The Fungi as Aids in the Taxonomy of the Flowering Plants

D. B. O. Savile

Botany and Plant Pathology Division, Science Service, Department of Agriculture, Ottawa, Ontario, Canada

THIS paper (*1*) is based on one prepared, by invitation, for the Sixth International Congress of Microbiology, and read there by proxy. As was indicated in the original text the invitation was, in truth, somewhat premature, for the development of techniques for using data from the parasitic fungi to reveal relationships in the flowering plants is still in its infancy and will require several years' elaboration before its full value can be assessed. Nevertheless, a few examples of the results obtained may be of general interest and serve to illustrate the methods involved.

Taxonomic mycology is a younger science than taxonomy of the flowering plants. Its development for a long period awaited improvements in the microscope. Even today its followers are fewer than those of phanerogamic botany, although the examination and comparison of microscopic specimens is more time-consuming than that of the flowering plants. Inevitably mycology lagged behind phanerogamic botany and accepted its dictates for a long period, although it has made great strides in recent years. For many years, mycologists concerned with evolution in the rust fungi tried to arrange them in chronological sequences based upon host relationship, relying, as was natural, on the older discipline. This method gave some initial assistance, for it was safe to assume that the rusts of ferns and conifers were in general more ancient than those of the flowering plants. Thus, if one could detect a continuous series of forms, it was sometimes possible to decide the direction of evolution. Attempts to refine the method, notably by Cunningham (*2*), met with scant success, because the host plants were generally arranged in the sequence of Engler and Prantl, which is now known to have several serious defects. Although we cannot yet present even an approximately complete phylogenetic diagram of the rusts, our understanding of them has progressed greatly, and the evolutionary trends within some genera are now well understood.

The difficulties that beset the student of the simpler, microscopic plants are occasionally compensated for by the fact that their simplicity strips them of a mass of confusing details and makes evolutionary sequences relatively easy to detect. Thus, as mycology matures, it may well be able to give more aid to phanerogamic botany than the science of phanerogamic botany formerly gave to mycology.

The examples discussed here fall into two categories, although additional studies may be expected to provide intergradation. First, there are detailed studies of small natural groups of parasites that may demonstrate relationship or relative age within a family or even a single genus of host plants. Second, there are broad, more or less statistical studies that may assist us in arranging the major groups of flowering plants.

Parasite relationship, if properly used, is a reliable biochemical tool; but obviously its value depends upon the achievement of a natural classification of the parasites. The responsibility for its use rests squarely with the mycologist. In the detailed study of a small group of parasites, we must base our classification on the most precise morphological study possible and attempt to find evolutionary trends, through developmental studies and by the demonstration of developing dispersal mechanisms or other valuable characters that will make plain the direction of evolution within a series. The details of host relationship are best ignored until the study of the parasites has been completed; otherwise one may disregard, through bias, apparent anomalies that may be vitally important. Reliable determination of the hosts is, of course, essential; and for this reason, if for no other, such studies must include only specimens personally examined and not literature records. Even when all these requirements are met, there is no assurance that parasite relationship will throw much light upon the phylogeny of the hosts. It will sometimes indicate the relative ages of the hosts without showing the evolutionary lines. Occasionally it will be of no assistance at all.

The second category of host-parasite study, that of broad general relationships, needs little explanation and is illustrated by the final example.

Phylogeny of Carex *and related genera.* The vast genus *Carex* and the smaller genera *Kobresia, Schoenoxiphium,* and *Uncinia* form a natural subfamily of the sedges (family Cyperaceae). In such a complex, the evolutionary clues tend to be hidden in a welter of confusing detail. Largely as the result of studies of some of the smuts that attack these plants, but also, of course, using more orthodox data, it has been possible (*3*) to achieve an improved arrangement for much of this complex, in particular in showing the existence and tracing the evolution of a strikingly natural subgenus of *Carex* hitherto unrecognized. The degree of success achieved was due to several favorable circumstances. An unusually long series of specimens was available (*4*); of these a high proportion was backed by adequate host specimens, whereby errors in host determination were reduced to a minimum. Most important of all, it chanced that species differentiation in the smut genus *Cintractia* took place relatively late in the evolution of *Carex*.

