermum,* but there is given in the synonomy *Aecidium fuscum* and the *Conjuror of Chalgrave's fern. Gymnosporangium Sabinae* occurs as *Tremella Sabinae* amongst algae and true Tremellas, just as the genus *Lycoperdon* also included true Lycoperdons and certain Myxomycetes.

In the 4th edition (1801), edited by Withering's son, we find under *Lycoperdon epiphyllum* a note which, from the date given, seems to be one by Withering himself. "The spots on *Sorbus aucuparia* consist of minute globules intermixed with wool-like fibres. On examining many of them in different states I at last found a small maggot in some of the younger spots, so that the globules are probably its excrement, and the fibres the woody fibres of the plant unfit for food." So much for *Gymnosporangium juniperinum.*

In the 7th edition, 1830, there is no alteration in the two species of *Lycoperdon* but five species of *Uredo* are given, and this only six years before the appearance of Berkeley's contribution to Smith's English Flora. Withering, in his Preface to this edition, apologises for the paucity of Cryptogamic material presented. He is evidently quite out of sympathy with "this overgrown class." "Experience warrants the conclusion that individuals far more highly gifted have hitherto failed to reduce these countless tribes to systematic order." Mycological studies especially "cannot be rendered palatable to the generality of Botanists. . . Experience evinces that this particular branch of science is almost daily becoming and must inevitably become, even to the proficient, a separate study, fully available only to the lynx-eyed few." By taking such a view Withering contrived to include just the same number of Uredineae for the whole of the British Isles as Relhan had in the Flora of Cambridge ten years before.

Persoon was the first to bring about anything like order in the study of the rusts. So much so that by the International Rules

Persoon's Synopsis (1801) is to be the starting point for the nomenclature of this group.

Puccinia, Uredo and *Aecidium* were three genera founded by Persoon. The first genus to be diagnosed was *Aecidium*, the diagnosis of which appeared in Gmelin's Linné Systema Vegetabilium, 1791. Eighteen species were described, including *Aecidium berberidis*, *A. tussilaginis* (given as equalling Linnaeus' old species *Lycoperdon epiphyllum*) and *Aecidium candidum*. The name *Aecidium* had previously been used by Hill in his History of Plants, 1751. Hill gives a description of his genus. It has a "tolerably firm structure and marked with round protuberances on the surface which are the coverings of certain cells . . . of the same nature with those of" *Xylaria*. It was because of the flask-shaped perithecia he bestowed the name. "We have called," he says, "this genus distinguished by its peculiar cells *Aecidium*, from the Greek ὰικιδιον, cellula." (Persoon did not correct the spelling of the name.) The genus includes certain large Pyrenomycetes such as *Nummularia*. The species grow either in the clefts and fissures of old trees or between the bark and the wood. Three species are fully described—male and female organs as well. The other species, ten in number, "will be easily distinguished by their names: they are the white thick Aecidium, the black thinner Aecidium, the hairy grey Aecidium growing on old Oaks," and so on. In spite of Hill's assertion no European botanist would pretend to know what these easily distinguished species are. This method of description is quite typical of John Hill, Sir John* as he called himself, being a member of the Swedish order of Vasa. He was a very versatile person, being somewhat of a player, apothecary, poet, botanist, playright, and, according to his contemporaries, rogue. He had controversies with very many notable people. Dr. Johnson had a very decided opinion about him. Christopher Smart, following some anonymous abuse by Hill of his work, composed "The Hilliad: an epic poem," in which he indulged in some rather free expressions. David Garrick wrote the famous couplet concerning him, "For physic and farces, his equal there scarce is, His farces are physic, his physic a farce is." He obtained the appointment of Superintendent of the Royal Gardens at Kew: the grant, however, does not appear to have been confirmed. He was a most voluminous writer and wrote the first Linnaean Flora of Britain. Concerning his botany Sir J. E. Smith wrote "sometimes, as Linnaeus says, a blind hen meets with a grain of corn."

Uredo was diagnosed in 1794 and four species given. They

* Mr. Claridge Druce has called my attention to a passage in Gent. Mag. 1774, p. 282, from which it is apparent that George III. acknowledged the title, for Hill, "was received at Court with the proper ensigns as knight."

are all good Uredos. The date usually given for *Uredo*, however, is 1795, when Persoon diagnosed the genus again. He was less successful this time. He described three species, the first two of which, *Uredo candida* and *Uredo mycophila*, are not now included in the Uredinales, the first being *Cystopus candidus* and the second *Sepedonium chrysospermum*.

The date, 1794, is also the correct one for the first use by Persoon of the name *Puccinia*. He described five specimens. The name *Puccinia* was first used by Micheli in his Nova Plantarum genera, 1729, the name being given in honour of Professor Puccini of Florence. Two species were described and figured, the one *Puccinia non ramosa, &c.*, being the present *Gymnosporangium juniperinum*, the other, *Puccinia ramosa, &c.*, being the Myxomycete *Ceratiomyxa fruticulosa*. The name *Puccinia* occurs several times between Micheli and Persoon in Micheli's sense, but Persoon redefined the genus taking out the myxomycete and adding a *Phragmidium* and three species of *Puccinia*, one of which is the famous *Puccinia graminis*. Link afterwards took out the *Uredo mucronata* (the *Puccinia non ramosa* of Micheli) and made it the type of his genus *Phragmidium*. No one apparently ever used the genus *Aecidium* in Hill's sense. Possibly the man who was forbidden Chelsea Physic Garden "for making too free use of the plants" could not be trusted to describe merely what he saw.

In the Tentamen, 1797, Persoon widely separated *Puccinia* from *Uredo* and *Aecidium*, which two he had placed together from the first. In his Synopsis he divides the fungus group into two classes, Angiocarpi and Gymnocarpi. The former class is divided into three orders, Sclerocarpi, Sarcocarpi and Dermatocarpi. The section Trichospermi of the last order includes the Gasteromycetes and Myxomycetes, while the section Gymnospermi includes *Aecidium*, *Uredo* and *Puccinia*, together with such genera as *Licea*, *Onygena* and *Trichoderma*. (The third section, Sarcospermi, includes only *Cyathus*). The grouping together of *Aecidium*, *Uredo* and *Puccinia* is the germ of the modern cohort Uredinales. The classification put forward in the Synopsis was followed by Albertini and Schweinitz in their Conspectus Fungorum, 1805, and by Sir W. J. Hooker in his Flora Scotica, 1821. In the Flore Française, 1805, De Candolle divided the fungi into Persoon's two main divisions, Angiocarpi and Gymnocarpi. He then subdivides the Angiocarpi into those genera without peridia (*Gymnosporangium*, which is here first diagnosed, *Puccinia* [species classified according to the number of compartments in the spore], *Bullaria* [*Puccinia*], *Uredo*); those genera with peridia in which there are no filaments (*Aecidium*, *Mucor*, *Licea*, *Tubulina*) and a third group where there are such filaments (Myxomycetes and Gasteromycetes).

The first reference which the present writer has been able to find to the Uredineae as a group occurs in Persoon's Traité sur les Champignons, 1818. It is not defined but he says "Une autre petite famille très-naturelle et très-riche en espèces est celle des *Urédinées*, toutes parasites sous l'épiderme des feuilles encore vertes, rarement sur les branches sèches, et quelques-unes dans les épis des céréales. . . Leur poussière est en proportion de leur petitesse très-abondante, mais sans filets; elle est aussi souvent dépourvue d'un péridié, et dans ce cas elle est entourée d'une partie de l'epidermie de la plante-mère, qui en fait la fonction, étant modifiée en faux-péridié. Leur grains paroissent être des capsules propres, qui dans le genre Puccinia sont cloissonnées. Les *Puccinia*, *Podisoma* Link., ou *Gymnosporangium* Decand.; les *Uredo* (Ustilago) et *Aecidium* (Roestelia), sont les genres les plus connus de cette division."

