

RIGHT AND WRONG CONCEPTIONS OF PLANT RUSTS.

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The plant rusts have been known both popularly and scientifically from the earliest times. Their study took the usual course of development of all cryptogamic plants up to the time that DeBary demonstrated that pleomorphism existed in many species in a more striking manner than known in other fungi. He showed that most if not all members of the genus *Æcidium* as recognized at the time were only stages in the life cycle of species of *Puccinia* and *Uromyces*, and other investigators soon followed with similar demonstrations for such genera as *Roestelia*, *Peridermium*, and *Cwoma*. It was in 1866 that he announced, with experimental proof, that one stage of a rust, as the *Æcidium*, often grows on a host wholly different from that on which the final stage grows, such rusts being called heterœcious.

Heterœcism, which was thus established by DeBary and confirmed by his contemporaries, was not generally accepted by mycologists for a score or more of years. That the *Æcidium poculiforme* of the barberry leaf, with its conspicuous cups filled with chains of verrucose spores, could not give rise to other similar cups on the barberry, but only to the powdery and echinulate spores of the red rust on wheat stems, as unlike the former as a caterpillar is unlike the pupa into which it is transformed, was such a strikingly new idea in botany, that when once it did find general credence, and was extended to many other species by culture work, it assumed undue prominence. This result was accelerated by the rather recent discovery of races, or so-called physiological species. When the well known *Puccinia graminis*, which has great economic importance by producing a destructive disease of cereals and grasses, became also one of the best illustrations of the division of a species into physiological strains or races, more or less well established, in some cases amounting to possible species, it assumed in the minds of many mycologists a typical position in reference to other rusts. It became common to speak of rusts as agreeing with *Puccinia graminis* in their life cycles and spore structures, or in showing a certain amount of deviation from it. This attitude has caused considerable distortion in the conception usually held

of the rusts, even by the foremost students of the order. It affects systematic work adversely, keeps the terminology in an antiquated and ambiguous form, and makes it difficult to institute legitimate comparisons between different genera, species, or spore structures.

One of the wrong conceptions, wrong when viewed in the light of present knowledge, is to make the genus *Puccinia* include all species that possess a two-celled, pedicelled and free teliospore (excepting those with teliospore imbedded in gelatinous matrix, separated under *Gymnosporangium*), irrespective of the other morphological characters, or of the complexity of the life cycle, and furthermore, as part of the same conception, to make the genus *Uromyces* include all species that possess the same kind of teliospore, only one-celled instead of two-celled. The writer believes that the length and nature of the life cycle, which is a more unvarying character in the rusts than the one or two-celled teliospore (recall the *Uromyces-Puccinia* species on *Allium*, *Sida*, and some other hosts), should be accepted as a character for genera, as it is now quite generally accepted for species. Recognizing this as a valid generic character, and taken in connection with other characters, the genus *Puccinia* can be separated into four genera (i. e., *Dicæoma*, *Allodus*, *Bullaria*, *Dasyscypha*), and the genus *Uromyces* also into four (i. e., *Nigredo*, *Uromycopsis*, *Klebahnia*, *Telospora*). If other characters, as well as the life cycle, mostly now generally ignored, are taken into account, *Puccinia Pruni-spinosæ* and its allies should form a genus (*Tranzschelia*) near to *Ravenelia*, on account of the adherent pedicels of the teliospores and peculiar structure of the urediniospores; *Uromyces rosicola*, on account of its evident spore structure, will go into a genus (*Ameris*) near to *Phragmidium*, but with a more limited life cycle; *Uromyces Terebinthi*, and its allies, on account of the remarkably distinctive characters of both urediniospores and teliospores, will form a genus somewhere between *Ravenelia* and *Tranzschelia*, while the similar *Uromyces effusus*, with a still more restricted life cycle, will go into another genus (*Discospora*). And in like manner quite a number of other species now commonly included under *Puccinia* and *Uromyces* could properly be separated and distributed to other genera, with much improvement in the nomenclature and great clarification of the systematic affinities. Other genera beside *Puccinia* and *Uromyces* could also be shown to be overburdened with species whose life cycle, or morphological structure, or both, entitle them to a different place in the systematic arrange-

ment, if the extent of the life cycle and characters other than those pertaining to the teliospore were called into account.

