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**PROCEEDINGS OF
A SYMPOSIUM ON "TAXONOMY AND PHYLOGENY OF UREDINALES"**

**Organized by
THE SECOND INTERNATIONAL MYCOLOGICAL CONGRESS
University of South Florida, Tampa, Florida, U.S.A.**

August 31, 1977

Edited by
Yasuyuki HIRATSUKA and Naohide HIRATSUKA

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Contents

Introduction	J.F. HENNEN
HENNEN, Joe F. and Pablo BURITICÁ C. : A brief summary of modern rust taxonomic and evolutionary theory	243
HIRATSUKA, Yasuyuki and Naohide HIRATSUKA : Morphology of spermogonia and taxonomy of rust fungi	257
URBAN, Zdeněk : Rust ecology and phytocenology as aids in rust taxonomy	269
SAVILE, D.B.O. : Ecology, convergent evolution, and classification in Uredinales	275
DURRIEU, Guy : Phylogeny of Uredinales on Pinaceae	283
HOLM, Lennart : The rusts on Rosaceae and their affinities	291
<hr/>	
BURITICÁ, P. : Teliospore ontogeny as a criteria for rust phylogeny (<i>Abstract</i>)	295
THIRUMALACHAR, M.J. : Taxonomic significance of teliospore germination types in rust fungi (<i>Abstract</i>)	296



Participants of a symposium on "Taxonomy and phylogeny of Uredinales", organized by the Second International Mycological Congress, Tampa, Florida, U.S.A., Aug. 31, 1977.

From left to right: Dr. J.A. PARMELEE (Canada), Dr. M.J. THIRULAMACHAR (U.S.A.), Dr. Guy DURRIEU (France), Dr. D.O.B. SAVILE (Canada), Dr. N. HIRATSUKA (Japan), Dr. Y. HIRATSUKA (Canada), Dr. J.F. HENNEN (U.S.A.), Dr. L. HOLM (Sweden), Dr. P. BURITICÁ C. (Colombia), Dr. D.O. EBOH (Nigeria).

Introduction

Prof. J.F. HENNEN

The Arthur Herbarium

Department of Botany and Plant Pathology

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West Lafayette, Indiana, U.S.A.

A symposium entitled "Taxonomy and Phylogeny of Uredinales" was held at the Second International Mycological Congress in Tampa, Florida, U.S.A., August 31, 1977. Seven papers were presented. The symposium was organized by Dr. Y. HIRATSUKA of Edmonton, Alberta, Canada. Sessions were chaired by Drs. J. F. HENNEN and J. A. PARMELEE, Ottawa, Ontario, Canada. Five papers that were presented at the symposium are published here and the two are represented in abstracts. The introductory paper given below is adapted and updated from introductory remarks given at the Tampa meeting, and a paper presented at the J. C. ARTHUR Memorial Lectures held on June 22, 1975 at Purdue University, Indiana, U.S.A. The symposium sessions were well attended and provided excellent opportunities for exchange of ideas on the taxonomy of rusts.

We are very glad that the papers presented at the symposium will be published in the Reports of the Tottori Mycological Institute, especially in the issue commemorating Dr. Naohide HIRATSUKA's 77th birthday. We were very pleased to meet him at the symposium and we admire his continued contribution to rust taxonomy. On behalf of the all participants of the symposium and many other uredinologists across the world, we extend our congratulations for his 77th birthday and wish him good health for years to come.

Symposia of IMC² (Tampa)

(August 31, 1977)

(Taxonomy and phylogeny of Uredinales)

Douglas Savile (Ottawa) celebrating the greatest assembly of the world's Uredinologists
 Joe F. Klenner - The 1st, but not last, International Symposium on Rust Taxonomy.

M. S. Thirumalachar - Uredinologists lead the way to further knowledge of fungi!

Jack Parmelee (Ottawa) - A great way to get to know one another

G. DURRIEU (Toulouse) - Aug. 31 - 1977 a new starting day in the study of rusts?

P. BURITICA (Colombia) - THE FIRST TIME THAT THE TROPICS ARE IN THE SCHEME!

L. Holm (Uppsala) - Tampa is like an oceanium - we get intellectually dicarotized.

Jan. D. Eboh - It is a great assemblage of (NIGERIA) rusters!

Zdeněk URBAN - we have an obligation for the future (Praha) to enlarge or reestablish rust taxonomy studies world-wide.

Yasu HIRATSUKA. Naohito Hiratsuka Toshiko Hiratsuka

A brief summary of modern rust taxonomic and evolutionary theory*

Joe F. HENNEN** and Pablo BURITICÁ C.***

This paper gives a short review of some of the important ideas of modern rust taxonomy and evolution, thus providing a basis for more detailed discussions. PETERSEN (1974) gives an extensive literature review for many of the topics discussed here.

Mycologists are continually amazed and intrigued by the enormous diversity and degree of host specificity of Uredinales. Frequently new taxa are still being discovered in many regions. Most tropical areas remain poorly collected for rusts. Recent collections from Brazil reveal a rate of one new taxon for each 70 specimens collected. Even in temperate regions most taxa still need critical study including field observations and experimental life cycle data. Detailed study of a large number of collections of a species often reveals intraspecific variations and specificities. A basic world inventory of extant morphological types and host and geographic ranges of rusts is far from complete. The lack of adequate information about extant rusts is an important obstacle to developing objective theories of rust classification and evolution.

There is little direct knowledge of the evolution of rusts and few ways of testing evolutionary hypotheses. Few researchers have speculated critically about a general scheme for rust evolution. Perhaps the complex nature of rusts and the seeming impossibility of knowing their geological past history accounts for so few evolutionary uredinologists. Few scientists have the inclination for critical evolutionary speculation combined with the broad knowledge of the many complex aspects of evolution to attempt to synthesize a believable, let alone verifiable, scheme that will explain the origin, relation to other fungi, evolutionary history, and reasons for the extant great diversity of rusts. Attempts at producing evolutionary schemes for rusts have resulted mainly in conflicting ideas. Most of the few taxonomic uredinologists prefer the more important practical and scientifically verifiable work of collecting, describing, classifying, cataloging, and learning the biology of rust species. They believe that critically monographing various groups of rusts based on detailed comparative study of developmental and mature morphology is the most important kind of work for now. Only through this kind of basic taxonomic research can sufficiently reliable data accumulate so that eventually sound theoretical hypotheses of evolution and phylogeny can be produced. Perhaps because there are few rust

* Journal paper of the Purdue Agricultural Experiment Station.

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taxonomists, few large rust herbaria, and so many rusts worldwide, we should expect that serious speculation about rust phylogeny should remain at a low intensity. However, the desire to produce the "one true natural classification" of rusts is strong, and considering the great significance of rusts to plant pathology, the tremendous intellectual challenge of their complexity, the availability of modern technologies for their study, and the intellectually and esthetically rewarding pursuit of uredinology, perhaps the near future will bring increased high quality theorizing about rust phylogeny. Therefore, symposia at international scientific meetings concerning phylogeny, evolution, and taxonomy of rust fungi should be encouraged so that various viewpoints can be elaborated, critically examined, and their weaknesses, strengths, and quality be determined.

The Order Uredinales

Rusts make up one of the largest natural orders of fungi with more than 5,000 species. They comprise more than a third of the Basidiomycetes (AINSWORTH 1971). Obviously, generalizations about Basidiomycetes must include rusts or be qualified to exclude them. Rusts probably parasitize more different vascular plants than any other order of fungi, nearly 200 families (ARTHUR Herbarium files). They attack nearly all kinds, from mosses, primitive ferns and gymnosperms, to various primitive and advanced families of monocots and dicots. The rusts must be a geologically ancient group with a long and complicated evolutionary history. An important assumption that uredinologists make is that rusts have coevolved with their hosts over very long geological time. A corollary of this assumption is that, generally speaking, rusts that parasitize the most primitive kinds of extant plants are themselves the most primitive kinds of rusts and those that parasitize the more advanced kinds of plants are the more advanced kinds of rusts. Rusts now occur on all of the continents except Antarctica, have invaded all the major ecosystems, and are most diverse in the tropics, which is, no doubt, their ancestral home. They have a bewildering array of spore forms with different functions and morphologies that they put together in various kinds of life-cycles, which puzzle and intrigue mycologists and plant pathologists. Uredinologists try to make sense out of what is essentially, at least in geological time, a very plastic group of organisms. They are able to change their hosts, spore forms, morphologies, and life cycles to suit the situation. Rusts are ecologically obligate parasites with seemingly strict host specialization. Their complete life cycles have never been grown in axenic culture. Because of this complexity, it is no wonder that uredinologists have been unable to unravel these puzzles very well, that they cannot agree on terminology for the diversity of spore forms and types of life cycles, that they cannot agree on the proper classification, and certainly that they cannot agree on rust phylogeny.

The most characteristic features of rusts are their basidia and parasitic nutrition with its specialized associated vegetative morphology. The other kinds of sori and spores that many rusts produce are also characteristic so that nearly always an uredinologist can determine that an unknown fungus is a rust by any one of its states. Rusts produce phragmobasidia which often have well differentiated probasidia, commonly known as

teliospores, and metabasidia upon which the basidiospores are formed. Many rusts are known to have the capacity of basidiospore germination by repetition. Rusts do not produce basidiocarps, as usually understood, but a number of rusts produce well developed sterile fungus tissue associated with basidial sori. Many species of *Prospodium*, for example, produce suprastomatal, basket-like sori (CUMMINS 1940) while a number of species of *Puccinia* produce loculate sori reminiscent of certain ascocarps. Neither clamp connections nor dolipore septa, structures characteristic of many other basidiomycetes, are known in rusts. With greater use of modern technology, perhaps other characters will be found that will aid in defining rusts. Electron microscopy has revealed the "pully-wheel septal pore" apparatus which may prove to be unique for Uredinales (LITTLEFIELD & HEATH 1979).

Table 1. Recent chronology of families proposed for Uredinales

DIETEL (1900)	P. SYDOW and H. SYDOW (1904~24)	DIETEL (1928) ARTHUR (1929, 1934)	GÄUMANN (cited in LEPPIK 1972)	(LEPPIK 1972)	(SAVILE 1976)
Cronartia- ceae			Pucciniastra- ceae	Pucciniastra- ceae	Pucciniastra- ceae
Melampsora- ceae	Melampsora- ceae	Melampsora- ceae	Cronartia- ceae	Cronartia- ceae	
Coleosporia- ceae	Coleosporia- ceae		Chryso- myxaceae	Chryso- myxaceae	
Puccinia- ceae	Puccinia- ceae	Puccinia- ceae	Melampsora- ceae	Melampsora- ceae	Melampsora- ceae
	Zaghouania- ceae		Coleosporia- ceae	Coleosporia- ceae	
			Puccinia- ceae	Puccinia- ceae	Puccinia- ceae
					Phragmidia- ceae
				Ravenelia- ceae	Ravenelia- ceae

Taxonomy of Uredinales

The most extensive taxonomic coverage of rusts is the monumental, four volume work of the father-son team of Paul and Hans SYDOW published between 1904~1924. Although badly out of date, this work is the starting point for modern taxonomic monographic rust studies. Unfortunately, it may also be the best reference available for identification of rust species in many parts of the world. Another important world wide coverage of rusts is DIETEL's 1928 classification for families, tribes, and genera. More recent works that include information on only genera are those of THIRUMALACHAR and MUNDKUR (1949, 1950), CUMMINS (1959), and LAUNDON (1973).