At this time *Puccinia*, *Uredo* and *Aecidium* were usually regarded as separate genera though certain botanists began to have serious doubts upon the subject. In the words of Sachs, "The lower, the small and simple Fungi, those especially which are parasitic on plants and animals, were the most attractive objects in the whole field of mycology. Here were difficulties in abundance, here were the darkest enigmas with which botany has ever had to deal, here was new ground to be slowly won by extreme scientific circumspection and foresight. In these forms, as in the Algae, the first thing to be done was to make out the complete history of development in a few species; but it was more difficult in the Fungi than in the Algae to discover what properly belonged to one cycle of development and to separate it from casual phases of development of other Fungi."

Sir Joseph Banks, in 1805, wrote a most interesting letter on the Blight in corn, which he distributed to those interested in Agriculture; it was afterwards republished in several scientific journals. Banks was then President of the Royal Society. It may be of interest to some to learn that the Department of Botany at the British Museum was originally known as the Banksian department and was established for the reception of the herbarium of Banks, who shortly before his death in 1820, bequeathed it to Robert Brown. When Brown died it was to become the property of the British Museum, although with Brown's consent the herbarium might be, and as a matter of fact actually was, removed to the Museum during his life-time. The books in the Department are always stamped on their cover with a representation of the genus *Banksia*.

In Banks' letter he suggests that the uredo and the teleutospore stage are connected though he does not definitely state how. He probably did not understand the proper nature of the relation. "It seems probable that the leaf is first infected in

the spring, or early in the summer, before the corn shoots up into straw, and that the fungus is then of an orange colour: after the straw is become yellow, the fungus assumes a deep chocolate brown." He thought the teleutospores contained a large number of seeds, "a sort of animated dust." Taking account of the large number of these spores he gives a very good idea of the struggle for existence. "Providence, however, careful of the creatures it has created, has benevolently provided against the extensive multiplication of any species of being; was it otherwise, the minute plants and animals, enemies against which man has the fewest means of defence, would increase to an inordinate extent; this, however, can in no case happen, unless many predisposing causes afford their combined assistance. But for this wise and beneficent provision, the plague of slugs, the plague of mice, the plagues of grubs, wire-worms, chafers, and many other creatures whose powers of multiplying is countless as the sands of the sea, would, long before this time, have driven mankind and all the larger animals, from the face of the earth." He also considers the case of the relation between the aecidium stage on Barberry and the stages on wheat. "It has long been admitted by farmers, though scarcely credited by botanists, that wheat in the neighbourhood of a barberry bush seldom escapes the Blight. The village of Rollesby, in Norfolk, where barberries abound, and wheat seldom succeeds, is called by the opprobrious appellation of Mildew Rollesby. Some observing men have of late attributed this very perplexing effect to the farina of the flowers of the barberry, which is in truth yellow, and resembles in some degree the appearance of the rust, or what is presumed to be the Blight in its early state. It is, however, notorious to all botanical observers, that the leaves of the barberry are very subject to the attack of a yellow parasitic fungus, larger, but otherwise much resembling, the rust in corn. Is it not more than possible that the parasitic fungus of the barberry and that of wheat are one and the same species, and that the seed transferred from the barberry to the corn, is one cause of the disease? Mistletoe, the parasitic plant with which we are the best acquainted, delights most to grow on the apple and hawthorn, but it flourishes occasionally on trees widely differing in their nature from both of these."

To the 2nd edition of Banks' letter, 1806, there is appended a letter from the famous horticulturist Thomas Andrew Knight, who afterwards became President of the Royal Horticultural Society, and who is well known to elementary students of physiological botany through their wearying efforts to understand the theory of Knight's wheel.

Knight writes as follows:—"An opinion prevailing very

generally in this, as in other districts, that the barberry tree communicates disease to wheat and other plants in its vicinity, I sowed, in the autumn of 1804, a row of wheat round a plant of that kind, which grew in my garden, the soil of which is a shallow loam or a limestone gravel; and I also sowed several small portions of seed of the same kind in a meadow, the soil of which was very similar to that of my garden, though situated at a considerable distance from it. All the plants continued perfectly healthy till the beginning of July, when those near the barberry bush showed evident symptoms of disease. . . . Examining the barberry bush attentively, I found upon its fruit a species of fungus similar in colour to that on the straws of the wheat; but its seed vessels were larger, and more spherical. I was, however, much disposed to believe the parasitical plants of the same species, and that the difference in the form and size of the seed vessels arose only from the difference of the nutriment they derived from the wheat, and from the acrid juice of the barberry. The plants of wheat, which grew at a distance from the barberry bush, remaining free from the disease, I carried a branch of barberry, with diseased fruit upon it, to one of them, and wetting it with water, I brushed the wheat plants with it, repeating this operation three successive days. I at the same time applied a part of the diseased straws which had grown near the barberry bush, to other plants of wheat, which were free from disease, leaving upon them so large a portion of the seeds and seed vessels of the mildew, as to be visible without the aid of a lens. In the course of ten days the plants of wheat, which I had endeavoured to infect by means of the barberry branches and fruit, became covered with disease, whilst those to which I had applied the mildewed straws were not sensibly affected. I attributed the health of these to the want of moisture necessary to make the seeds of the mildew vegetate, and I therefore sprinkled them plentifully with water in the three succeeding days; and at the end of ten days I found them all diseased as in the preceding cases."

Knight seems to have thus been the first to try inoculation experiments on heteroecism. He sifted his ideas in an intelligent manner, but was quite led astray by his previous notions. He continues: "As water had been applied in each of the preceding experiments, it became necessary to ascertain how far that fluid alone might be capable of inducing disease without the aid either of the barberry, or diseased straws; and I therefore, whilst repeating the experiment last described, sprinkled a remaining portion of plants at the same hour with water only." He significantly adds, "and I was not very much surprised to find that these became as much diseased, within the same period of time, as any of those I have described." He states

that very cold water was applied early in the afternoon of warm and bright days; the ground in which the plants grew was very dry, therefore there was probably a considerable absorption of water, and to this and a sudden change of temperature as secondary causes, Knight was disposed to attribute the appearance of the disease. He does not attempt to solve whether the spores of the fungus were carried by the water or were already there. He states that the applications of water to any plant on which the sun is shining strongly is very injurious to its health and therefore likely to give increased activity to any disease to which the plant is subject. Nevertheless, he holds that "the opinion so generally entertained both in this kingdom and on the continent, by practical farmers, that barberry trees are injurious to corn, deserves very considerable attention." That this was not Knight's first experiment with fungus spores is seen by the note in Sowerby's Fungi, 1803, where under *Farinaria pomacia* it is recorded that he "observed that on shaking the [diseased apple] leaf over a piece of talc or glass he detected little oval bodies which shrivelled a little in drying. Some of these were transferred to other trees, and the disorder along with each, every one producing its own species."

De Candolle (1807) agreed with Banks that the Uredo and Puccinia stages were connected, the *Uredo* becoming a *Puccinia* on further growth, but later he suggested the two might be definite stages in the life history.

Prévost, in a remarkable paper in 1807, records that he has seen *Uredo* and *Phragmidium* in the same sorus. He had at first thought that the spores of *Phragmidium* were male organs. He thinks the mycelium the first stage, from which spring the teleutospores, the uredospores arising in the loculi of these. The important work of Prévost, however, was in connection with the germination of spores. He germinated the uredospores of *Uredo linearis* and *Uredo Alliorum*. On germinating the spores of *Albugo* or *Cystopus candidus*, then called by Persoon's name *Uredo candida*, he found that they gave rise to zoospores, a fact that was taken no notice of by systematists till the time of de Bary.

In the first half of the nineteenth century there were great controversies as to the relation existing between the uredo-stage and the teleuto-stage.