The full significance of the latter circumstance was not realized until later, when I tried to use the North American rusts of *Carex* to secure further phylogenetic evidence. Sedges in various sections and often in two or three subgenera proved to be hosts for rust after rust. It was further found that, within each major host group, a rust tends to be restricted to a few closely related species. Evidently most species of rusts that attack *Carex* became differentiated very early in the evolution of the host genus. As the various subgenera and sections of *Carex* differentiated, races of the parasites developed on certain of them; but these races have since undergone little or no morphological differentiation.

Relationship of Sparganium *and* Acorus. The bur-reeds (*Sparganium*) and sweet flag (*Acorus*) are placed in the families Sparganiaceae and Araceae, respectively. In the system of Engler and Prantl these families were considered to be very widely separated, although some botanists, notably Hutchinson (*5, 6*), have believed them to be more closely related. The flowers of most species of *Sparganium* have a single style, but those of *S. eurycarpum* possess two styles. Because reduction in the number of styles or other flower parts is a well-recognized evolutionary trend, we consider that *S. eurycarpum* is the most primitive of the existing bur-reeds. The members of the family Araceae are characterized by a spikelike inflorescence usually partly surrounded by a spathe such as that of the skunk cabbage and jack-in-the-pulpit. In *Acorus* the spathe is simply a sword-shaped prolongation of the scape and might be considered either primitive or reduced.

It has long been realized that *Uromyces sparganii,* the rust that attacks *S. eurycarpum* but no other members of the genus, and *U. pyriformis,* which attacks *A. calamus,* are virtually indistinguishable. Recent studies (*7*) have shown that these rusts have a common host for the aecial stage and are not only morphologically identical but are cross-inoculable; that is, they are physiologically identical. A given race of a rust may not infrequently attack plants in closely related genera, but for one to atack plants in widely separated families would be astonishing. Examination, furthermore, shows striking similarity of the leaves and individual fruits, although not the whole inflorescence, of *A. calamus* to *S. eurycarpum* but much less to those of other *Sparganium* spp. The probable explanation is that *A. calamus* and *S. eurycarpum* are the most primitive representatives of their respective families, that the families are more closely related than even Hutchinson suggested, and that the two plants in question are more or less direct descendants of a common ancestor.

Taxonomic position of Allium. The genus *Allium,* comprising the onions, leeks, and so forth, has been placed by most authors in the family Liliaceae, but Hutchinson (*5*) considered that its affinities lay with Amaryllidaceae. Arthur (*8*) recorded that *Puccinia asparagi,* the rust of asparagus, which is an accepted member of Liliaceae, will slightly infect *A. cepa,* the common onion. This fact seems to offer some slight support for the retention of *Allium* in Liliaceae.

Relative age in Saxifragaceae. There are several short-cycled species of *Puccinia* that attack various genera of Saxifragaceae. It has recently been shown (*9*) that most of these rusts can be arranged in a reasonably clear evolutionary series. By plotting the host records of each rust, some idea can be obtained of the relative ages of the ten host genera concerned. Furthermore, three morphologically homogeneous rusts, *P. heucherae* var. *heucherae, P. heucherae* var. *austroberingiana,* and *P. heucherae* var. *saxifragae* occur on plants in five, four, and three genera, respectively. Thus we can tell the approximate relative ages of individual species in different genera. It is felt that, when accumulated phytogeographic data can be adequately interpreted, these clues from the rust relationships will allow a much clearer picture of evolution in this family.

Evolution of Puccinia *and relative age in the flowering plants.* Although a detailed picture cannot yet be presented, considerable progress has been made in our understanding of the large genus *Puccinia.* For our immediate purpose we may include *Uromyces,* having one-celled teliospores, with *Puccinia,* in which the teliospores are two-celled. *Puccinia* is one of the more modern genera of the family Pucciniaceae and is certainly much more modern than most genera of Melampsoraceae, universally accepted as the more primitive of the two families into which the rusts are usually divided. Nevertheless, *Puccinia* has a long developmental history, and in it there are many evolutionary lines. Although we cannot unravel all these lines, some of them are clear enough to demonstrate that one trend is common to most if not all.