The third epoch in the study of plant rusts (the second one being ushered in by DeBary's demonstration of heterœcism and the first epoch preceding that time), may be considered to have started with the study of the nucleus and its behavior. This was begun by the work of Sappin-Trouffy and of Poirault and Raciborski some fifteen years ago, and ably continued by Blackman, Christman, Holden and Harper, Olive and others. The nuclear history in the rusts is still in a very incomplete state, and part of what has been gone over needs further substantiation. Enough has been demonstrated, however, to modify profoundly our ideas of the significance of the different spore forms, the relation of the spore structures, and the possibility of sexuality.

While it may be interesting to review the present knowledge of nuclear changes in the rusts and show the bearing on taxonomy, it will suffice for the present purpose to bring up briefly a few points. It has been rather clearly shown that the rusts possess well marked antithetic alternation of generations. The gametophytic generation has uninucleated mycelium, and gives rise to two kinds of spores, basidiospores and pycniospores, both uninucleated, and these are the only truly asexual spores formed in the life cycle. The sporophytic generation begins shortly after the pycnia mature, being inaugurated by a sexual fusion of cells. This act introduces the binucleated condition. In many species of rusts only one spore form (teliospore) is produced in the sporophytic generation. In other species there is an initial spore form (œciospore), and usually a repeating form, in addition to the teliospore. All spores of this generation are binucleated. In the gametophytic generation all species behave essentially the same. It is in what follows during the sporophytic generation that the great diversity of the rusts is shown.

If the first binucleated spores arising after sexual cell fusion are teliospores, no other spore forms in this generation are produced, and the life cycle is a brief one. But if the first binucleated spores are formed in what has been called an *æcidium*, *œcoma*, or primary uredo, they are essentially of the same physiological nature, whatever form they may take. Any such sorus may be called an *æcium*, and the spores *œciospores*, this being an extension in the previous application of the terms to cover the primary uredo. Possibly new terms would be less liable to introduce am-

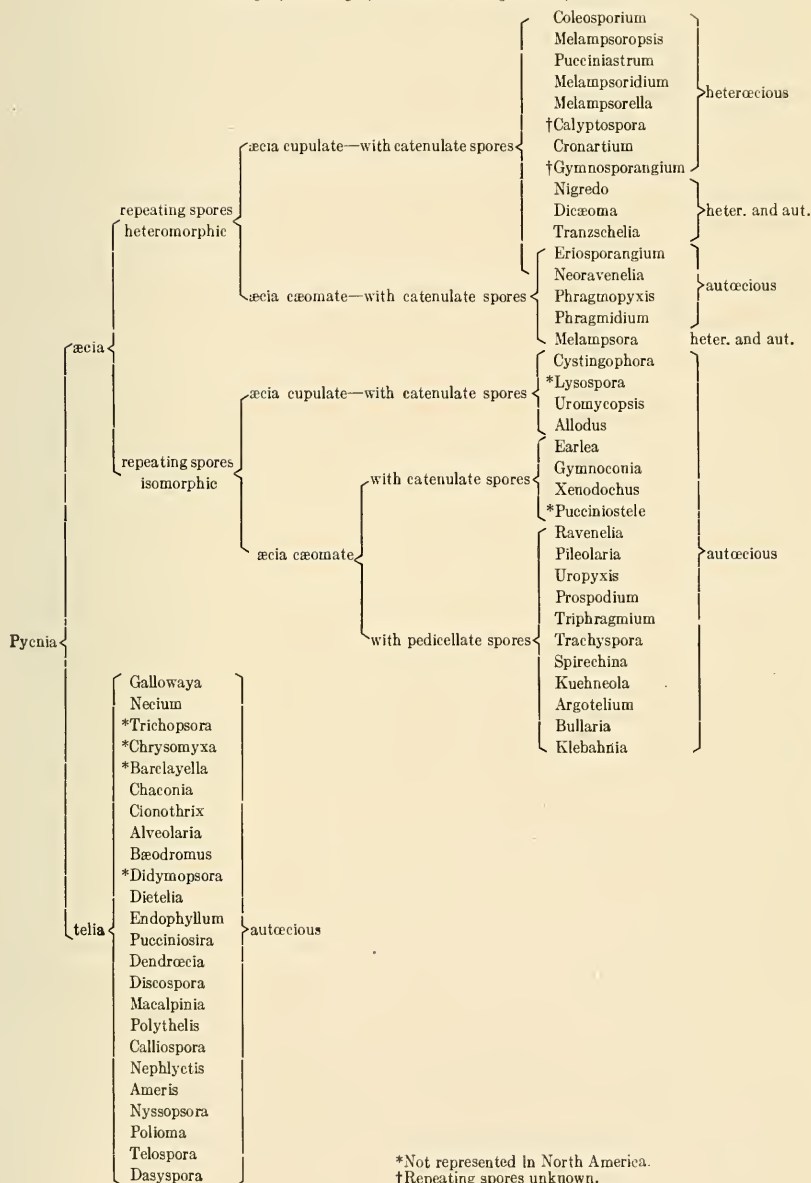
biguity in subsequent discussions, but in this paper æcia will be understood to be the initial spore structures following the pycnia, when these structures are not telia. Such æcia are of varying complexity, the simplest being of the uredo-type with spores borne on pedicels and no peridium, intermediate forms being of the cœoma-type, with spores in chains and no peridium, and the most highly developed being of the æcidium-type with a well-formed peridium. There is a wide difference in complexity of structure between the lowest uredo-type of æcia (*e. g.*, those of the so-called *Chrysomyxa albida*) and the highest æcidium-type (*e. g.*, those of *Æcidium poculiforme* belonging to *Puccinia graminis*). But whatever the degree of complexity they are all strictly comparable in their relation to the life cycle of the different species to which they belong.