Albertini and Schweinitz stated that *Uredo* always appears before *Phragmidium* and from the fact that sometimes sori occur which consist of pure *Phragmidium*, the latter must develop at the expense of the detritus of the *Uredo*.

Corda, Fries, Schlechtendal and Léveillé on the other hand held that the uredospore was parasitic on the teleutospore.

Eysenhart stated that *Uredo* and *Phragmidium* often live

together without apparent prejudice. His opinion was that the *Uredo* changed into the *Phragmidium*, but this change was not seen because it was brought about too quickly—a very modern-sounding explanation. Schwabe also assented to this explanation and did not even trouble to separate the genera.

Unger did not agree with this idea. He held the two kinds of spores to be contemporaneous and associated productions though independent and holding no necessary relation to one another. He gave seven or eight species of *Phragmidium* habitually accompanied by *Uredo*.

In 1841, Henslow, then professor of Botany at Cambridge, turned his attention to the Uredineae owing to the failure of the candidates for a prize essay offered by the Royal Agricultural Society to bring forth anything of worth. He stated that he had satisfied himself " by direct observation, that the fungus which first produces the orange-coloured spores of *Uredo rosae*, also gives rise to other spores of a very different form . . . *(Aregma mucronatum)* " and talking of Mildew he says: " I have observed this fungus intermixed with the rust-fungi in a way which strengthens my opinion that they are identical." In a later paper of the same year "On the Specific Identity of the Fungi producing Rust and Mildew " he gives additional evidence for this opinion. Also he states: " As the fact of the berberry occasioning some sort of blight in wheat, but more especially mildew, has been forcibly brought before me from several quarters since my last report was written, I am bound to suppose that there must occasionally exist some relation between the presence of this shrub and the occurrence of mildew in wheat. At present I have met with no evidence which can explain the nature of this relation." He suggests, however, that it may be due to some ingredient in the soil, some different form of development belonging to the same fungus or to bad odours!

In 1847 L. R. Tulasne published his first Mémoire on the Ustilagineae and Uredineae in collaboration with his brother. He gives a practically complete résumé of previous work on the structure of the group. He first made clear the nature of the paraphyses in *Phragmidium*, which Unger had thought to be young spores of *Uredo*, Corda had thought to be basidia and Prévost had regarded as young pericarps, from which the uredospores had escaped prematurely.

He also continued the work begun by Prévost on germination. Corda meanwhile had attempted to germinate the spores of *Aecidium Tussilaginis*. Tulasne germinated the spores of *Uredo suaveolens* and *Uredo Rosae;* and asserted definitely that the *Uredo* which was known to accompany *Phragmidium* was a definite spore form of the same species.

In Tulasne's 2nd ' Mémoire ' (1854), he definitely proves that

Uredo and *Phragmidium* are different stages of the same species. His previous studies on the polymorphism of other fungi was of great help to him in understanding this problem. If the two are not definite stages of the same fungus then he holds their occurrence together must be accidental and of no physiological character, or one must be a necessary parasite on the other. He thinks the relation too obvious for the first explanation and too close for the second for either to be probable.

Tulasne also studied the spermogonia of the Uredinales, giving this name to them as he had previously done to similar structures in other fungus groups and in Lichens. Unger in 1838 had worked out the structure of these organs and noted that they appeared slightly before the aecidia. He thought they were separate fungi and gave them the name *Aecidiolum exanthematum.* Meyen in 1841 thought they might be male organs, although he fully realised that fertilisation of the ordinary type could not possibly occur in the group. Tulasne agreed with this suggested function, but did not attempt to explain the method of fertilisation. From 1851 he grouped the Uredinales amongst those fungi possessing spermogonia. In 1852 de Bary proved that the spermogonia and the aecidia arose from the same mycelium. It is interesting to note that Sowerby at the beginning of the century had more or less suggested this function for the spermogonia. Speaking of the "troublesome parasite" *Aecidium cancellatum* he states that "This Fungus, which grows under the leaves has been considered as a distinct species; but from these specimens it seems scarcely doubtful that they are analogous to the diœcious class of plants, and are of one and the same species. Those on the upper side of the leaf might have been considered, if alone, as a *Sphaeria,* but as they may belong to the opposite parasite, they must be included as one dioecious species." He adds: "The peculiarities of particular Fungi will afford much entertainment." Tulasne worked out what he called the dimorphism in thirteen genera of the Uredinales and gave the results of his germination experiments with teleutospores, aecidiospores and uredospores, and the determining factors controlling the germination of each. He homologised the promycelium produced on the germination of the teleutospore with the basidium of *Auricularia.*

In 1821 there appeared Gray's Natural Arrangement of Plants, the first of the British Floras to break away from the traditional Linnaean classification. We have seen how the younger Withering, even so late as 1830, had only managed to find room in his four volumes for seven species of the Uredineae. That Gray had a wide conception of what constitutes botany is

shown in a charming manner in the section of his book labelled " Introduction to Botany," where he informs us that " Anne of Cleves, when transformed by Act of Parliament from the wife into the sister of Henry [VIII.], endeavoured to forget the slights of the monarch in the cultivation of vegetables." He includes over fifty species of rusts in his family Protomyceae. The family is divided up into sections. Coeomideae *(Roestelia, Aecidium, Ustilago, Uredo, Albugo* [much better known under Léveillé's name *Cystopus* proposed twenty-six years later], *Coeomurus* [*Uromyces*], *Dicaeoma* [*Puccinia*], *Puccinia* [*Phragmidium*] and *Podisoma* [*Gymnosporangium*]). Stilbosporideae *(Fusidium, Stilbospora).* Xylomideae *(Xyloma* [*Rhytisma*]). Gymnosporangideae *(Gymnosporangium).* Aegeritideae *(Aegerita, Fusarium)* and Tuberculariadae *(Tubercularia).*

This classification is very similar to that of Nees von Esenbeck in his System der Pilze (1816-7). Here the fungi are divided into certain groups. The group Protomyci has several divisions, one of which, the Coniomyci has a section Entophyti composed of *Caeoma (Roestelia, Aecidium, Ustilago, Uredo, Dicaeoma), Puccinia* and *Podisoma.* The division Sphaeromyci section Entophyti contains simply *Gymnosporangium.* The Liberi sections of these divisions include such genera as *Fusidium* and *Fusarium.* Martius (Flora Cryptogamica Erlangensis 1817) has a very similar classification. His ' Coniomycetes elementares entophyti ' are the same as Nees' Coniomyci entophyti but *Xyloma* is added: Coniomycetes elementares liberi consist of *Fusidium, Stilbospora,* &c. In the Coniomycetes suffulti the section evoluti contains *Tubercularia, Calycium* and *Gymnosporangium.*

In 1821 Fries began the publication of his Systema Mycologicum. In his introduction he divides the Fungi into Coniomycetes, Hyphomycetes, Gasteromycetes, and Hymenomycetes. The Coniomycetes are then sub-divided into Entophytae, Sporodesmia, Coniosporia and Tuberculariae. The Entophytae are further divided into Hypodermia (parasitic on living plants: *Coeoma, Spilocaea, Phragmidium, Podisoma)* and Stilbosporei (endophytic on dead plants: *Melanconium, Fusidium, Stilbospora, Naemaspora).* Sporodesmia consisted of *Seiridium, Sporodesmium, Exosporium,* and *Gymnosporangium.*

The classification followed in the body of the book (the Coniomycetes were included in the portion published 1832) is somewhat different.