Families of Uredinales

Developing family or other suprageneric concepts for rusts has been only partially satisfactory. Table 1 shows a chronology and interrelations of the most important

proposals for families of rusts (ONO 1978). So far, the morphological characteristics by which families and tribes have usually been defined are not always practical for routine identification. In fact, a good host-pathogen index is still the most efficient tool for identifying rusts, provided of course that it is complete, accurate, and the host is correctly identified, conditions seldom attained in many parts of the world. Thus, THIRUMALACHAR and MUNDKUR (1949, 1950), CUMMINS (1959), and LAUNDON (1973) did not include the family concept in their works. CUMMINS proposed that his method of dividing the genera of rusts into ten morphological sections based mainly on characteristics of teliospores, but without formal taxonomic status, is more practical for identification purposes. However, he stated that family concepts can be developed for rusts. Likewise, LAUNDON attempted to provide a key to all rust genera that would have practical application. He states that "because of uncertainties in classifying rusts, I prefer to avoid presenting any particular system herein."

The Melampsoraceae and its segregates

Table 1 shows that the number of families proposed for rusts varies from two to seven, with the Melampsoraceae and Pucciniaceae being the two key families. Many uredinologists accept the concept that the Melampsoraceae is for the most part a natural group of phylogenetically related genera. Also, it can be divided into a number of smaller natural groups which at one time or another have been classified as tribes or families, with the taxonomic level of these groups being perhaps arbitrary. These rusts have mostly expanded life cycles that alternate between gymnosperms, as spermogonial and aecial hosts, and various ferns and angiosperms, as uredinial and telial hosts. However, many species of *Melampsora* are autoecious on several families of angiosperms. These autoecious species are thought to be more phylogenetically advanced. Very few Melampsoraceae are known to have fully reduced life cycles (i.e., only spermogonia and telia, or only telia). The Melampsoraceae are mainly North Temperate or Boreal in distribution and all have *Aecidium*-like or modified *Aecidium*-like aecia, usually termed "peridermoid". Except for *Coleosporium*, their basidia are usually well differentiated into pro- and metabasidia with the probasidia usually forming well developed teliospores. Their probasidia are sessile and either single or united into one or several layered cushions, crusts, or thread-like columns. The Melampsoraceae include only about 15 genera of North Temperate or Boreal rusts, which have been studied taxonomically relatively well by northern hemisphere uredinologists (ARTHUR 1929, DIETEL 1928, HIRATSUKA 1958, KUPREVICH & TRANZSCHEL 1957, PETERSON 1973, P. & H. SYDOW 1904~24, ZILLER 1974).

The genus *Uredinopsis* in the Pucciniaceae is considered traditionally to be the most primitive extant rust. The assumption is that the most primitive extant rusts parasitize the most primitive types of extant hosts, in this case the fern family Osmundaceae and the genus *Abies* in the Pinaceae. Correlated with this is the relatively unspecialized telial stage of *Uredinopsis* consisting of single simple teliospores scattered within the fern host tissue.

Beginning with *Uredinopsis* as the most primitive, SAVILE (1955) constructed presumable evolutionary lines that gave rise to some of the main genera or suprageneric groups of Melampsoraceae. LEPPIK (1973) reviewed the geographic distribution of conifers in relation to Northern and Southern Hemisphere groups of genera. This distribution, for the most part, is accounted for by continental drift theory. LEPPIK concluded that the association of Melampsoraceous rusts with Northern Hemisphere conifers indicates that these rusts had their origin and coevolution in the Laurasian super-continent that later split into the main parts of Eurasia and North America.

Future research will undoubtedly strengthen the theory that the Melampsoraceae and its segregates are good taxonomic groups.

The Pucciniaceae and its segregates

The Pucciniaceae has included traditionally a large group of 75~80 or more genera that is much more diverse than the Melampsoraceae. The family is defined by the characteristics of teliospores usually pedicellate and laterally free, or if laterally united then pedicellate. Perhaps a more workable definition is that if a rust cannot be placed in the Melampsoraceae, then it belongs in the Pucciniaceae.

DIETEL (1928) divided the Pucciniaceae into 14 tribes. While some of these tribes are composed of mostly obviously closely related genera, few detailed studies have been made to test the soundness of these groups. Recently two of the tribes have been considered as families (LEPPIK 1972, SAVILE 1976).

Among the most thorough recent studies of the tribes of Pucciniaceae are those of the Puccinosiireae by BURITICÁ (1974), BURITICÁ and HENNEN (1980), and of the tribe Oliveae and its relatives by ONO (1978). BURITICÁ made a comparative developmental study of the telia of 19 genera within or allied to the tribe Puccinosiireae. His study places this tribe on a firm morphological foundation and shows convincingly that the evolution of Puccinosiireae has occurred polyphyletically by life cycle reduction through the endophylloid pathway from ancestors in the Pucciniaceae with *Aecidium*-like aecia.

ONO's work (1978) deals with the taxonomy of 13 genera and nearly 60 species. These rusts have one or usually several colorless, thin-walled, one-celled probasidia, with or without pedicels, produced on basidiogenous cells in basidiosori. Some of the genera previously have been placed in Melampsoraceae and some in Pucciniaceae. Under favorable conditions the probasidia form metabasidia without noticeable interruption of growth and development. The metabasidia are mostly simple apical extensions of the probasidia without the intervention of germination pores. The metabasidia may occupy the upper portion of either fully or partly elongated probasidia or may replace the entire probasidia with no or only slight morphological change. These rusts parasitize a wide variety of vascular plant families in mainly tropical and subtropical regions.

In another study, LEPPIK (1955) suggested that *Desmella*, *Hemileia*, *Cystopsora*, and *Gerwasia*, some of which belong to DIETEL's tribe Hemileieae, the coffee rust tribe, could be united with certain theoretical ancient fern rusts into a single group, the Stomatosporeae.

This group shows marked similarity with primitive Auriculariales on ferns such as *Herpobasidium* and *Platycarpha*, as well as *Jola* and *Eocronartium* on mosses. The name Stomatosporae is derived from the characteristic way in which some of these fungi form their basidial sori from mycelium that emerges through stomates. LEPPIK did not make this as a formal taxonomic proposal nor did he present it as a critical taxonomic study. However, it is an imaginative hypothesis that stimulates further consideration. There are, for example, no characteristics that separate the auriculariaceous genera, *Jola*, *Eocronartium*, *Herpobasidium*, and *Platycarpha* from Uredinales. These fungi have been placed traditionally in Auriculariales presumably because their basidiosori are on mycelium that emerges onto the host surface. Certain suprastomatal rusts, however, are known to have emergent hyphae on which sporogoneous or basidiogenous cells are formed (HENNEN & ONO 1978, ONO 1978).

DONK (1972) proposed that certain genera, *Herpobasidium*, *Kriegeria*, and *Kweilingia*, traditionally regarded as members of the Auriculariales, are best recognized as monocyclic rusts.

These suprastomatal and auriculariaceous rusts are mostly tropical and either lack *Aecidium*-like aecia in their life cycles, or their life cycles are unknown. While the life cycles of these rusts are still speculative, LEPPIK theorized that *Aecidium*-like aecia have never occurred in this group and they represent an evolutionary line even more primitive than the Melampsoraceae. Because of their tropical ancestry, hosts, and adaptations, they never developed *Aecidium*-like aecia nor heteroecism, which are presumed to be adaptive responses to climatic regions with long droughts. This group of genera certainly deserves more critical taxonomic study, including life cycle and nuclear determinations. Such studies would help solve the question of the relationships of the auriculariaceous rusts.

SAVILE (1976), however, rejects the idea that these rust-like auriculariaceous genera should be considered as rusts, but no one has yet given characteristics of the Uredinales that would exclude them. Further, SAVILE believes that all extant rust genera with suprastomatal sori have evolved by convergence from only distantly related rust ancestors and cannot be placed closely together taxonomically.

Among the most important research studies that will aid in guiding the making of natural groups of rust genera is the comparative study of spermogonial types by HIRATSUKA and CUMMINS (1963) and HIRATSUKA and HIRATSUKA (1980). This work shows that the morphology of spermogonia is relatively stable within and among certain groups of presumably related genera. The six well defined groups for spermogonia proposed in these studies will prove useful in guiding the definition of suprageneric taxa. The quality, naturalness, or phylogenetic significance of these groups will improve as other characters are found that correlate with spermogonial type.

While spermogonial type of rusts may prove useful in showing phylogenetic relationships, they are of relatively little value for practical identification because of their infrequent or non occurrence in many rusts. If there was a group of primitive rusts that never evolved spermogonia, and if representatives of this group still exist, we cannot expect to find

spermogonia in all lineages of rusts.

Evolutionary pathway mechanisms in rusts

How have rusts managed to attain their present diversity? How can we reconcile the strict host specialization of species and physiological races on the one hand and extremely wide host range of the order on the other? Obviously rusts possess evolutionary mechanisms that permit them to become obligately adapted to a very narrow ecological niche, as physiological races, yet the order as a whole is highly diversified as to climatic adaptation, hosts, types of life cycles, and spore morphology. Do rusts possess any unique mechanisms of evolution that may help explain their diversity?

No significant fossil record is known for rusts, but because of the strict obligate and host specialized parasitism, the coevolution of rusts along with their hosts is a primary consideration for rust evolution. Obviously, if the rusts are as geologically ancient as their oldest groups of extant hosts, the ferns and mosses, then they have had ample time to accomplish the complexity they now possess.

Modern attempts to describe and explain rust evolution have come mainly from the works of JACKSON (1931, 1944), LEPPIK (1953, 1955, 1956, 1959, 1965, 1967, 1972, 1973), and SAVILE (1955, 1976).

These papers do not deal with microevolutionary mechanisms such as specific chromosomal, genetic, physiological, or biochemical changes. These phenomena are studied effectively usually only by experimental methods. Only a few rusts that are important pathogens have been studied intensively along these lines.

SAVILE (1955, 1976) has effectively warned of the numerous pitfalls of evolutionary speculation and especially the need to attempt to recognize similar patterns of adaptive selection in different groups of rusts and convergent evolution.

Only the main ideas of these papers are summarized or augmented here in a more or less integrated form. Four interrelated general types of evolutionary pathway mechanisms are proposed. They are: 1. Divergence and radiation with hosts. 2. Jumps to new unrelated hosts, 3. life cycle expansion, and 4. life cycle reduction.

Divergence and radiation is a standard descriptive mechanism of evolution that applies to many organisms but the other three must be relatively restricted to only a few groups of organisms.