In most genera having species with initial æcia more rapid and extensive dissemination is brought about by means of repeating spores, often called summer spores. A few genera, like *Gymnosporangium* and *Calypsotheca*, have no repeating spores in present known species. The repeating spore structures are either isomorphic with the æcia, and are known as secondary æcia and secondary uredinia, or they are heteromorphic, and are known simply as uredinia. In either case the repeating spores arise from an infection by initial æciospores, and are not immediately preceded by pycnia. Repeating spores are binucleated, but do not arise from fusing uninucleated hyphæ, as the initial æciospores do, for the mycelium on which they are seated is already binucleated, having been derived from a binucleated spore.

The accompanying chart enumerates the best understood genera of the rusts, arranged in such a way as to show the essential features in the life history of the species. It embraces about three-fourths of all genera of the Uredinales recognized at the present time. The chief value of the chart is to emphasize the need of taking into account the full life cycle in order to compare or to contrast genera. It will be seen that many genera, possibly a third of all known, have no æcia or repeating spores, but the formation of telia follows immediately upon the maturity of the pycnia. In the genera with æcia increasing complexity of development is shown by the presence of heteromorphic repeating spores, cupulate æcia with catenulate æciospores, and heteroecism while comparative simplicity of development is shown by isomorphic repeating spores, cœomate æcia with pedicelled æciospores, and autoecism.

DIAGRAM

Showing life history of 59 best known genera of rusts.



It is evidently a right conception, in view of the foregoing statement, to regard *Puccinia graminis* (a better name is *Dicoma poculiforme*) as a representative of the highest development of rusts. But to regard it as typical of all rusts, or even of all rusts having aecia, is clearly asking too much of an illustration, and likely to involve grave misconceptions of structure and relative values. If the most essential features of the rusts were to be illustrated by the smallest permissible number of examples of common and well known species, I should select *Polythelis Thalictri* (*Puccinia Thalictri*) for the forms without aecia, *Kuchneola albida* (often called *Chrysomyxa albida*) for the forms with aecia and isomorphic repeating spores, and *Dicoma poculiforme* (*Puccinia graminis*) for the highly developed forms with aecia and heteromorphic repeating spores.