Ordo I. Tuberculariní. *Tubercularia, Volutella, Fusarium, Blennoria, Coryneum, Dicoccum, Schizoderma.*

Ordo II. Stilbosporei. *Naemaspora, Septoria, Fusidium, Cryptosporium, Stilbospora, Didymosporium, Melanconium.*

Ordo III. Sporodesmiei. *Conoplea, Phragmotrichum, Sporidesmium, Aregma, Xenodochus, Torula, Spilocaea.*

Ordo IV. Hypodermii s. Entophyti. *Gymnosporangium, Podisoma, Puccinia, Epitea, Aecidium, Uredo, Ustilago.*

Fries certainly had not a very great opinion of the Hypodermii. The characters he gives to the order are " Vegetatio propria nulla. Sporidia ex anamorphosi telae cellulosae *plantarum vivarum* orta; sub earum epidermide enata et per hanc erumpentia." They are *fungi inferioris ordinis.*

The influence of Fries was such that his lead was followed even in the classification of a group which he little understood and apparently rather despised. In this country Berkeley used the classification in the section he wrote of Smith's English Flora, 1836. He says, however: " I cannot adopt the character of Fries, which begins 'no proper vegetation, *sporidia* arising from an anamorphosis of the cells of living vegetables.' If this were really the case, however interesting in a physiological point of view, these productions ought to be excluded entirely from the list of Fungi on the same principle by which the exclusion of *Erineum* is justified."

Corda (1842) divided the Fungi up as Fries had done but the group Myelomycetes replaced the Gasteromycetes. He subdivided his larger groups into families. The Caeomaceae and the Phragmidiaceae were included in the Coniomycetes. The Aecidiaceae, however, were placed in the Myelomycetes amongst Mucoroideae, Gasteromycetes, Tuberaceae, Pyrenomycetes, Fungi Imperfecti, &c.

Berkeley (Introduction to Cryptogamic Botany 1857), had as two of the divisions the Coniomycetes, Caeomacei of Corda, and Pucciniae. In Outlines of British Fungology, 1860, his divisions were Pucciniaei and Aecidiacei.

Cooke, who sat at the feet of Berkeley and inherited all the latter's conservatism, combined these two classifications in his Handbook of British Fungi 1871. Uredineae, still included with the Sphaeronemei and Melanconiae in the Coniomycetes, are divided into Pucciniaei, Caeomacei and Aecidiacei. Even at this date *Tilletia, Ustilago* and *Cystopus* were included in the Caeomacei.

Greville's Flora Edinensis was published in the year 1824. His classification of fungi is somewhat strange. There are three divisions, Fungi Link, Grev., Gastromyci Link, Grev. and Byssoideae Grev. In the Gastromyci, Division II. is composed of

the Uredineae, consisting of *Puccinia* (29 species), *Uredo* (45 species) and *Aecidium* (20 species). The descriptions are accompanied by very valuable notes. I have searched through the works of Link but his Gastromyci group is, in all cases, different from Greville's, which latter contains amongst other genera, *Tremella, Stilbum, Pilobolus, Erysiphe,* together with the Myxomycetes.

Link's best known classification is that contained in the fourth edition of Linné's, Species Plantarum 1824.

I. Hyphomycetes.

II. Gymnomycetes.
- Series 1. *Caeoma, Puccinia, Triphragmium, Phragmidium* and several other genera such as *Melanconium* and *Fusidium.*
- Series 2. *Fusarium, Isaria, Ceratium,* &c.
- Series 3. *Podisoma, Gymnosporangium* with *Sporidesmium, Coryneum,* &c.

III. Gasteromycetes.

IV. Sarcomycetes.

In this work *Triphragmium* and *Phragmidium* were diagnosed, the genus *Uromyces* having already been founded by Link (1816).

Brongniart (1824) attempted a natural classification of the fungi. He gives five families: Uredineae, Mucedineae, Lycoperdaceae, Champignons and the Hypoxyleae. The Uredineae (which are more or less the equivalents of the Coniomycetes) are divided into four tribes, Urédinées vraies, Fusidiées, Bactridiées and Stilbosporées. The grouping of the true Uredineae together was an advance on many of the contemporary classifications, but the inclusion of the other tribes in the Uredineae made for great confusion.

Léveillé (1839) wrote a paper on the development of the Uredineae. He divided the group into three families. 1. Aecidineae: *Roestelia, Aecidium, Peridermium, Endophyllum.* 2. Uredineae: *Phragmidium, Triphragmium, Puccinia, Uredo, Gymnosporangium,* " auxquels on peut joindre sans inconvénient " *Coryneum, Exosporium, Sporidesmium.* 3. Ustilagineae: *Ustilago, Sporisorium* and perhaps *Sepedonium* and *Testicularia.* These families are " trop distinctes " he said to form a single one under the Uredineae or entophytes. They cannot be confounded since in the first the spores are enclosed in " receptacles propres " which open in different ways: in the second the spores, or better still sporangia, are free and fixed on a stroma which is more or less developed, while in the third the spores have neither receptacle nor stroma but coexist with

byssoid filaments of which the mutual relation is not yet known. The chief fault of this attempt at classification was that many genera foreign to the group were added to Brongniart's "Urédinées vraies."

In 1847 Léveillé had another attempt at classifying the rusts. He states that these fungi are named chiefly from their hosts—a statement which is not surprising. Therefore he holds that the same fungus on different hosts has different names and different fungi on the same host the same name. He considers, with what might be regarded as optimism, that his system would enable one to name the fungus when isolated from the plant which gives it support. He divides the group into 1. Uredineae without cystidia: *Uromyces, Pileolaria, Cystopus, Uredo, Polycystis, Tilletia, Microbotryum, Ustilago, Thecaphora, Coleosporium.* 2. Uredineae with cystidia: *Lecythea, Physonema, Podosporium.* 3. Doubtful Uredineae: *Protomyces, Spilocaea, Melampsora.* It will be noticed that the Ustilagineae find their way back to the Uredineae and that *Melampsora* loses its place. It is not regarded as having true spores. Léveillé's conception of many of the genera was remarkable and in the thirty-six species which he gives of *Uromyces* he includes at least three other well-known genera.

It is to Tulasne that we owe the clearing up of ideas on the group in classification as in morphology. The classification given by Tulasne in his second memoir (1854) is as follows:—

I. Albuginei (candidi s. melini, heterospori). *Cystopus.*
II. Aecidinei (peridiati, homoeospori). *Caeoma, Aecidium, Roestelia, Peridermium.*
III. Melampsorei (solidi, pulvinati, biformes). *Melampsora, Coleosporium.*
IV. Phragmidiacei (pulverulenti, biformes, infuscati; ordinis centrum). *Phragmidium, Triphragmium, Puccinia, Uromyces, Pileolaria.*
V. Pucciniei (carnosi, ligulati v. tremelliformes, nudi et fructibus uniformes; ordinis magnates). *Podisoma, Gymnosporangium.*
VI. Cronartei (peridiati, biformes, ligulati, omnium fortassis prae structura nobilissimi). *Cronartium.*

This classification is the basis of all the modern systems. The Ustilagineae are removed from the group. The Albuginei are placed in the group with some doubt. Tulasne had not been able to confirm Prévost's account of the formation of zoospores in *Cystopus*, the confirmation of which came later from de Bary. A point of interest is that the genus *Puccinia* is included in the Phragmidiacei, while the Pucciniei consists of *Podisoma* and *Gymnosporangium.* The inclusion of the group