1. *Divergence and radiation with hosts* This phenomenon is the most straight forward, and probably accounts for most rust species. Simply stated, as hosts have evolved, diversified, or become extinct, their rust parasites have followed. This mechanism can be accounted for by the microevolutionary theory of physiological or biological race formation followed by various sexual isolating mechanisms, such as genetic, ecological, and geographical. The results of the process become obviously manifest to rust taxonomists at a higher level when they find that certain genera or families of flowering plants, such as Compositae, support large numbers of species of *Puccinia* that are morphologically different but obviously closely related (CUMMINS 1978). Each host genus or species may have its

own species of rust. If a single host species has more than one species of a rust genus, these are often adapted to different ecological regions of the host's geographic range. *Zea mays* for example, is host for two species of *Puccinia* each of which is best adapted to a different climatic zone. A genus of rust is often specialized on species of a single or several closely related host genera. The new world rust genus *Cumminsia*, for example, has eight species, each of which parasitizes either a single species or a group of closely related species of the host genus *Mahonia* or *Berberis* in the *Berberidaceae* (BAXTER 1957). Another new world rust genus, *Prospodium*, has nearly 30 species, most of which parasitize species or groups of closely related species of *Bignoniaceae* (CUMMINS 1940). A few occur on *Verbenaceae*.

Certain host families may support certain groups of related rust genera. The *Rosaceae* and *Leguminosae* are well known in this regard (LEPPIK 1972, SAVILE 1976).

2. *Jumps to new, unrelated hosts* This mechanism is difficult to document and explain. How is it that an autoecious rust species that is genetically host specialized can jump to a new host in a plant family taxonomically far removed from the first? Of course, heteroecious rusts have the genetic capacity for a two host specialization in different phases of their life cycles. Thus, perhaps it is not so speculative to imagine that given sufficient time and proper circumstances, an autoecious rust can produce by chance the proper genetic capability to occasionally jump to some unrelated host family.

SAVILE (1969) discusses host jumping by autoecious rusts in some detail. As an example, he speculates that the immediate ancestor of *Puccinia palmeri*, a rust on *Penstemon* spp. in the *Scrophulariaceae*, made a jump to *Pedicularis* sp., in a different subfamily of the *Scrophulariaceae*, subsequently evolving into a new closely related species, *Puccinia rufescens*.

Host jumping in heteroecious rusts has been proposed by LEPPIK (1953) to be the most important mechanism by which rusts have been able to invade so many different vascular plant families. According to his detailed "hologenetic ladder" hypothesis, heteroecious rusts have climbed or "jumped" their way through various families of vascular plants in a phylogenetic sequence, beginning with primitive and continuing to the more advanced. His basic idea is derived from the observation that heteroecious rusts always have one stage of their life cycle on a particular host family of one phylogenetic age and the other stage on a host family of a different phylogenetic age. Thus, the ferns support the uredinial and telial stages of many rusts whose spermatophytes and aecia are on the phylogenetically more advanced gymnosperms. Another example is the numerous species of heteroecious rusts whose uredinia and telia are on the *Gramineae* and whose spermatophytes and aecia are on various families of dicots and a few monocots of presumably more advanced phylogenetic age than the *Gramineae*. His explanation for this observation is that heteroecious rusts can change hosts of only one of its stages at a time. That is, for example, during evolutionary change, an uredinial and telial stage may remain constant on a particular host but the spermatophytes and aecia may become labile. They can switch to either the same host on which occur the uredinia and telia, and thus the rust would become autoecious, or

they can switch to some other family phylogenetically younger than the uredinal and telial host family, thus remaining heteroecious.

In other circumstances, the uredinal and telial stage may become the labile phase and "jump" to either the spermogonial and aecial host, the population thus becoming autoecious, or they can switch to some other family phylogenetically younger than the spermogonial and aecial host family. Thus along the way of climbing the hologenetic ladder some rust populations may become permanently autoecious. Other rusts continue to be heteroecious, although changing their hosts, while in other cases autoecious populations may revert to heteroecism.

3. *Life cycle expansion* Most early ideas about rust evolution proposed that the most primitive rusts and their ancestors were pleomorphic and long cycled, such as is found in many extant long cycled rusts. However, both SAVILE and LEPPIK speculate that the phenomenon of life cycle expansion explains some of the earliest evolution in rusts. According to these ideas, the earliest rusts were obligately parasitic and produced only the basidial stage. During their early evolutionary period they expanded their life cycles to include spermogonia, uredinia, and aecia. The development of each of these structures brought adaptive advantages by which eventually the Uredinales were able to attain the diversity they now have.

SAVILE (1955) suggests that an ascomycetous *Taphrina*-like ancestor, which parasitized some early fern or fern ally, gave rise to the first rusts. LEPPIK (1955) uses the older idea that rusts arose originally from some auriculariaceous fungus, which was parasitic on some primitive ferns. With slight modification, these ideas can be combined, as SAVILE (1976) has done, to suggest that some plant parasitic proto-*Taphrina* gave rise to protobasidiomycetes which in turn produced Uredinales, which remained plant parasitic, and Auriculariales, which became saprobic. An important aspect of this idea is that rusts have been plant parasites from their beginning and the earliest rusts were parasitic on ferns or perhaps mosses. Also, the first rusts had simple life cycles, adapted to a warm, moist, tropical environment with little or no seasonal climatic fluctuations. These early rusts were probably heterothallic but had no specialized gametes, sexual fusions occurring by hyphal anastomoses. They had no special dispersal spores except for basidiospores, and no protective or other adaptive features for various climatic or other hazards. The most similar living relatives of these primitive rusts seem to be the auriculariaceous rust genera *Jola*, and *Eocronarrium* on mosses, and *Herpobasidium* and *Platycarpha* on ferns. These fungi produce only basidial stages, but no experimental work has been done to determine their sexual or nuclear life cycles. As rusts continued to evolve in this early period, spermogonial, uredinal, and aecial stages and structures arose as adaptive responses, improving the efficiency of genetic exchange, clonal dispersion, and dispersion of new genetic combinations, respectively. By attaining these new features, plus the inherent plasticity of the basidial stage, rusts now possessed the basic tools for great expansion out of the climatically uniform tropics and into new climatic and host ranges.

Both SAVILE and LEPPIK see heteroecism originating as a response to climatic shifts

that made fern hosts of primitive tropical rusts less susceptible or even resistant to infection by basidiospores during the time of their liberation, while at the same time certain conifers growing in close proximity produced young, susceptible, vegetative growth. After a period of adjustment the heteroecious condition became stabilized. It proved to be important for rusts invading the great Northern Hemisphere coniferous forest ecosystems and much later the great savannas and prairies composed of angiosperms.

This early life cycle expansion hypothesis raises several questions. Did some primitive tropical rusts never or only partially expand their life cycles? Are their descendants to be found as extant relict auriculariaceous or tropical suprastomatal rusts? Was there only one general expansion or several? Did they all end in heteroecism and further evolution of rusts proceed from there? Is it possible that more recent expansions have occurred or will occur from primitive tropical rusts?

According to this evolutionary life cycle expansion hypothesis, it is possible to categorize life cycles based upon the degree of expansion. Thus, those rusts that have never expanded their life cycles and have only the basidial stage are the unexpanded type. Those that have attained one or two stages in addition to the basidial, but not the total possible, are the partially expanded type, while those rusts that have the full complement of stages are the fully expanded type.

As shown in the next section, similar characteristics of the number of stages in the life cycle also determine the degree to which life cycles become reduced. Therefore, the differentiation between expanded and reduced life cycles presents a problem. Secondary considerations, which are presented below, help solve this problem.

4. *Life cycle reduction* Life cycle reduction was reviewed and analyzed critically by JACKSON (1931). His analysis is based mainly on North American species. He designated two general kinds of life cycle reduction. The first is a change from heteroecism to autoecism, which reduces the number of hosts in the life cycle. Second is the loss of various stages from the life cycle. Correlated with these reductions, changes may also occur in the number of cells in teliospores. The two-celled teliospores characteristic of the genus *Puccinia*, for example, may become transformed into one-celled teliospores of *Uromyces*.

Among the most instructive of JACKSON's analyses were those of species with "unstable life cycles". Actually these are species that possess more than one kind of life cycle. Two of the variations he found were: 1. species with *Aecidium*-like aecia may infrequently produce *Uredo*-like aecia, and 2. species that are full cycled may infrequently have reduced life cycles. JACKSON (1931) concludes that the natural occurrence of these variants supports his hypothesis that the different kinds of stabilized, reduced life cycles have evolved by natural selection of these variants. Several similar life cycle variants have been observed in experimental rust cultures, which further supports this idea (JOHNSON & NEWTON 1938).

JACKSON concluded that most full cycled, autoecious rusts are derived from full cycled heteroecious rusts, which have transferred all of their stages to the original aecial host. Only a few seem to have transferred all of their stages to original telial hosts. This

conclusion makes up an important part of LEPPIK's (1953) hologenetic ladder hypothesis as discussed above.

JACKSON (1931) concluded that rusts with life cycles in which various stages are missing are derived from full cycled rusts. He did not consider the idea that perhaps some rusts have unexpanded or only partly expanded life cycles, which could also account for some stages missing from the life cycles.

One of the best known and most common types of life cycle reduction is accounted for by "TRANZSCHEL's law". This law states that when heteroecious, full-cycled rusts form a stable, reduced life cycle variant, the new form will occur on the original aecial host. The teliospores of the new short cycled rust usually resemble the teliospores of the parental species but occasionally they may resemble the aeciospores of the parental species. The latter kind of rusts are termed endo forms and are usually placed in special convenience genera such as *Endophyllum* and *Kunkelia*. This process of life cycle reduction has been called the endophylloid pathway. When a group of rust species occurs, each member having a different life cycle, but all thought to be related by direct derivation from a long cycled parental form, they are termed correlated species. ARTHUR (1934) made use of this concept, so that correlated species are placed together in groups to better show their relationships.

Summary of evolutionary pathways of rust life cycles

Although JACKSON's ideas about the derivation of various kinds of reduced life cycles from full-cycled, heteroecious rusts must be true for many rusts, we must also consider the propositions by SAVILE and LEPPIK that the earliest rusts possessed only the basidial stage and underwent life cycle expansion. Perhaps some of the primitive types of life cycles have persisted in relict tropical rusts in which the life cycles are unexpanded or only partially expanded. In connection with this, LEPPIK (1955) further proposed that in addition to the line of evolution in which *Aecidium*-like aecia occur and in which heteroecism developed, there very likely exists another rusts evolutionary line in which *Aecidium*-like aecia and heteroecism never developed.

Figure 1 summarizes diagrammatically some possible interconnections between evolutionary pathways of rust life cycles. The Roman numerals O, I, II, III represent spermogonial, aecial, uredinal, and basidial stages, respectively, as defined by HIRATSUKA (1973). The lower left III represents the most primitive unexpanded life cycle. The arrow leading up to the III in the middle left of the figure indicates that the unexpanded life cycle may still exist in morphologically unspecialized, mostly tropical, relict auriculariaceae species on mosses, ferns and some angiosperms (*Eocronartium*, *Jola*, *Platycarpha*, *Herpobasidium*, and perhaps some species of *Goplana*). Life cycles became partly expanded by the evolutionary development of either spermogonia, uredinia, or aecia.