In the most primitive species, the teliospores serve to overwinter the fungus and are the site of fusion of the paired haploid nuclei, but they do not serve as dispersal agents. They are firmly compacted in the sorus and have smooth walls, thickened at the apex, and strongly persistent pedicels. The more advanced species have teliospores with walls of nearly uniform thickness, often sculptured, and with deciduous pedicels. The latter spores are effective dispersal agents. In series after series, we can trace the evolution from the first to the second teliospore type, with ample evidence that evolution has actually been in this direction.

Examination of the North American species of *Puccinia* shows that nearly all attack monocotyledons or herbaceous dicotyledons. In contrast a high proportion of Melampsoraceae attack ferns and conifers, acknowledged as being in general older than the flowering plants, or woody dicotyledons. Most botanists agree that herbaceous plants have generally been derived from woody. Hutchinson (*10*), while supporting such a tendency, has suggested that, almost from their origin, the dicotyledons were split into two groups, one mainly woody and the other mainly herbaceous. Their rust relationships suggest that the herbaceous dicotyledons are, in general, more modern than the woody members. Further support for this belief is found in the host relationships of the smut fungi and of the ascomycetous genus *Taphrina*. It appears probable that the separation seen by Hutchinson is chronological rather than genetic.

If we divide the species of *Puccinia* and *Uromyces* in Canada and the United States into three groups—primitive, intermediate, and advanced—on the basis of teliospore morphology and count the numbers that occur on (i) herbaceous dicotyledons, (ii) Glumiflorae (grasses, sedges, and rushes), and (iii) Liliaceae (*sensu lato*), Amaryllidaceae, and Iridaceae, we may hope to get some idea of the relative ages of these various plants. Such a division is shown in Table 1. The exact distribution must depend upon one's species concept and estimate of the latitude of each category, but the disposition is doubtful for only a few species. It is generally recognized today that the monocotyledons split off from the dicotyledons at an early stage when most members of the latter were woody. Thus the monocotyledons are all more modern than the most ancient dicotyledons, but it is not so clear how the more advanced members of each class compare.

Among the monocotyledons, the Glumiflorae represent one evolutionary line, adapted to wind pollination, and the Liliaceae and related families with showy flowers represent another line in which insect pollination has predominated. The figures in Table 1 strongly suggest that the Glumiflorae are, on the average, older than the herbaceous dicotyledons. The data for the Liliaceae, Amaryllidaceae, and Iridaceae are somewhat scanty, but these families appear to be more modern than the Glumiflorae. This finding may come as a surprise to many botanists, as it did to me, for we think of the reduced flowers of the grasses, sedges, and rushes as being highly advanced and thus modern. The explanation may lie in the fact that most Glumiflorae flower in the first or second year from seed, thus having a much shorter generation time than many of the lilies and their allies that do not flower until they are about 5 to 7 yr old. Thus evolution in the Glumiflorae may have proceeded very rapidly.

Table 1. Telial hosts of North American species of *Puccinia* and *Uramyces*.

Type of rust	Herbaceous dicotyledons	Glumiflorae	Liliaceae, Amaryllidaceae, and Iridaceae
Primitive	91	113	9
Intermediate	21	9	5
Advanced	168	3	21

Conclusion. These observations make only a trifling contribution to phanerogamic taxonomy in proportion to the many and serious phylogenetic problems that remain to be solved. Yet I feel that they are useful examples of the profitable results to be expected from more detailed studies of this sort. It must be repeated that the reliability of the method depends on the validity of the classification of the parasites; and thus the responsibility for its use falls fully on the mycologist.

References and Notes

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Revised Symbols for the New Unstable Particles[*]

R. W. Thompson

Department of Physics, Indiana University, Bloomington

ONE of the most interesting developments in physics in recent years has been the discovery of a surprising number of new heavy, unstable particles. There is no reason to think the list is yet complete; in fact, at the moment, the rate at which new particles are being found (about two per year) appears to be increasing as a result of concentrated effort in a large number of laboratories in many different countries.

The new particles are produced, directly or indirectly, in nuclear collisions of energy of the order of 1 Bev or more. For this reason, the new particles have been detected and studied primarily in cosmic radiation, although during the last year, artificial production has been achieved with the Brookhaven cosmotron. The methods of observation are quite varied; the principal experimental techniques are the nuclear emulsion, the magnetic cloud chamber, the multiple-plate