Aecidinei was justifiable in that it was not then known that *Aecidium*, *Peridermium*, &c., were only stages in the life history of other fungi. This was first shown to be the case by de Bary (1863) working with the autoecious eu-form *Uromyces Fabae*. He germinated teleutospores in artificial media and inoculated bean plants with the sporidia obtained. After nine days spermogonia appeared and aecidia shortly afterwards. About a month after inoculation teleutospores and uredospores were formed. It was certain that these were produced by the same mycelium as the aecidia and spermogonia. The next step taken by de Bary was to prove that the aecidia and spermogonia could be produced on one plant, whereas the uredospores and teleutospores were borne on another. This work on heteroecism began with *Puccinia graminis* in 1865. We have seen how various observers had fumbled about with the idea, but it remained for de Bary to scientifically prove that such a remarkable phenomenon existed. By inoculating barberry leaves with sporidia produced by germinating teleutospores he obtained aecidia and spermogonia. Then when aecidiospores are placed on wheat plants, uredospores and afterwards teleutospores were produced. The work of de Bary soon bore fruit, but many mycologists who totally failed to apprehend the significance of cultural methods criticised the doctrine rather freely. All cultural experiments were not of course successful. The correct conditions for infection were not realised, and modern cultural work on biological species points out another factor which must certainly have caused negative results. Many mycologists seem to think that the fact that farmers had thought there was some connection between the barberry and the wheat mildew was an essential part of the proof of heteroecism. In this country Cooke strongly opposed the idea, but Plowright gave it great support and conducted numerous experiments. W. G. Smith could say in 1884 "Men of science of the present day do not generally try to support their views by quoting what other observers thought one or two hundred years ago, particularly when those observers were not specialists. Old observers were doubtless right in many of their ideas, but no support is given to modern views by quoting the opinions of old authors who were but poorly acquainted with their subject. . . . . Some rustics believe that mushrooms spring from salt, because 'experience has taught' the practical farmer that a dressing of salt over a non-productive pasture will generally cause a good crop of mushrooms to appear. The result in this instance, however unvarying, does not prove genetic relationship," and so on. Whatever might be said of our older British mycologists it cannot be affirmed that their style of writing lacked vigour.

Schroeter in 1879 suggested dividing each genus of the Uredineae into sub-genera or forms depending upon the number of spore forms present in its life cycle. Thus using the initial letters to represent the spores, those forms with S, A, U, T are *eu*-forms, S, A, T-opsis, S, U, T, *Brachy*- U, T, *Hemi*-, T, *Micro*- or *Lepto*- (e.g. Eupuccinia, Pucciniopsis, &c.) the first four teleutospores requiring a period of rest before germinating, while in the last case the teleutospores germinate at once. This convenient classification has been adopted in most systematic works.

Winter in Rabenhorst's Cryptogamic Flora (1884) uses this division of the genera and was the first to apply the facts obtained by cultural experiments to relate up the various spore forms in the life cycle of each species. He does not arrange the genera in families, however, but merely lists them. Plowright in his Monograph (1889) followed this method but his sequence of genera is somewhat different.

Schroeter (Cohn's Kryptogamen Flora von Schlesien 1885) made a forward step in dividing the group. His classification is as follows:—

I. Pucciniei. *Uromyces, Puccinia.*
II. Phragmidiei. *Trachyspora, Triphragmium, Phragmidium.*
III. Endophyllei. *Endophyllum.*
IV. Gymnosporangiei. *Gymnosporangium.*
V. Melampsorei. *Melampsora (Pucciniastrum, Thecospora), Melampsorella, Calyptospora, Coleosporium, Chrysomyxa, Cronartium.*

Appendix. *Uredo, Caeoma, Aecidium.*

This classification was followed by von Tavel in his Morphologie der Pilze 1892. In 1896 appeared Dietel's first classification of the Uredinales in Engler's Pflanzenfamilien. They are classed with the Auriculariales in the Auriculariineae. The divisions here are I. Endophyllaceae, II. Schizosporaceae, III. Melampsoraceae, a. Chrysomyxeae, b. Cronartieae, c. Coleosporieae, d. Melampsoreae, IV. Pucciniaceae. In the "Nachtrag" to the volume (1900) he rearranged his families and this latter classification is the one now usually followed. I. Melampsoraceae, II. Coleosporiaceae, III. Cronartiaceae, IV. Pucciniaceae. The positions of the second and third families can be seen by glancing at the first system. The Endophyllaceae, Schizosporaceae (which include no British representatives) and the Chrysomyxeae are placed in the Cronartiaceae. Fischer (Die Uredineen der Schweiz, 1904) adopts this classification but his Pucciniaceae has three subfamilies, Puccinieae, Gymnosporangieae and Phragmidieae. It is also followed by Hariot, (Les Urédinées 1908) and Trotter (Flora Italia Cryptogamia, 1908).

In the key to the genera given below the modifications of the last named with regard to subfamilies have been adopted.

In Saccardo's Sylloge Fungorum (1888) De Toni follows Saccardo's well-known method of arranging genera in different spore groups. This grouping, which is very useful in the case of the Fungi Imperfecti, is strikingly artificial when applied to the Uredineae. As the work is supposed to give descriptions of all fungi which have been published, the different spore forms are kept distinct. We even find descriptions of two species of *Aecidiolum*. The four large divisions of Saccardo are utilised I. Amerosporae, teleutospores continuous, unilocular: *Uromyces*, ? *Hemileia*, *Melampsora*, *Melampsorella*, *Cronartium*. II. Didymosporae, spores one-septate or two-celled: *Puccinia*, *Uropyxis*, *Gymnosporangium*. III. Phragmosporae, spores many septate, i.e., three to many-celled: *Phragmidium*, *Xenodochus*, *Coleosporium*, *Chrysomyxa*, *Pucciniastrum*, *Thecopsora*, *Calyptospora*, *Endophyllum*, *Milesia*. IV. Dictyosporae, spores septate in various directions: *Triphragmium*, *Aecidiolum*, *Aecidium*, *Roestelia*, *Peridermium*, *Uredo (Caeoma)*. That this classification was realised by the author himself to be artificial seems to be shown by the fact that an additional key by Schroeter is given which has a much more natural appearance.

Other classifications that have been proposed are those of de Bary, van Tieghem, Maire and Arthur. De Bary (1884) divided the Uredineae into aecidia-forming Uredineae and tremelloid Uredineae, to which latter the Leptopuccinieae and Leptochrysomyxa belong, and possibly the Micropuccineae. Van Tieghem published two different classifications. The one (1891), constructed before his work on the homologies of the promycelium, divided the Uredineae into three families. 1. Puccinieae, with teleutospores non gelatinous, free: *Uromyces*, *Puccinia*, *Triphragmium*, *Phragmidium*, *Endophyllum*. 2. Gymnosporangieae, teleutospores gelatinous, confluent, with tardive germination: *Melampsora*, *Thecopsora*, *Calyptospora*, *Gymnosporangium*. 3. Coleosporieae, teleutospores gelatinous, confluent, germinating immediately: *Cronartium*, *Chrysomyxa*, *Coleosporium*. His second classification (1898) was much influenced by his having realised the homology between the promycelium in the Uredineae and the basidium in the Basidiomycetes. The Uredineae (now the Pucciniaceae) are in this work divided into two families, the Coleosporieae for those genera where the teleutospore becomes itself a promycelium, and the Puccinieae for those genera in which the teleutospore sends forth a promycelium.

Maire (1902) in his "Recherches cytologiques et taxo-

nomiques sur les Basidiomycètes," divided his ' Protobasidiomycètes Stichobasidiés ' into Uredineae and Auricularineae. The former were subdivided into Pucciniaceae, (Puccinieae, Melampsoreae), Coleosporiaceae, Zaghouaniaceae, Endophyllaceae. The Zaghouaniaceae contains only the one genus Zaghouania, the teleutospore of which differs from that of the Pucciniaceae " par son caractère kystique peu accentué et sa germination semi-interne."

None of these latter classifications have been used by systematists.

With regard to the delimitation of genera it has been often pointed out that too much importance is being placed upon the teleutospore, and more stress should be laid upon the cycle of development. Arthur (1906) has applied this principle to the classification of the group. He makes the aecidium of greater importance than the teleutospore. He divides each tribe into four groups according to the spore stages present, each genus possessing only species which have the same types of fructification. The parasitical relation between fungus and host is also considered. Unfortunately Arthur makes many remarkable changes in the nomenclature of the genera. *Gymnosporangium* figures as *Aecidium*, *Melampsora* as *Uredo*, and so on; also many of the early ill-defined genera which had fallen out of use are revived. When a system which professes to be a natural one appears, it is annoying to find that it has such a forbidding aspect, the author having undertaken to revise both terminology and nomenclature. Arthur has worked out his system to its logical conclusions in the North American Flora which is at present appearing.