The earliest expansion of rust life cycles that SAVILE (1955, 1976) and LEPPIK (1955) proposed are represented in the left central part of the diagram by arrows leading from the unexpanded III to the II III, O III, and O I III. We suggest that some of these life

cycles may be represented in extant tropical rust genera with suprastomatal sori such as *Desmella* on ferns, *Edythea* on *Berberidaceae*, certain *Goplana* species, *Cerradoa* on *Palmae*, and *Hemileia* species. LEPPIK (1955) suggested that no *Aecidium*-like aecia, characterized by drought resistant sori, developed in this line of evolution because of their tropical habitats. If these kinds of partly expanded or fully expanded life cycles, in which no *Aecidium*-like aecia have occurred, have persisted, then conceivably some of them have also become reduced. This is indicated in the upper central part of the diagram by the perpendicular arrow leading to the reduced type of life cycle at the top of the diagram. The (0) in the reduced type of life cycle indicates that spermogonia may be present or absent in these short cycled rusts.

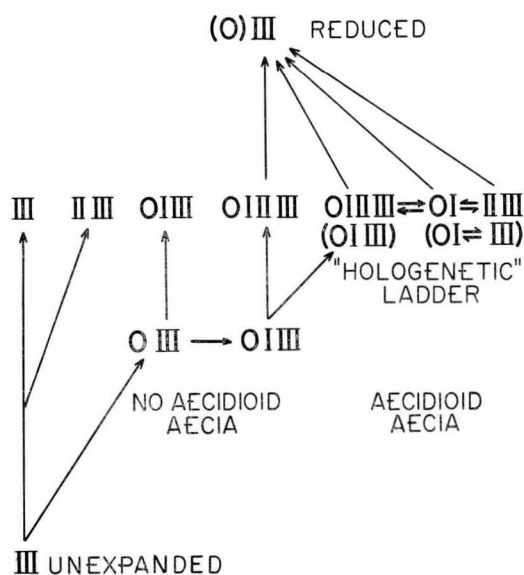


Fig. 1. Evolutionary pathways of rust life cycles.

SAVILE (1976) believes that none of these primitive types of unexpanded, partly expanded, or fully expanded life cycles in which non *Aecidium*-like aecia occurred have persisted. His hypothesis suggests that all extant rusts have lineages that have passed by way of the *Aecidium*-like aecial route. This route is shown on the right and upper part of the diagram. It seems highly probable that the great majority of extant rusts belong in this group which now have, or their ancestors have had, *Aecidium*-like aecia. This concept of *Aecidium*-like aecia also includes various morphological modifications such as *Peridermium*-like, *Roestelia*-like, and *Caecoma*-like. The diagram shows the interchanges of fully expanded rust life cycles from autoecism (O I II III) to heteroecism (O I \rightleftharpoons II

III), to reduced life cycles, with or without spermogonia ((O) III). It is this ability for complex changes of life cycles that JACKSON (1931), SAVILE (1955, 1976), and LEPPIK (1955) postulate to be responsible for much of the extant great diversity in host range and types of life cycles. During changes from autoecism to heteroecism phylogenetically younger host groups may be gained. As heteroecious rusts change hosts for only part of their life cycles they gain phylogenetically younger hosts. Life cycle reduction may occur from either autoecious or heteroecious rusts. Life cycle reduction may follow several pathways. One kind may be called the teloid pathway because the derived species with a reduced life cycle possesses a basidial stage that resembles the basidial stage (telia) of the parental species. Another kind may be termed the endophylloid pathway because the derived species with a reduced life cycle possesses a basidial stage that resembles the *Aecidium*-like aecial stage of the parental species. The term endophylloid is used because *Endophyllum* is a

convenience genus used for these kinds of rusts.

The characteristics of rust life cycles based upon evolutionary expansion or reduction can be summarized as follows.

1. UNEXPANDED-primitive tropical relicts without morphological specializations, with auriculariaceous, suprastomatal, or otherwise unspecialized basidiosori (*Jola*, *Eocronartium*, *Herpobasidium*, etc.).

2. PARTLY EXPANDED-somewhat less primitive than the unexpanded type with some morphological specializations, especially clonal dissemination (urediniospores), mostly tropical or subtropical with probably mostly suprastomatal sori (*Desmella*, *Hemileia*, *Goplana*, etc.).

3. FULLY EXPANDED-more advanced with numerous morphological and host specializations, worldwide (*Cronartium ribicola*, *Melampsora lini*, *Puccinia coronata*, *Cumminsella mirabilissima*, etc.).

4. PARTLY REDUCED-advanced, similar to fully expanded but not as numerous and lacking one or two stages, usually uredinia (*Gymnosporangium clavipes*, etc.).

5. REDUCED-highly advanced, with highly specific morphological and host specializations, worldwide (*Puccinia malvacearum*, *Endophyllum sempervivi*, *Chardoniella gynoxidis*, etc.).

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Morphology of spermogonia and taxonomy of rust fungi

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Abstract

Based on the examination of 224 species in 73 genera, the morphology of spermogonia is discussed in relation to taxonomy and phylogeny of rust fungi. The 11 morphological types of spermogonia proposed by HIRATSUKA and CUMMINS (1963) are redefined, and a new type, which is characterized by a well-developed beak and a large indeterminate deep-seated cavity, is described. The new type (Type 12) is found in *Mikronegeria alba*, *M. fagi*, *Caecoma deformans*, and *C. peltatum*. Six well-defined subdivisions are recognized among rust fungi based on the morphological types of spermogonia. Spermogonial morphology is a dependable characteristic for taxonomy and phylogeny of rust, especially at generic and suprageneric levels.

Introduction

In this presentation we would like to review the morphological types of the spermogonia of rust fungi and their relationship to taxonomy and phylogeny. This presentation is based on the examination of 224 species in 73 genera, which include 136 species described in HIRATSUKA & CUMMINS (1963).

One of the unique features of the rust fungi is that they have up to six functionally and morphologically different spore states in their life cycles. The situation is further complicated because they not only have many different spore states but gametophytic states and sporophytic states often grow on two unrelated groups of host plants. Spermogonia are structures produced on gametophytic haploid mycelium and are responsible for dikaryotization.

Taxonomy, especially suprageneric classification, has been heavily dependent on the morphology of teliospores, probably because telial state is considered as the perfect state of Uredinales according to the International Code of Botanical Nomenclature (1972), and its description is necessary for proper nomenclature of a species. However, to arrive at the more natural classification of rust fungi, examinations and comparisons of other spore states, including spermogonia, are desirable and necessary. This paper is an attempt to draw attention to the value of spermogonial morphology to the taxonomy of rust fungi.

Terminology

Before going into the discussion of morphology of spermogonia and their relationship to taxonomy, we would like to discuss the terminology of these structures. They have

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been variously called "spermogonia" (TULASNE 1851; ARTHUR 1904; CUMMINS 1959; HIRATSUKA & CUMMINS 1963), "pycnia" (ARTHUR 1905; LAUNDON 1974; SAVILE 1976), "pynciosori" (CUNNINGHAM 1931), and "pyncidia" (BULLER 1950). Among these terms, pynciosori is merely a variation of pycnia and has never been used extensively. The term pyncidia was used by BULLER (1950) and some others, but very few use this term now because of the confusion it could create with pycnidia of the imperfect state of Ascomycetes. The term pycnia was created by ARTHUR (1905) to designate pyncidia-like organ of rust fungi and is derived from the same Greek word 'πυκνος' (= dense or compact). Until then, ARTHUR had used the term spermogonia, which was first used by TULASNE in 1851 (ARTHUR 1904). ARTHUR (1905) at the time argued that this organ is very inefficient one and does not have an infectious or sexual function; therefore, he decided not to use the term spermogonia, which suggests sexual function. After the discovery of the sexual function of the organ (CRAIGIE 1927), ARTHUR himself, who had created the term pycnia, used the term spermogonia again (ARTHUR 1934). Many contemporary mycologists prefer the term pycnia to spermogonia (LAUNDON 1974; SAVILE 1971 & 1976), because they do not recognize this organ as only a male gamete producing structure. Shortly after CRAIGIE discovered the function of the organ, he reported and emphasized the presence and possible function of so-called "flexuous hyphae" as receptive structures. Flexuous hyphae are fragile hyphae protruding from the spermogonia and can be observed commonly. Mycologists who insist on using the term pycnia believe that the organ is not only the structure to produce sperm cells (spermatia), but also contains receptive female parts (flexuous hyphae) together in the same organ; therefore, the structure is hermaphroditic. SAVILE (1976) considered the organ analogous to an entomophilous perfect flower of higher plants because it also produces nectar. We agree with CUMMINS (1959) and CAIN (1972) that aecial primordia, not flexuous hyphae, should be considered the female receptive organs of rust fungi.

Presence and possible function of "flexuous hyphae" are discussed at length in BULLER's most interesting work, "*Researches of fungi*", Volume VII (1950), but as he admitted, there is no proof or evidence of nuclear migration from flexuous hyphae to the base of aecial primordia. On the other hand, ALLEN (1934) and ANDRUS (1931 & 1933) pointed out that many fragile hyphal tips have been observed to protrude through stomata or between cells close to the aecial primordia. SAVILE (1939) recognized that these hyphae were especially common in moist chambers, but concluded that they could seldom function in nature because they were pinched off by closing of the stoma. BULLER (1950), who strongly disputed the idea of a possible receptive mechanism in such hyphae, recognized their presence and illustrated them in his book (p. 130, Fig. 40). From our own observations, spermogonia and aecial primordia are not always positioned closely together. We observed many such hyphae; therefore, we do not believe that dikaryotization through flexuous hyphae is a main occurrence in rust fungi. Furthermore, all spermatia observed so far are phyalospores (MIMS *et al.* 1976), and homology of this organ to the spermogonia of Ascomycetes is obvious (CAIN 1972).

From the above considerations, we believe that the term spermogonia is preferable to pycnia.

Morphological types of spermogonia

Because of the inconspicuous nature of the spermogonia and minuteness of spermatia, the morphology of spermogonia as a useful character has received little attention from rust taxonomists, but the conservative nature of the morphology has been noted by several mycologists (HUNTER 1936; KAMEI 1940). HIRATSUKA & CUMMINS (1963) showed that morphology of spermogonia is useful and important to the taxonomy and phylogeny of the rust fungi. They distinguished 11 morphological types based on the presence or absence of a bounding structure, shape of the hymenium, position in the host tissue, and type of growth. Much additional information has been accumulated, and several modifications have become necessary to their system. We think, however, the criteria used in their work are basically sound, and we would like to discuss morphological types of spermogonia without changing numbers used by HIRATSUKA & CUMMINS (1963). We also would like to add a new type as Type 12.

Simple definitions of the 11 types mentioned in HIRATSUKA & CUMMINS (1963) are as follows:

Type 1 The spermogonia are subepidermal in position and have strongly concave hymenia. They are immersed in the mesophyll and generally are globoid or depressed globoid. The absence of a bounding structure distinguishes this type from Type 4.