A wrong conception, which is doing much harm to the taxonomic study of the rusts, is the view that aeciospores and urediniospores are of the nature of conidia, that is, asexual spores, comparable to the conidia so abundantly produced by many ascomycetous fungi. Cytological studies show, however, that in the rusts the only truly asexual spores, other than the basidiospores, are the pycniospores, and to these only can the term conidia be applied with approximate accuracy. The sexual process begins by the fusion of uninucleated hyphal cells, which immediately, or almost immediately, develop some kind of binucleated spore-structure. If only one kind of binucleated spore is produced by the species, it is properly called a teliospore. Such a teliospore has two nuclei in each cell, derived by a short succession of divisions from the two nuclei of the fusing cells. These two spore nuclei fuse into one nucleus prior to germination of the teliospore, thus completing the sexual process. If more than one kind of binucleated spore is produced, the initial kind may be called an aeciospore, whatever the morphological structure in which it is formed. It has arisen as the consequence of sexual cell fusion, just as in the preceding case, and has the physiological character of greatly stimulated growth associated with sexuality. This initial aeciospore gives rise to a binucleated mycelium, which in turn generally produces binucleated repeating spores of the same or of a different form, and so on, until finally a teliospore is produced in which nuclear fusion takes place, as in the first instance mentioned. The sexual process in this class of rusts extends from the cell fusion at the base of the aecia through all the succession of hyphal cells and repeating spores to the fusion of nuclei in the mature teliospore.

All rusts at present known fall into one of these two classes: the sporophytic generation gives rise either to a single spore-form, or else to initial and final spore-forms, with usually intermediate repeating forms. Whether one or more than one spore-form arises between the cell fusion and final nuclear fusion, constituting the sexual period, all such spores, of whatever morphological structure, are of a sexual nature, the initial form (whether of the *aecidium*-type, *caecoma*-type, primary uredo-type, or when none of these is produced, the teleuto-type) being the one which most clearly shows the stimulus of fertilization.

The above facts, especially when taken in connection with the highly differentiated structures associated with the initial and repeating spores, often being quite equal or superior to those of the teliospores, show every reason that may be based upon morphology and development for considering the initial and repeating spores as practically of equal taxonomic rank with the teliospores. To illustrate, a genus founded upon a repeating stage, like the genus of imperfectly known fern rusts, *Milesia*, should be as valid as if founded on the telia. This genus has recently been rechristened *Milesina* on the ground that the original name, given in 1870, is invalid because it was only applied to the uredinia and not to the telia. Again, now illustrating with a specific name, the heteroecious rust which was first specifically called *poculiforme* was described in its aecial stage under *Aecidium*, and according to the preceding argument on the importance of the initial spores, this name having priority, although not at the time made to include the telia, should be used, whatever genus name be considered the best, as *e. g.*, *Dicoma poculiforme* or *Puccinia poculiformis*, not *Puccinia graminis*.

From the foregoing it will be seen that for purposes of taxonomy names applied to the pycnia (spermogonia) may properly be ignored, on the ground that they apply to asexual or conidial structures, but that names applied to aecia and uredinia (*Aecidium*, *Caecoma*, *Peridermium*, *Uredo*, and other such forms) should have the same standing as names applied to telia (teleutospore stage).

I have tried to show that the main features in the life cycle of all rusts exhibit essential uniformity, there being two large groups, one with a single form of spore (teliospore) in the sporophytic generation, and the other with additional initial and (usually) repeating spores, and that the great diversity lies in the details of their structural development. It is

difficult to give a clear and concise account of the general features of the rusts on account of the inadequate and ambiguous terminology at present in use. It appears to be unquestionably established that the spore structures of the rusts are not to be homologized with those of the Ascomycetes, and that taxonomic practice in the rusts should not be influenced by what is correct or expedient in the Ascomycetes or other fungi with strongly marked conidial and sexual forms, but be based upon the unique characters of their own development.

Right conceptions of the rusts, according to the writer's position, are those based upon the full life histories of the species, taking into account all the present known facts, and wrong conceptions are based upon partial life histories, and on ideas derived from other fungi and formerly supposed to apply to the rusts but now known to be inapplicable and misleading.

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