In drawing up the following key to the genera and the list of species of British Uredineae the writer is particularly indebted to the works of Plowright, Dietel, Fischer, Hariot and Sydow.* The letters S, A, U, T, following the names of the species indicate whether spermogonia, aecidia, uredospores and teleutospores are known or not in that species. Heteroecious species are italicised. An asterisk indicates that biological forms are known, or that the species as given has been split up into many morphologically very similar. The species in square brackets are not yet definitely recorded for this country, although their presence is practically certain. In the genus *Melampsora*, the species on willows and poplars, *(M. farinosa*, *M. mixta*, *M. aecidiodes*, *M. Populina*, *M. vitellina*, *M. Tremulae*, and *M. epitea)*, have been divided into a number of species principally by Klebahn, working with inoculation methods. Most, if not all, of these species undoubtedly occur in this country, although few of them have yet been recorded.

The nomenclature followed is that of the standard works on

the group and, only in those cases where there is disagreement has the question been entered into as to which names must be accepted according to the International Rules. These rules, as far as they relate to fungi, are as follows:—

"Art. 19. Botanical nomenclature begins for—

e. Fungi: Uredinales, Ustilaginales and Gastromycetes 1801 (Persoon, Synopsis methodica Fungorum).

f. Fungi caeteri. 1821-32 (Fries, Systema mycologicum)."

"Art. 49 bis. Among Fungi with a pleomorphic life-cycle the different successive states of the same species (anamorphoses, status) can bear only one generic and specific name (binomial) that is the earliest which has been given, starting from Fries, Systema, or Persoon, Synopsis, to the state containing the form which it has been agreed to call the perfect form, provided that the name is otherwise in conformity with the rules. The perfect state is that which ends in the ascus stage in the Ascomycetes, in the basidium in the Basidiomycetes, in the teleutospore or its equivalent in the Uredinales and in the spore in the Ustilaginales.

"Generic and specific names given to other states have only a temporary value. They cannot replace a generic name already existing and applying to one or more species, any one of which contains the 'perfect' form.

"The nomenclature of Fungi which have not a pleomorphic life cycle follows the ordinary rules."

BRITISH UREDINALES.

I. PUCCINIACEAE.

Teleutospores pedicellate (stalk sometimes short or deciduous), uni- or pluricellular, in pulverulent, compact or gelatinous sori; promycelium septate, segments with sporidia-bearing sterigmata; sporidia ovoid or reniform, generally hyaline. Uredospores solitary, not catenulate, pedicellate. Aecidium with, or without pseudoperidium.

(1) PUCCINIEAE.

Teleutospores uni- or bi-cellular, in pulverulent or compact sori. Aecidium usually provided with a pseudoperidium.

Teleutospores mostly one-celled.

Uredospores smooth on one surface, warted on other ..... *Hemileia.*

Uredospores echinulate, warted or smooth over whole surface ..... *Uromyces.*

Teleutospores mostly two-celled ..... *Puccinia.*

(2) GYMNOSPORANGIEAE.

Teleutospores usually bicellular, with long pedicels embedded in gelatinous masses. Aecidium with pseudoperidium ..... *Gymnosporangium.*

(3) PHRAGMIDIEAE.

Teleutospores bi- or pluri-cellular in pulverulent sori. Aecidium *(Caeoma)* without pseudoperidium.

Teleutospores mostly three to more celled, cells in a row ..... *Phragmidium.*

Teleutospores three-celled, cells arranged in form of triangle ..... *Triphragmium.*

II. CRONARTIACEAE.

Teleutospores sessile, unicellular, arranged in series (simulating pluricellular spores) separating from one another, or arranged in cylindrical, lenticular or wart-like sori. Promycelia as above; sporidia subglobose, small, hyaline. Aecidium with pseudoperidium.

Teleutosorus without pseudoperidium.

Teleutospores composed of series of superimposed cells, forming flat or slightly elevated waxy crusts ..... *Chrysomyxa.*

Teleutospores compacted into a cylindrical body *Cronartium.*

Teleutosorus with pseudoperidium, resembling an aecidium ..... *Endophyllum.*

III. COLEOSPORIACEAE.

Teleutospores sessile or with lateral pedicel, dividing into four superposed cells, each with a simple sterigma bearing a large sporidium (about 20μ diam.). Promycelium usually internal. Teleutospores confluent in flat waxy masses of one or two layers. Aecidia provided with variously constituted pseudoperidia.

(1) ZAGHOUANIEAE.

Teleutospores with lateral pedicel. Promycelium internal only at the beginning .....*Zaghouania.*

(2) COLEOSPORIEAE.

Teleutospores sessile, promycelium internal.

Teleutospores with short sterigmata; sporidia fusiform; uredospores scattered; aecidium with cup-shaped pseudoperidium ..... *Ochropsora.*

Teleutospores with long sterigmata; sporidia elliptical; uredospores in chains; aecidium with inflated torn pseudoperidium ..... *Coleosporium.*

IV. MELAMPSORACEAE.

Teleutospores sessile, one- or many-celled, loose in tissue of host plant or united in a flat layer under the epidermis: Ger-

mination as in I.; sporidia globosc, small, about 10μ diam. Uredospores single. Aecidium and uredosorus with or without pseudoperidium.

Teleutospores vertically septate.

Teleutospores forming a crust, subepidermal or in the epidermal cells.

Teleutospores with brown membrane; aecidium and uredosorus provided with pseudoperidium *Pucciniastrum.*

Teleutospores with hyaline membrane; uredosorus with or without pseudoperidium; no aecidium *Hyalopsora.*

Teleutospores dispersed in the mesophyll: uredosorus with pseudoperidium ..... *Uredinopsis.*

Teleutospores not septate.

Uredospores surrounded by paraphyses which are thickened at the summit: uredosorus and aecidium (Caeoma) without pseudoperidium *Melampsora.*

Uredospores without paraphyses: uredosorus and aecidium with pseudoperidium.

Teleutospores with brown membrane *Melampsoridium.*

Teleutospores with hyaline membrane *Melampsorella.*

UROMYCES Link.

Ficariae (Schum.) Lév. U., T.

caryophyllinus (Schr.) Schroet., A., U., T.

Behenis (DC.) Unger, S., A., T.

sparsus (K. et Sch.) Lév., S., A., U., T.

Geranii (DC.) Otth. S., A., U., T.

Kabatianus Bubak, S., A., U., T.

Anthyllidis (Grev.) Schroet., U., T.

Ervi (Wallr.) Westend., A., U., T.

Loti Blytt., S., A., U., T.

**striatus* Schroet., S., A., U., T.

Orobi (Pers.) Plow., S., A., U., T.

appendiculatus (Pers.) Link, S., A., U., T.

**Pisi* (Pers.) Schroet., S., A., U., T.

Phaseoli (Pers.) Wint., S., A., U., T.

Trifolii (Hedw.) Lév., S., A., U., T.

Trifolii-repentis (Cast.) Lindroth, S., A., U., T.

flectens Lagerh., T.

*Fabae (Pers.) de Bary, S., A., U., T.

Alchemillae (Pers.) Lév., U., T.

Valerianae (Schum.) Fuck., S., A., U., T.

Scrophulariae (DC.) B. et Br., S., A., T.

Limonii (DC.) Lév., S., A., U., T.

Armeriae (Schlecht.) Lév., S., A., U., T.

Betae (Pers.) Tul., S. A., U., T.