Type 2 The spermogonia are subepidermal, determinate, and have flat hymenia. There is no bounding structure. The spermogonia of some species are produced in substomatal cavities, and the stomates serve as ostioles. In such species the spermogonia sometimes appear superficial and may be erroneously interpreted as subcuticular.

Type 3 The spermogonia are subcuticular, determinate, and have flat hymenia. They have no bounding structure.

Type 4 The spermogonia are subepidermal, determinate, and have strongly concave hymenia. Well-developed periphyses comprise the bounding structures.

Type 5 The spermogonia are subepidermal, determinate, and have flat hymenia. Bounding structures, either periphyses or peridia, are present. This type differs from Types 6 and 7 in position in the host.

Type 6 The spermogonia are intraepidermal, determinate, and have flat hymenia. Bounding structures are present.

Type 7 The spermogonia are subcuticular, determinate, and have flat hymenia. There are two kinds of bounding structures, periphyses or peridia.

Type 8 The spermogonia are subepidermal, indeterminate, and have flat hymenia. They develop between the epidermis and the mesophyll and split the tissues apart.

Type 9 The spermogonia are intracortical, indeterminate, and have flat hymenia. The position is designated as intracortical but actually is between the periderm and the cortex of the stem. Intracortical spermogonia are known to occur in *Cronartium* only.

Table 1. Rust species examined and type of spermogonia

<i>Achrotelium lucumae</i> CUMM.	7	<i>Cystomyces costaricensis</i> SYD.	5
<i>Arthuria catenulata</i> JACKS. & HOLW.	7	<i>Dasturella divina</i> (SYD.) MUND. &	
<i>Baeodromus eupatorii</i> (ARTH.) ARTH.	4	KHESWALLA	7
<i>Baeodromus holwayi</i> ARTH.	4*	<i>Dasyscypha gregaria</i> (KUNZE) P. HENN.	5
<i>Baeodromus senecionis</i> SYD.	4*	<i>Diabole cubensis</i> (ARTH.) ARTH.	7
<i>Caeoma deformans</i> (BERK. & BR.) TUB.	12*	<i>Dicheirinia superba</i> JACKS. & HOLW.	7
<i>Caeoma peltatum</i> C.G. SHAW III &		<i>Didymopsora africana</i> CUMM.	4
C.G. SHAW	12*	<i>Didymopsora solani-argentii</i> (P. HENN.)	
<i>Caeoma torreyae</i> BONAR	4*	DIET.	4
<i>Cerotelium dicentrae</i> MAINS &		<i>Didymopsorella lemanensis</i> (DOIDGE)	
H.W. ANDERSON	7	HIRAT. f.	5
<i>Chaconia ingae</i> (SYD.) CUMM.	7	<i>Diorchidium piptadeniae</i> DIET.	7
<i>Chardoniella andina</i> (LAGERH.) BURIT. &		<i>Endophyllum sempervivi</i> (ALB. & SCHW.)	
HENN.	4*	DBY.	4
<i>Chardoniella gynoxidis</i> KERN	4	<i>Frommea obtusa</i> (STRAUSS) ARTH.	10
<i>Chrysocelis lupini</i> LAGH. & DIET.	4	<i>Gerwasia rubi</i> RAC.	6
<i>Chrysocyclus cestri</i> (DIET. & P. HENN.)		<i>Gymnoconia peckiana</i> (HOWE) TROTT.	6**
SYD.	4	<i>Gymnosporangium andinum</i>	4*
<i>Chrysomyxa arctostaphyli</i> DIET.	2	<i>Gymnosporangium bethelii</i> KERN	4*
<i>Chrysomyxa cassandrae</i> TRANZ.	2	<i>Gymnosporangium clavariiforme</i> (PERS.)	
<i>Chrysomyxa empetri</i> (PERS.) SCHROET.	2	DC.	4*
<i>Chrysomyxa ledi</i> (ALB. & SCHW.) DBY.	2	<i>Gymnosporangium clavipes</i> CKE. & PK.	4
<i>Chrysomyxa ledicola</i> (PK.) LAGH.	2	<i>Gymnosporangium connersii</i> PARMELEE	4*
<i>Chrysomyxa piperiana</i> SACC. & TROTT.		<i>Gymnosporangium cornutum</i> ARTH. ex	
ex CUMM.	2*	KERN	4*
<i>Chrysomyxa woroninii</i> TRANZ.	2*	<i>Gymnosporangium fuscum</i> HEDW. f.	4*
<i>Chrysospora gynoxidis</i> LAGH.	4	<i>Gymnosporangium globosum</i> FARL.	4
<i>Cionothrix jacksoniae</i> (P. HENN.) SYD.	4	<i>Gymnosporangium haraeaeum</i> SYD.	4*
<i>Cionothrix praelonga</i> (WINT.) ARTH.	4	<i>Gymnosporangium juniperi-virginianae</i>	
<i>Coleosporium asterum</i> (DIET.) SYD.	2**	SCHW.	4*
<i>Coleosporium jonesii</i> (PK.) ARTH.	2**	<i>Gymnosporangium nelsonii</i> ARTH.	4*
<i>Coleosporium paraphysatum</i> DIET.	2*	<i>Gymnosporangium nidus-avis</i> THAXT.	4*
<i>Coleosporium phellodendri</i> DIET.	2*	<i>Gymnosporangium tremelloides</i> HARTIG	4*
<i>Coleosporium vernoniae</i> BERK. & CURT.	2**	<i>Hamaspora longissima</i> (THUEM.) KOERN.	8
<i>Coleosporium xanthoxyli</i> DIET. &		<i>Hapalophragmium derridis</i> P. HENN.	7
P. SYDOW	2*	<i>Hapalophragmium millettiae</i> SYD.	5
<i>Cronartium coleosporioides</i> ARTH.	9*	<i>Hapalophragmium mysorense</i> THIRUM.	7
<i>Cronartium comandrae</i> PK.	9*	<i>Hapalophragmium ornatum</i> CUMM.	7
<i>Cronartium comptoniae</i> ARTH.	9*	<i>Hapalophragmium ponderosum</i> SYD. &	
<i>Cronartium fusiforme</i> HEDGC. & HUNT		BUTL.	5
ex CUMM.	9*	<i>Hapalophragmium setulosum</i> (PAT.) SYD.	7
<i>Cronartium occidentale</i> HEDGC. et al.	9	<i>Hyalopsora aspidiotus</i> (MAGN.) MAGN.	2
<i>Cronartium quercuum</i> MIYABE ex SHIRAI	9*	<i>Kuehneola uredinis</i> (Lk.) ARTH.	11
<i>Cronartium ribicola</i> J.C. FISCH.	9	<i>Kunkelia nitens</i> (SCHW.) ARTH.	6**
<i>Crossospora sawadae</i> (SYD.) ARTH. &		<i>Lipocystis caesalpiniae</i> (ARTH.) CUMM.	7
CUMM.	7	<i>Maravalia ascotela</i> (SYD.) MAINS	4
<i>Cumminsella mirabilissima</i> (PK.) NANNF.	4	<i>Maravalia elata</i> (SYD.) MAINS	4
<i>Cumminsella standleyana</i> CUMM.	4*	<i>Masseella capparis</i> (HOBSON) DIET.	7*
<i>Cumminsella stolpiana</i> (DIET. & NEG.)		<i>Masseella narisimhanii</i> THIRUM.	7
BAXTER	4*	<i>Melampsora abieti-capraearum</i> TUB.	2
<i>Cumminsella texana</i> (HOLW. & LONG)		<i>Melampsora albertensis</i> ARTH.	3
ARTH.	4*	<i>Melampsora arctica</i> ROSTR.	2

Table 1. *Continued*

<i>Melampsora euphorbiae-dulcis</i> OITH.	2	<i>Puccinia enixa</i> CUMM.	4*
<i>Melampsora lini</i> (PERS.) LÉV.	2	<i>Puccinia farinacea</i> LONG	4*
<i>Melampsora medusae</i> THUEM.	2*	<i>Puccinia globosipes</i> PK.	4
<i>Melampsora occidentalis</i> JACKS.	3	<i>Puccinia graminis</i> PERS.	4
<i>Melampsora paradoxa</i> DIET. & HOLW.	3*	<i>Puccinia grata</i> ARTH. & CUMM.	4*
<i>Melampsora pinitorqua</i> (DBY.) ROSTR.	3	<i>Puccinia helianthi</i> SCHW.	4
<i>Melampsorella caryophyllacearum</i>		<i>Puccinia hystereum</i> (STR.) RÖHL.	4*
SCHROET.	3	<i>Puccinia impedita</i> MAINS	4*
<i>Melampsoridium betulae</i> (SCHUM.) ARTH.	3	<i>Puccinia inaudita</i> JACKS. & HOLW.	4*
<i>Mikronegeria alba</i> OEHRENS & PETERSON	12*	<i>Puccinia inclusa</i> SYD.	4*
<i>Mikronegeria fagi</i> DIET. et NEG.	12*	<i>Puccinia intermixta</i> PK.	4*
<i>Milesina fructuosa</i> (FAULL) HIRAT. f.	1	<i>Puccinia jonesii</i> PK.	4*
<i>Milesina laeviuscula</i> (DIET.) HIRAT. f.	1	<i>Puccinia laschii</i> LAGERH.	4*
<i>Milesina polypodophila</i> (BELL) FAULL	1	<i>Puccinia leptochloae</i> ARTH. & FROMME	4
<i>Milesina vogesiaca</i> (FAULL) HIRAT. f.	1*	<i>Puccinia longicornis</i> PAT. & HARIOT	4*
<i>Miyagia anaphalidis</i> MIYABE	4	<i>Puccinia massalis</i> ARTH.	4*
<i>Ochropsora ariae</i> (FCKL.) SYD.	7	<i>Puccinia menthae</i> PERS.	4*
<i>Ochropsora kraunhiae</i> (DIET.) DIET.	7*	<i>Puccinia mitrata</i> SYD.	4*
<i>Olivea tectonae</i> THIRUM.	7	<i>Puccinia nigrescens</i> PECK	4*
<i>Olivea capituliformis</i> ARTH.	7	<i>Puccinia otopappicola</i> JØRST.	4*
<i>Peridermium ephedrae</i> CKE.	3*	<i>Puccinia ostryoderridis</i> JØRST.	7
<i>Phakopsora ampelopsidis</i> DIET. & SYD.	7*	<i>Puccinia proba</i> JACKS. & HOLW.	4*
<i>Phakopsora crotonis</i> (CKE.) ARTH.	7	<i>Puccinia phragmitis</i> (SCHUM.) KOERN.	4
<i>Phragmidiella africana</i> CUMM.	7	<i>Puccinia recondita</i> ROB. ex DESM.	4
<i>Phragmidium americanum</i> (PK.) DIET.	11	<i>Puccinia salviae-runcinatae</i> DOIDGE	4*
<i>Phragmidium barnardi</i> PLOWR. & WINT.	10	<i>Puccinia salviicola</i> DIET. & HOLW.	4*
<i>Phragmidium horkeliae</i> GARRETT	10	<i>Puccinia smilacis</i> SCHW.	4
<i>Phragmidium ivesiae</i> SYD.	11*	<i>Puccinia sonorae</i> PARMELEE	4*
<i>Phragmidium sanguisorbae</i> (DC.)		<i>Puccinia sparganii</i> CLINT. & PK.	4*
SCHROET.	10	<i>Puccinia sporoboli</i> ARTH.	4
<i>Phragmopyxis accuminata</i> (LONG) SYD.	7	<i>Puccinia vertisepta</i> TRACY & GALL.	4*
<i>Phragmopyxis deglubens</i> (BERK. & CURT.)		<i>Puccinia vertiseptoides</i> CUMM.	4*
DIET.	7*	<i>Pucciniastrum americanum</i> (FARL.) ARTH.	3*
<i>Phragmopyxis noelii</i> J.W. BAXTER	7*	<i>Pucciniastrum arcticum</i> TRANZ.	3*
<i>Physopeila hansfordii</i> (CUMM.) CUMM. &		<i>Pucciniastrum epilobii</i> OTH	3*
RAMACHAR	7	<i>Pucciniastrum goeppertianum</i> (KUEHN)	
<i>Pileolaria brevipes</i> BERK. & RAV.	7	KLEB.	3*
<i>Pileolaria effusa</i> PK.	7	<i>Pucciniastrum hydrangeae</i> (BERK. & CURT.)	
<i>Pileolaria inscrustans</i> (ARTH. & CUMM.)		ARTH.	3
THIRUM. & KERN	7	<i>Pucciniosira anthocleista</i> P. HENN.	4
<i>Polioma unilateralis</i> (ARTH.) J.W.		<i>Pucciniosira brickelliae</i> DIET. & HOLW.	4
BAXTER & CUMM.	4	<i>Pucciniostele clarkiana</i> (BARCL.) DIET.	7
<i>Polioma nivea</i> (HOLW.) ARTH.	4	<i>Pucciniostele mandshurica</i> DIET.	7*
<i>Puccinia balsamorhizae</i> PK.	4*	<i>Pucciniostele philippinensis</i> CUMM.	7*
<i>Puccinia batesiana</i> ARTH.	4*	<i>Ravenelia arizonica</i> ELL. & TRACY.	7
<i>Puccinia caborcensis</i> PARMELEE	4*	<i>Ravenelia brevispora</i> HIRAT. f. & HASH.	7
<i>Puccinia caricina</i> DC.	4*	<i>Ravenelia brongniartiae</i> DIET. & HOLW.	7
<i>Puccinia caulicola</i> TRACY & GALL	4*	<i>Ravenelia epiphylla</i> (SYD.) DIET.	5
<i>Puccinia codyi</i> SAVILE	4*	<i>Ravenelia fragrans</i> LONG	7
<i>Puccinia coronata</i> CDA.	4	<i>Ravenelia hieronymi</i> SPEG.	7
<i>Puccinia diutina</i> MAINS & HOLW.	4*	<i>Ravenelia lonchocarpi</i> LAGH. & DIET.	7
<i>Puccinia eatoniae</i> ARTH.	4	<i>Ravenelia mera</i> CUMM.	7