Salicorniae (DC.) de Bary, A., U., T.
Chenopodii (Duby) Schroet., S., A., U., T.
Polygoni (Pers.) Fuck., S., A., U., T.
Rumicis (Schum.) Wint., U., T.
Acetosae Schroet., S., A., U., T.
*scutellatus (Schrank) Lév., S., U., T.
tuberculatus (Fuck.) Magn. S., A., U., T.
ambiguus (DC.) Lév., U., T.
Urticae Cooke, T.
Ornithogali Lév., T.
Gageae Beck., T.
Colchici Mass., T.
Lilii (Link) Fuck., S., A., T.
Scillarum (Grev.) Wint., T.
Alliorum (DC.) Cooke, T.
Junci (Desm.) Wint., S., A., U., T.
**lineolatus* (Desm.) Schroet. (= U. Scirpi (Cast.)), S., A., U., T.
maritimae Plow., S., A., U., T.
**Dactylidis* Otth, S., A., U., T. (= Aecid. Ranuculacearum DC. pp.).
**Poae* Rabenh., A., U., T. (= Aecid. Ranuculacearum DC. pp.).

PUCCINIA Pers.

fusca (Relh.) Wint., S., T.
Calthae Link, S., A., U., T.
Zopfii Wint., S., A., U., T.
Thalictri Chev., T.
*Violae (Schum.) DC., S., A., U., T.
aegra Grove, A., U., T.
Fergussoni B. et Br., T.
Arenariae (Schum.) Wint., T.
Silenes Schroet., S., A., U., T.
Spergulae DC., T.
Malvacearum Mont., T.
argentata (Schultz) Wint., S., A., U., T.
**Pruni-spinosae* Pers., S., A., U., T.
pulverulenta Grev. (= Epilobii-tetragoni (DC.) Wint.), S., A., U., T.
*Epilobii DC., T.
Circaeae Pers., T.
Umbilici Guép., T.
Rhodiolae B. et Br., T.
*Ribis DC., T.
*Saxifragae Schlecht., T.
Pazschkei Diet., T.
Chrysosplenii Grev., T.
Aegopodii (Schum.) Mart., T.
*Angelicae (Schum.) Fuck., S., U., T.
Apii Desm., S., A., U., T.
Bulbo-castani (Cum.) Fuck., A., T.
Bupleuri Rud., S., A., U., T.
*Chaerophylli Purt., S., A., U., T.
Cicutae Lasch, S., A., U., T.
Conii (Str.) Fuck., U., T.
tumida Grev. (= P. Bunii (DC.) Wint.), T.
Heraclei Grev., S., A., U., T.
Hydrocotyles (Link) Cooke, A., U., T.
Aethusae Mart., S., U., T.
*bullata (Pers.) Schroet., S., U., T.
Pimpinellae (Str.) Mart., S., A., U., T.
Saniculae Grev., S., A., U., T.
Smyrnii Biv., S., A., T.
albescens Grev., S., A., U., T.
Adoxae Hedw. fil., T.
*punctata Link (= P. Galii Schw.), S., A., U., T.
Asperulae-odoratae Wurth., A., U., T.
Celakovskiana Bubak, S., U., T.
*Valantiae Pers., T.
*Millefolii Fuck., T.

Absinthii DC., U., T.
Tripolii Wallr., T. (=P. Asteris Duby).
Carduorum Jacky, U., T.
Cardui-pycnocephali Syd., U., T.
Carlinae Jacky, U., T.
Cyani (Schleich.) Pass., U., T.
*Centaureae Mart., S., U., T.
Cichorii (DC.) Bell., U., T.
Chrysanthemi Roze, U., T. (=Uredo Chrysanthemi Roze.).
obtegens (Link) Tul. (=P. suaveolens Rost.), S., U., T.
Cirsii Lasch, U., T.
Cnici-oleracei Pers., T. (=P. Cardui Plow.).
Andersoni B. et Br.
major Diet., S., A., U., T.
Crepidis Schroet., S., A., U., T.
*Hieracii (Schum.) Mart., U., T.
Hypochaeridis Oud., U., T.
Chondrillae Corda, A., U., T.
Lampsanae (Schultz.) Fuck., S., A., U., T.
Bardanae Corda, U., T.
Leontodontis Jacky, U., T.
Leucanthemi Pass., T.
Senecionis Libert, A., T.
glomerata Grev., T.
tinctoriicola Magn., U., T.
Virgaureae (DC.) Libert, T.
Sonchi Roberge, U., T.
Tanaceti DC., U., T.
variabilis Grev., S., A., U., T.
Taraxaci Plow., U., T.
Tragopogi (Pers.) Corda, S., A., U., T.
Campanulae Carm., T.
Primulae (DC.) Duby., A., U., T.
Soldanellae (DC.) Fuck., S., A., U., T.
Vincae (DC.) Berk., S., U., T.
Gentianae (Str.) Mart., S., A., U., T.
Convolvuli (Pers.) Cast., A., U., T.
Veronicae Schroet., T.
Veronicarum DC., T.
Betonicae (A. et S.) DC., T.
Glechomatis DC., T.
*Menthae Pers., S., A., U., T.
*annularis (Str.) Schlecht., T.
caulincola Schneid., T.
Oxyriae Fuck., U., T.
Polygoni A. & S., S., A., U., T.
Polygoni-amphibii Pers., S., A., U., T.
Polygoni-vivipari, Karst., A., U., T.
**Bistortae* (Str.) DC., S., A., U., T.
Acetosae (Schum.) Koern., U., T.
Thesii (Desv.) Chaillet, S., A., U., T.
Buxi DC., T.
asarina Kunze, T.
Porri (Sow.) Wint., A., U., T.
Asparagi DC., S., A., U., T.
*Liliacearum Duby, S., A., T.
Iridis (DC.) Wallr., U., T. (=Uredo Iridis (Thüm.) Plow.).
Schroeteri Passer., T.
oblongata (Link) Wint., U., T.
obscura Schroet., A., U., T.
**Caricis* (Schum.) Rebent, S., A., U., T.
Pringsheimiana Kleb., S., A., U., T.
Magnusii Kleb., S., A., U., T.
dioicae Magn. S., A., U., T.
sylvatica Schroet, S., A., U., T.
Schoeleriana Plow. et Magn., S., A., U., T.
arenariicola Plow., A., U., T.

extensicola Plow., A., U., T.
paludosa Plow., S, A., U., T.
uliginosa Juel., A., U., T. (= Aecidium Parnassiae Grev.)
Scirpi DC., S., A., U., T.
**graminis* Pers., S., A., U., T.
**coronata* Corda., S., A., U., T.
**Lolii* Niels (=P. coronifera Kleb.) S., A., U., T.
**glumarum* (Sch.) Erikss. et Henn., U., T.
**dispersa* Erikss. et Henn., A., U., T.
agropyrina Erikss., U., T.
holcina Erikss., U., T.
Triseti Erikss., U., T.
triticina Erikss., U., T.
Bromina Erikss., S., A., U., T.
Agrostidis Plow., S., A., U., T.
perplexans Plow., A., U., T.
*Anthoxanthi Fuck., U., T.
Arrhenatheri (Kleb.) Erikss., S., A., U., T.
Baryi (B. et Br.) Wint., U., T.
**Festucae* Plow., S., A., U., T.
simplex (Koern.) Erikss. et Henn., U., T.
paliformis Fuck., T.
**Moliniae* Tul., A., U., T.
**sessilis* Schneid., S., A., U., T.
Orchidearum-Phalaridis Kleb., S., A., U., T.
Winteriana Magn. (=P. Allii-Phalaridis Kleb.) S., A., U., T.
Phalaridis Plow., S., A., U., T.
Phlei-pratensis Erikss. et Henn., U., T.
Magnusiana Koern., A., U., T.
Phragmitis (Schum.) Koern., A., U., T.
Trailii Plow., A., U., T.
Poarum Niels., S., A., U., T.
Agropyri Ell. et. Everh., A., U., T. (=Aecidium Clematidis DC.).
persistens Plow., S., A., U., T.

HEMILEIA B. et Br.
Phaji Syd., U., T.
Oncidii Griff. et Maubl., U., T.
americana Mass., U., T.