Table 1. *Continued*

<i>Ravenelia roemerianae</i> LONG	7	<i>Uromyces dolichosporus</i> DIET. & HOLW.	4
<i>Ravenelia similis</i> (LONG) ARTH.	7	<i>Uromyces euphorbiae</i> CKE. & PK.	4
<i>Ravenelia talpa</i> (LONG) ARTH.	5	<i>Uromyces fabae</i> (GREV.) DBY. ex CKE.	4
<i>Ravenelia thornberiana</i> LONG	7	<i>Uromyces hedysari-obscuri</i> DC.	4*
<i>Ravenelia versatilis</i> (PK.) DIET.	7	<i>Uromyces holwayi</i> LAGERH.	4*
<i>Scopella echinulata</i> (NIESSL) MAINS	7	<i>Uromyces iresines</i> LAGERH.	4
<i>Skierka cristata</i> (SPEG.) MAINS	5	<i>Uromyces lapponicus</i> LAGERH.	4*
<i>Skierka holwayi</i> ARTH.	5	<i>Uromyces phaseoli</i> (PERS.) WINT.	4*
<i>Sorataea amiciae</i> SYD.	7	<i>Uromyces striatus</i> SCHROET.	4*
<i>Sorataea baphiae</i> (VIEN.-BOURG.) SAVILE	7***	<i>Uromycladium fusisporum</i> (CKE. & MASS.)	
<i>Spumula heteromorpha</i> J.W. BAXTER	7*	SAVILE	5***
<i>Tegillum fimbriatum</i> MAINS	7	<i>Uromycladium simplex</i> MCALP.	5
<i>Teloconia kamtschatkiae</i> (ANDERS.)		<i>Uropyxis amorphae</i> (CURT.) SHROET.	7
HIRAT. f.	11**	<i>Uropyxis daleae</i> (DIET. & HOLW.) MAGN.	
<i>Tranzschelia pruni-spinosae</i> (PERS.) DIET.	7	var. <i>eysenhardtiae</i>	7*
<i>Triphragmium ulmariae</i> (HEDW. f.) LK.	11	<i>Uropyxis disphysae</i> (ARTH.) CUMM.	7*
<i>Uraecium holwayi</i> (ARTH.) ARTH.	3*	<i>Uropyxis farlowii</i> (ARTH.) J.W. BAXTER	7*
<i>Uredinopsis hashiokai</i> HIRAT. f.	1*	<i>Uropyxis nissoliae</i> (DIET. & HOLW.)	
<i>Uredinopsis longimucronata</i> FAULL	3*	MAGN.	7*
<i>Uredinopsis phegopteridis</i> ARTH.	3*	<i>Uropyxis petalostemonis</i> (FARL.) DET.	7*
<i>Uredinopsis osmundae</i> MAGN.	2	<i>Uropyxis roseana</i> ARTH.	7*
<i>Uredinopsis pteridis</i> DIET. & HOLW.	3	<i>Xenodochus carbonarius</i> SCHROET.	10
<i>Uredinopsis struthiopteridis</i> STOERM. ex		<i>Zaghouania phillyae</i> PAT.	4
DIET.	3*		

* Not listed in HIRATSUKA & CUMMINS (1963).

** Changed from HIRATSUKA & CUMMINS (1963).

*** Generic transfer since HIRATSUKA & CUMMINS (1963).

Type 10 The spermogonia are intraepidermal, indeterminate, and have fiat hymenia. They originate within the epidermal cells and establish the hymenium within the epidermal cells. Sometimes it is difficult to decide whether spermogonia belong to this type or to Type 11.

Type 11 The spermogonia are subcuticular, indeterminate, and have flat hymenia. They usually originate subepidermally, but the mycelium grows outward between the epidermal cells and establishes the hymenium under the cuticle. Often, hyphae split the epidermal cells apart, and the cells appear as isolated circles in the sections.

Type 12 A new type, which is designated "Type 12", has been recognized. It is characterized by deep-seated hymenia with indefinite growth and well-developed beaks. Detailed features of the type and examples of species having this type of spermogonia will be discussed later.

According to the definitions mentioned above, the types of spermogonia of 224 species belonging to 73 genera have been examined and listed in Table 1. The list includes 136 species described in HIRATSUKA & CUMMINS (1963), with few changes in assignment of types.

Among the morphological characteristics of spermogonia that are used to designate types, the position of the organ in the host tissue is least significant in indicating the relationship among rust fungi. On the other hand, such characteristics as presence or absence of

bounding structures or pattern of growth (definite or indefinite) seem to be important. Considering the above, we recognize six distinct groupings of types that seem to suggest natural subdivisions of the rust fungi (Fig. 1).

The six groups are as follows:

Group I: Types 1, 2, and 3

Group II: Type 9

Group III: Type 12

Group IV: Types 6, 8, 10, and 11

Group V: Type 4

Group VI: Types 5 and 7

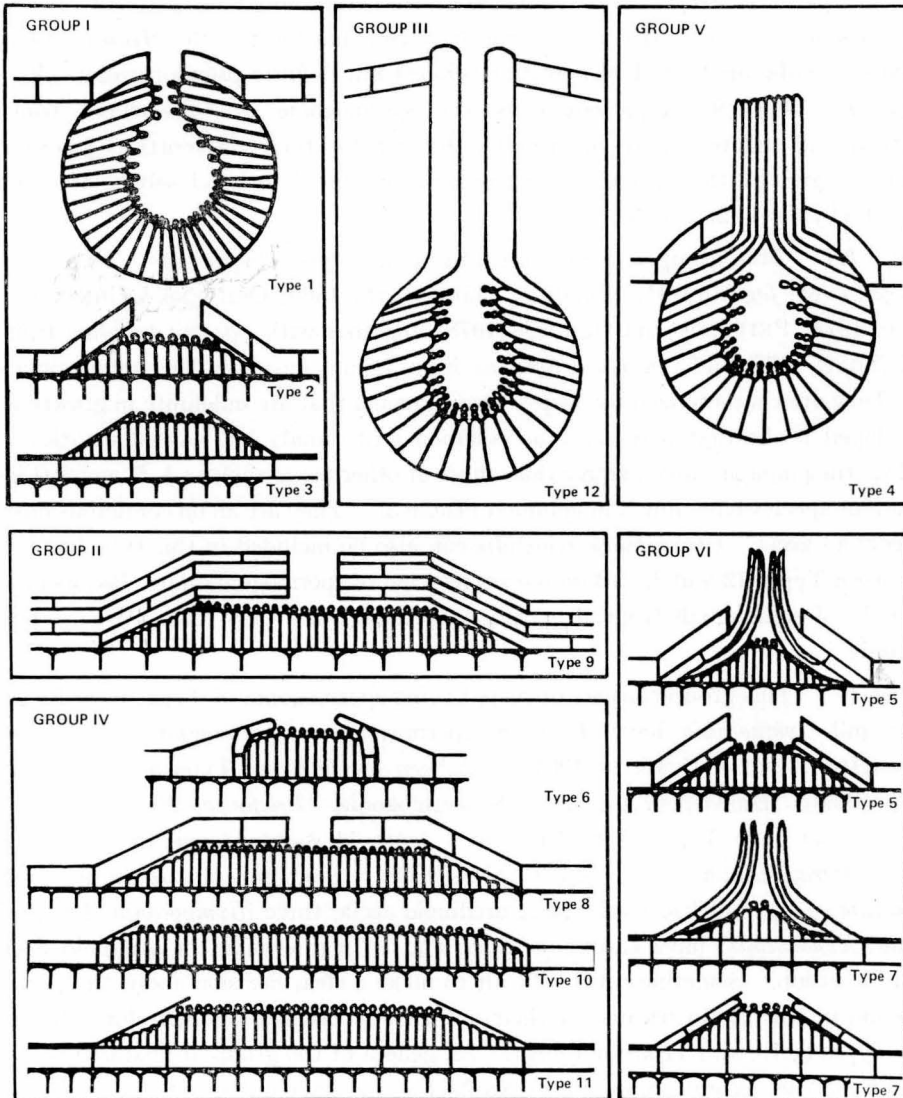


Fig. 1. Six groups of morphological types of spermogonia

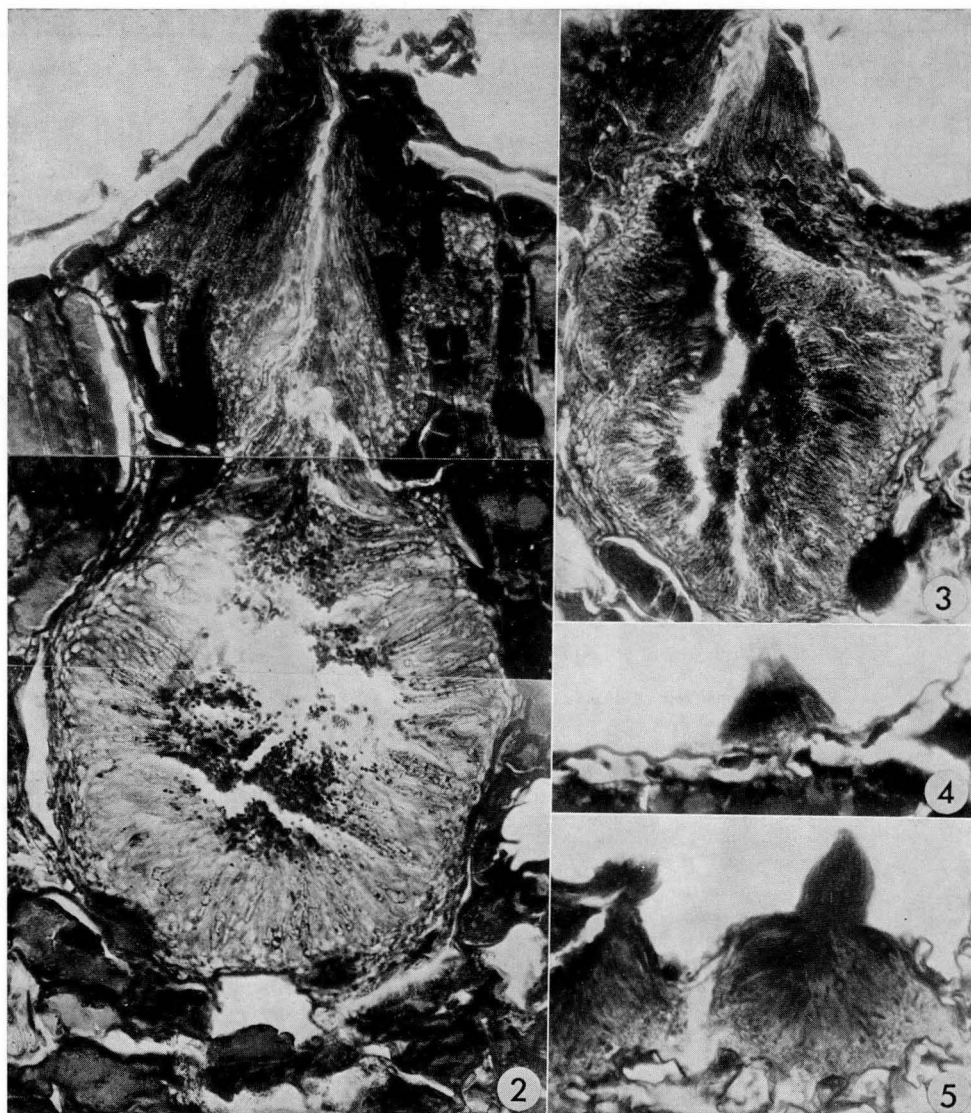
Group I: This group represents the simplest types of spermogonia without bounding structures such as peridia or periphyses. Type 1 is found only in the genus *Milesina*. Type 2 spermogonia are known in *Hyalopsora*, *Chrysomyxa*, *Melampsora* (p.p.), *Uredinopsis* (p.p.), and *Coleosporium*. Spermogonia of *Coleosporium* were considered to have indefinite growth and were assigned to Type 8 (HIRATSUKA & CUMMINS 1963), but we now consider them to have Type 2 spermogonia with definite growth. Type 3 spermogonia occur in *Melampsora* (p.p.), *Melampsoridium*, *Pucciniastrum*, and *Uredinopsis* (p.p.). Rusts belonging to this group are predominantly heteroecious, and gametophytic states occur on coniferous hosts, except parts of *Melampsora*. All genera have peridermioid aecia except *Melampsora*, which has caeomoid aecia. It is interesting, however, that most of the *Melampsora* species examined on coniferous hosts had poorly developed but definite pseudoperidial cells.

Group II: Type 9 is represented by the spermogonia of *Cronartium*, which are intercortical and indeterminate in growth. Except for their intercortical position and indeterminate growth, this type of spermogonia is considered to be closely related to those of Group I (Types 1, 2, and 3).

Group III: This group is represented by a new type, "Type 12". Two species of *Mikronegeria* (*M. fagi* and *M. alba*) from Chile (BUTIN 1969; OEHRENS & GONZÁLEZ 1977; PETERSON 1974; PETERSON and OEHRENS 1978), together with *Caeoma peltatum* from New Zealand (SHAW 1976) and *Caeoma deformans* from Japan, have similar spermogonia (Figs. 2 & 3). They are characterized by deep-seated hymenia that are indefinite in growth and by well-developed beaks that may serve as common exit canals for several cavities. Also, Type 12 spermogonia are much larger than those of other types such as 4, 5, and 7 (Figs. 1~5). The four species have much in common (Table 3). They are all on coniferous hosts and have caeomoid aecia. *Chrysopsora gynoxidis* can also be included in this type but is somewhat between Types 12 and 4. Close re-examination of spermogonia now classified as Type 4, especially of some small tropical genera, may show that they also possess Type 12 spermogonia.

Group IV: This group consists of rusts having spermogonia of Types 6, 8, 10, and 11. *Gerwasia* and *Gymnoconia* have Type 6 spermogonia. Spermogonia of *Gymnoconia peckiana* (HIRATSUKA & CUMMINS 1961) have been classified as Type 5 in HIRATSUKA & CUMMINS (1963). *Hamasporea* has Type 8 spermogonia. *Frommea*, *Phragmidium* (p.p.), and *Xenodochus* have Type 10 spermogonia. Type 11 spermogonia are represented in *Kuehneola*, *Phragmidium* (p.p.), and *Triphragmium*. Four genera [*Gerwasia*, *Frommea*, *Phragmidium* (p.p.), and *Kuehneola*] have uredinoid aecia, three [*Gymnoconia*, *Phragmidium* (p.p.), and *Xenodochus*] have caeomoid aecia, and no peridermioid or aecidioid aecia are found in the group. Sometimes it is difficult to make a clear decision about the position of spermogonia in this group because of their ontogenetic progression; therefore, distinctions between Types 8, 10, and 11 are not clear. All genera of the group are parasitic on plants of family Rosaceae, except few species of *Kuehneola*, and have autoecious life cycles.

Group V: Type 4 spermogonia are characterized by strong concave hymenia with well-developed periphyses at the mouth of the organ. At least 20 genera have Type 4



Figs. 2~5. Spermogonia of rust fungi all $\times 340$

Fig. 2. Type 12 spermogonia of *Caeoma peltatum* C.G. SHAW III & C.G. SHAW on *Phyllocladus trichomanoides* D. DON.

Fig. 3. Type 12 spermogonia of *Caeoma deformans* (BERK. & BR.) TUB. on *Thujopsis dolabrata* SIEB. & ZUCC.

Fig. 4. Type 7 spermogonia of *Phakopsora ampelopsidis* DIET. & SYD. on *Meliosma myriantha* SIEB. & ZUCC.

Fig. 5. Type 4 spermogonia of *Puccinia recondita* ROB. ex DESM. on *Thalictrum* sp.

spermogonia. Examples are *Puccinia*, *Uromyces*, *Gymnosporangium*, *Miyagia*, *Cumminsella*, *Baeodromus*, *Cionothrix*, *Chrysocelis*, *Chardoniella*, *Maravalia*, *Didymopora*, *Polioma*, *Zaghouania*, *Gambleola*, *Puccinosira*, and *Endophyllum*. Most of the genera have aecidioid

Table 2. Summary of six groups of spermogonia types

Group	Types of spermogonia	Representative genera	Type of aecia	Life cycle	Remarks
I	1, 2, 3	<i>Milesina</i> , <i>Uredinopsis</i> , <i>Hyalop-sora</i> , <i>Chrysomyxa</i> , <i>Melampsora</i> , <i>Coleosporium</i> , <i>Melampsoridium</i> , <i>Pucciniastrum</i> , <i>Melampsorella</i>	peridermioid (caeomoid)*	heteroecious (autoecious)	* <i>Melampsora</i> only O, I on conifers except <i>Melampsora</i> (p.p.)
II	9	<i>Cronartium</i>	peridermioid	heteroecious	O, I on <i>Pinus</i>
III	12	<i>Mikronegeria</i> , <i>Caeoma</i> (p.p.)	caeomoid	heteroecious	O, I on conifers
IV	6, 8, 10, 11	<i>Gerwasia</i> , <i>Gymnoconia</i> , <i>Hamaspora</i> , <i>Frommea</i> , <i>Phragmidium</i> , <i>Xenodochus</i> , <i>Kuehneola</i> , <i>Triphragmium</i> , <i>Kunkelia</i> , <i>Teloconia</i>	uredinoid caeomoid	autoecious	All on <i>Rosa-ceae</i> except few species of <i>Kuehneola</i>
V	4	<i>Puccinia</i> , <i>Uromyces</i> , <i>Gymnosporangium</i> , <i>Miyagia</i> , <i>Cumminsella</i> , <i>Baeodromus</i> , <i>Cionothrix</i> , <i>Chrysopsora</i> , <i>Chrysocelis</i> , <i>Chardoniella</i> , <i>Maravalia</i> , <i>Didymopsora</i> , <i>Polioma</i> , <i>Zaghouania</i> , <i>Gambleola</i> , <i>Puccinosira</i> , <i>Endophyllum</i>	aecidioid (uredinoid)	heteroecious autoecious	
VI	5, 7	<i>Achrotelium</i> , <i>Arthuria</i> , <i>Cerotelium</i> , <i>Chaconia</i> , <i>Crossopsora</i> , <i>Dasturella</i> , <i>Diabole</i> , <i>Dicheirinia</i> , <i>Diorchidium</i> , <i>Hapalophragmium</i> , <i>Lipocystis</i> , <i>Masseella</i> , <i>Ochropsora</i> , <i>Olivea</i> , <i>Phakopsora</i> , <i>Phragmidiella</i> , <i>Phragmopyxis</i> , <i>Physo-pella</i> , <i>Pileolaria</i> , <i>Pucciniostele</i> , <i>Ravenelia</i> , <i>Scopella</i> , <i>Sorataea</i> , <i>Spumula</i> , <i>Tegillum</i> , <i>Tranzschelia</i> , <i>Uropyxis</i> , <i>Cystomyces</i> , <i>Dasyspora</i> , <i>Didymosporella</i> , <i>Poliotelium</i> , <i>Skierka</i> , <i>Uromycladium</i>	uredinoid (caeomoid) (aecidioid)	autoecious (heteroecious)*	*Some species of <i>Cerotelium</i> , <i>Ochropsora</i> and <i>Tranzschelia</i> are heteroecious

Table 3. Species having Type 12 spermogonia

Rust species	O, I hosts	II, III hosts	Locati
<i>Mikronegeria fagi</i> DIET. & NEG.	<i>Araucaria araucana</i> (MOL.) K. KOCH (Araucariaceae)	<i>Nothofagus</i> spp. (Fagaceae)	Chile
<i>Mikronegeria alba</i> OEHRNS & PETERSON	<i>Austrocedrus chilensis</i> (D. DON) FLORIN & BOUTELGE (Cupressaceae)	<i>Nothofagus</i> spp. (Fagaceae)	Chile
<i>Caeoma deformans</i> (BERK. & BR.) TUB.	<i>Thujaopsis dolabrata</i> SIEB. & ZUCC. (Cupressaceae)	Not known	Japan
<i>Caeoma peltatum</i> C.G. SHAW III & C.G. SHAW	<i>Phyllocladus trichomanoides</i> D. DON. (Podocarpaceae)	Not known	New Zealand

aecia, and very few have uredinoid aecia. It is also noteworthy that many microcyclic genera such as *Gambleola*, *Puccinosira*, *Baeodromus*, and *Endophyllum* that have catenulate telia, which are considered to be derived from catenulate aecia, also have Type 4 spermogonia. Only two genera, *Polioma* and *Chrysocelis*, have caeomoid aecia in this group.