GYMNOSPORANGIUM Hedw. fil.
clavariaeforme (Jacq.) Reess, S., A., T.
Juniperi Lk., S., A., T.
Sabinae (Dick.) Wint., S., A., T.
confusum Plow., S., A., T.

TRIPHRAGMIUM Link.
Ulmariae (Schum.) Link., S, A., U., T.
Filipendulae (Lasch) Pass., A., U., T.

PHRAGMIDIUM (including Xenodochus) Link.
Potentillae (Pers.) Wint., S., A., U., T.
Fragariastri (DC.) Schroet., S., A., U., T.
Sanguisorbae (DC.) Schroet., S., A., U., T.
*subcorticium (Schrank) Wint., S., A., U., T.
tuberculatum Müll., S., A., U., T.
fusiforme Schroet. (=P. Rosae-alpinae (DC.) Wint.), A., U., T.
albidum (Kühn.) Ludw. (= Chrysomyxa albida Kühn, Kühneola Magn.), U., T.
Rubi (Pers.) Wint., A., U., T.
violaceum (Schultz) Wint., S., A., U., T.
Rubi-Idaei (Pers.) Karst., S., A., U., T.
carbonarium (Schlecht.) Wint. (=Xenodochus carbonarius Schlecht.), A., T.

Tormentillae Fuck., A., T. (=Xenodochus Tormentillae (Fuck.) Magn.).
?curtus (Cooke) (=Xenodochus curtus Cooke), T.

COLEOSPORIUM Lév.
Cacaliae (DC.) Wagner (=Peridermium Magnusianum Fisch., P. Magnusii Wagn.), S., A., U., T.
**Campanulae* (Pers.) Lév. (=Peridermium Rostrupi Fisch., P., oblongo-sporum Kleb., P. Kosmahlii Wagn.), S., A., U., T.
Euphrasiae (Schum.) Wint. (= Peridermium Stahlii Kleb.), S., A., U., T.
Melampyri (Rebent) Kleb. (=Peridermium Soraueri Kleb.), S., A., U., T.
Petasitis de Bary (=Peridermium Boudieri Fisch., P. Dietelii Wagn.), S., A., U., T.
**Senecionis* (Pers.) Fr. (=Peridermium oblongosporum Kleb., P. Pini Chev., P. acicolum Link, P. Piniacicola Hartig), S., A., U., T.
Sonchi-arvensis (Pers.) Lév. (=Peridermium Fischeri Kleb.), S., A., U., T.
Tussilaginis (Pers.) Kleb. (=Peridermium Plowrightii Kleb.), S., A., U., T.

OCHROPSORA Diet.
[*Sorbi* (Oud.) Diet.] (=Aecidium leucospermum DC., Endophyllum leucospermum (DC.) Soppitt), S., A., U., T.

ZAGHOUANIA Pat.
[Phillyreae Pat.] (=Uredo Phillyreae Cooke, Aecidium Phillyreae DC.), A., U., T.

CRONARTIUM Fries.
asclepiadeum (Willd.) Fr. (=C. flaccidum (A. et S.) Wint.), (=Peridermium Cornui Kleb.), S., A., U., T.
ribicolum Dietr. (=Peridermium Strobi Kleb.), S., A., U., T.

CHRYSOMYXA Unger.
Empetri (Pers.) Rostr., U., T.
Pyrolae (DC.) Rostr., U., T.

PUCCINIASTRUM Otth. (including Thecopsora Magn. and Calyptospora Kühn).
Circaeae (Schum.) Schroet., U., T.
Agrimoniae (DC.) Tranzschel., U., T.
Epilobii (Pers.) Otth, S., A., U., T.
Galii (Link) Fisch. (Thecopsora), U., T.
Padi (K. et Sch.) Diet. (Thecopsora), A., U., T. (=Aecidium strobilinum A. et S.).
Vacciniorum (Link) Diet. (Thecopsora), U., T.
Goeppertianum (Kühn). Kleb. (Calyptospora), A., T. (=Aec. columnare A. et S.).

HYALOPSORA Magn.
[Adianti-Capilli-Veneris (DC.) Syd.], U., T. (=Uredo Polypodii Pers. pp.)
Polypodii (Pers.) Magn., A., U., T. (=Uredo Polypodii Pers. pp.).
Aspidiotus (Peck) Magn., A., U., T.

UREDINOPSIS Magn.
Scolopendrii (Fuck.) Rostr. (=Uredo (Milesia) Scolopendrii Fuck. pp.), U., T.
[filicina (Niessl.) Magn.].

MELAMPSORA Cast.
*Helioscopiae (Pers.) Cast., S., A., U., T.

*Hypericorum (DC.) Schroet., A., T.
Lini (Pers.) Desm., S., A., U., T.
Amygdalinae Kleb., S., A., U., T.
arctica Rostr., U., T.
Saxifragarum (DC.) Schroet. S., A., U., T. (=M. vernalis Niessl.).
[*Larici-pentandrae* Kleb.], A., U., T.
[*Allii-Salicis-albae* Kleb.] (= Caeoma alliorum Link pp.), S., A., U., T.
[*Allii-fragilis* Kleb.] (= Caeoma alliorum Link pp.), S., A., U., T.
[*Galanthi-fragilis* Kleb.] (= Caeoma Galanthi Unger), S., A., U., T.
Larici-Caprearum Kleb., A., U., T.
**Larici-Epitea* Kleb., A., U., T.
Orchidi-repentis (Plow.) Kleb. (=Caeoma Orchidis (Mart.) Wint.), S., A., U., T.
[*Euonymi-Caprearum* Kleb.] (=Caeoma Euonymi Mart.), S., A., U., T.
[*alpina* Juel] (=Caeoma Saxifragae Strauss pp.), S., A., U., T.
[*Ribesii-purpureae* Kleb.] (= Caeoma confluens (Pers.) Schroet. pp.), S., A., U., T.
[*Ribesii-auritae* Kleb.] S., A., U., T.
[*Ribesii-viminalis* Kleb.] (= Caeoma confluens (Pers.) Schroet. pp.), S., A., U., T.
[*Larici-Tremulae* Kleb.] (= Caeoma Laricis Hartig pp.), A., U., T.
[*pinitorqua* Rostr.] (= Caeoma pinitorquum Braun.), A., U., T.
[*Magnusiana* Wagner] (= Caeoma Chelidonii Schw., C. Fumariae Link), S., A., U., T.
Rostrupii Wagn. (=Caeoma Mercurialis (Mart.) Link pp.), S., A., U., T.
[*Larici-populina* Kleb.] (= Caeoma Laricis Hartig pp.), A., U., T.
[*Alii-populina* Kleb.] (= Caeoma alliorum Link pp.), S., A., U., T.

MELAMPSORIDIUM Kleb.
betulinum (Pers.) Kleb., A., U., T.

MELAMPSORELLA Schroet.
Caryophyllacearum (DC.) Schroet. (=M. Cerastii (Pers.)), S., A., U., T.
Symphyti (DC.) Bubak (= Uredo Symphyti DC.), S., A., U., T.
Blechni Syd. (=Uredo (Milesia) Scolopendrii Fuck. pp., Milesina Magn.), U., T.
Dieteliana Syd. (=Uredo Polypodii Pers. pp., Milesina Magn.), U., T.

UREDO Pers.
Quercus Brond. (=Cronartium Quercus (Brond.) Schroet.).
Tropaeoli Desm.
Lynchii (B. et Br.) Plow.
Plantaginis B. et Br.
Pyrolae Grev. (=Puccinias-trum Pyrolae (Gmel.) Diet.

CAEOMA Tul.
Ari-italici Duby.

AECIDIUM Pers.
Ranuculacearum DC. var. Linguae DC.
Hellebori Fisch.
dracontii Schw.
incarceratum B. et Br. (=? Doassansia Sagittarieae (Fuck.) Fisch.
Poterii Cooke.
pseudo-columnare Kühn.