Group VI: Types 5 and 7 spermogonia are considered to be closely related, and the only difference is the position in the host tissue. Type 5 spermogonia are found in eight genera [*Cystomyces*, *Dasyscypha*, *Didymospora*, *Hapalophragmium* (p.p.), *Polioteliium*, *Ravenelia* (p.p.), *Skierka*, and *Uromycladium*]. Twenty-five genera are known to have Type 7 spermogonia. They are *Achroteliium*, *Arthuria*, *Ceroteliium*, *Chaconia*, *Crossopsora*, *Diabole*, *Dicheirinia*, *Diorchidium*, *Hapalophragmium*, *Lipocystis*, *Masseella*, *Ochropsora*, *Olivea*, *Phakopsora*, *Phragmidiella*, *Phragmopyxis*, *Physopella*, *Pileolaria*, *Pucciniostele*, *Ravenelia* (p.p.), *Sorataea*, *Spumula*, *Tegillum*, *Tranzschelia*, and *Uropyxis*. In both Types 5 and 7, 20 genera have uredinoid aecia, 6 genera have caeomoid aecia, and only 5 genera have aecidioid aecia. Most of the species in this group are autoecious, but a few species belonging to *Ceroteliium*, *Ochropsora*, and *Tranzschelia* are heteroecious.

Discussion and conclusions

Six well-defined groups are recognized within Uredinales based on the morphological types of spermogonia (Table 2). These groupings are closely parallel to several recent proposals for a supergeneric classification of rust fungi made by LEPPIK (1972), SAVILE (1976), and AZBUKINA (1974). No attempt is made to discuss and propose subdivisions of rust fungi in this presentation, but the authors would like to emphasize the importance of morphological types of spermogonia as dependable criteria for the taxonomy of this group of fungi.

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Rust ecology and phytocenology as aids in rust taxonomy

Zdeněk URBAN*

Ecology is usually understood to be the interrelationship between organisms and both abiotic and biotic life conditions. The ecology of rust fungi should thus be studied from this point of view. I mentioned some aspects of rust ecology in earlier papers (URBAN 1952, 1958, 1965). Recently, MÄKINEN (1966) discussed some definitions in ecology of parasitic fungi (rust fungi included). He defined microecology as the relationship of parasite to host when the latter represents the immediate environment for the parasite. The environment thus influences the parasite through the host only. The macroecology, on the other hand, is the study of the direct influence of the environment on the pathogen (rust fungus), without the interaction of the host. The main macroecological factor, according to MÄKINEN, is the climate; he only incidentally gives attention to the possibility of interaction with more external factors.

In my experience, ecology of many parasitic fungi (and rust fungi especially) includes the interrelation between the parasite and the vegetation type, which is always a natural or artificial plant community (phytocenosis). In nature various phytocenoses exist either side by side or they penetrate each other. The parasite (rust fungus) always exists in a definite phytocenosis. The parasite can occasionally be introduced into another plant community; there it finds either restricted possibilities for existence or, on the contrary, very good ones. In this last case the parasite seems to be indigenous (autochthonous). On the other hand, the natural vegetation spreads (and sometimes very recently) as definite phytocenoses. Similarly some artificial phytocenoses (agrophytocenoses) spread in the past as communities of definite plant species. Some parasites migrated together with plant communities; that is why the historic point of view, historic areography, and knowledge of evolution of phytocenoses should be introduced into the ecology of parasites (and also into the study of their taxonomic units).

Rust fungi, being obligately and specifically parasitic, are very closely connected with vascular plant ecology and history of their communities. The existence, history, and geographic distribution of plant communities sometimes limit the distribution of rusts. However, sometimes these restrictions are overcome by interaction of man (agrophytocenoses). Thus adaptation to new environmental conditions is required and this leads to the origin of new species or infraspecific units.

The species concept in rust fungi and the problem of specific diversity based on ecological characteristics, besides other criteria, was exemplified previously by *Puccinia*

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graminis. In my conclusions, I have considered results in stem rust race hybridization and compatibility from both Canada and the United States, from many records of French authors, from personal experiments carried out with Czech and Slovakian stem rust populations. Also ideas on stem rust genealogy presented by LEPPIK (1961) were taken into account.

Puccinia graminis s.l. in Eurasia originally spread from central Asia (together with plant communities containing *Berberis* and convenient grasses) to the East and West. The Near East and the Mediterranean are secondary evolutionary centers of *Berberis* (*B. cretica*, *B. hispanica*, etc.). The montane plains of central Asia are, however, also the primary evolutionary center of cereals (wheat, barley). In my opinion, the ancestral form of *P. graminis* parasitized various grass genera, *Triticum* included. Thus it also parasitized ancestors of our recent wheats: *T. boeoticum* ($2n=14$), *T. dicoccoides*, and *T. timopheevi* ($2n=28$). About 8000~9000 years ago Man took the genus *Triticum* into cultivation. Successively he developed the first cultivated wheats: *T. monococcum* ($2n=14$), *T. dicoccum* ($2n=28$), and *T. spelta* ($2n=42$). The ancestral form of the stem rust also parasitized these wheats and advanced together with them to the Near East and to the Mediterranean, i.e. to the secondary evolutionary centers of both *Berberis* and wheats. Gradually soft wheats were created. Simultaneously, the acreage of wheat monoculture became greater and greater. In this way, a suitable precondition was formed for long-distance spread of *P. graminis* on cultivated wheats by means of urediospores. Owing to this ecological change, the importance of *Berberis* as an alternate host diminished in many countries. Under the influence of Man, plant breeder, the secondary physiologic form of the stem rust evolved from the ancestral one. As it evolved further, it was influenced by microecological (cultivated wheat) and macroecological (loss of obligate heteroecism, current long-distance spread by urediospores) conditions into a new, morphologically distinct cerealicolous subspecies *graminis*. The wild central Asiatic *Triticum* species together with some cultivated ancestral wheats are immune or highly resistant to the new subspecies.

On the contrary, in the Mediterranean (the secondary evolutionary center of *Berberis* and wheats) we find physiological races parasitizing both cultivated wheats and some wild grasses growing in plant communities with *Berberis*: *Aegilops*, *Bromus*, *Haynaldia*, *Hordeum*, *Agropyrum*. Similarly, in the high mountains about Bakur'jansk of the Georgian SSR, *Triticum timopheevi* bears heavy infection of the stem rust.

More or less natural stands of *Berberis vulgaris* in Czechoslovakia (central and southern Bohemia, western Slovakia) house the graminicolous *Puccinia graminis* subsp. *graminicola* URBAN, which does not attack cereals. It persists in the locality owing to its obligate heteroecism and because it parasitizes grasses of the same phytocenosis: *Dactylis*, *Poa*, *Agrostis*, *Festuca*, *Calamagrostis*, *Arrhenatherum*, etc.

According to AZBUKINA (1974), *Puccinia graminis* in the Soviet Far East is a complex of cerealicolous subsp. *graminis* and graminicolous subsp. *graminicola*.

The use of ecological criteria in taxonomy has practical consequences: (1) it gives new points of view on eradication measures of *Berberis* in natural plant communities removed from cultures of cereals; (2) it recommends, in the search for stem rust resistance genes, the

use of urediospore inoculum originating from primary or secondary evolutionary centers.

Another example is the taxonomy of brown rusts of grasses, including leaf rust of wheat. In Europe this complex embraces obligately heteroecious rusts (in Ranunculaceae, Boraginaceae) together with other taxonomic units living without host alternation. It seems that in this complex there are both brachysporous (ratio of teliospore length to lower cell width=2:3) and dolichosporous forms (ratio 3:4 and more). It is probable that both characteristics mentioned are genetically fixed. This suggestion seems to be supported by the following facts. Just recently we have found in western and southern France, Spain, North Africa, and in other parts of Europe, brachysporous and dolichosporous rust fungi having both stages on the same host genera or species. I suppose that here we are meeting rusts in which brachyspory or dolichospory are not in strong correlation with specific or generic status of the monocaryophyte and dicaryophyte host. This may be exemplified on obligately heteroecious rusts on *Milium effusum*. *Puccinia milii-effusi* DUPIAS from southwestern Pyrenees (*Isopyrum thalictroides*-*Milium effusum*) was described as conspicuously dolichosporous. The characteristic mentioned distinguishes it from another, but brachysporous, rust fungus discovered recently in eastern Slovakia (MARKOVÁ 1976) which parasitizes the same host species and probably belongs to the complex of autochthonous brachysporous rusts on *Agropyrum caninum* and *Hordelymus europaeus* (O+I on *Actaea*, *Thalictrum*, *Cimicifuga*).

The study of Czechoslovak populations of brown rust is not yet finished. Nevertheless, it seems that there are at least *two* taxonomic units: the brachysporous *Puccinia persistens* PLOW. subsp. *persistens* and the dolichosporous subsp. *agropyrina* (ERIKS.) URBAN et MARKOVÁ. Both subspecies probably embrace additional lower taxonomic units, both heteroecious and autoecious. *Puccinia persistens* var. *persistens* on *Agropyrum repens* in Czechoslovakia lives without host alternation. On the contrary, *P. persistens* subsp. *agropyrina* on *A. intermedium* is obligately heteroecious (aecia on *Thalictrum* and *Lithospermum*). Some rye cultivars and some other grass genera are resistant to moderately susceptible to urediospores of both rusts. Cultivars of wheat species (*T. aestivum*, *T. dicoccum*, *T. durum*) are, on the contrary, immune to highly resistant.

I suppose that brown rusts came into central Europe as members of plant communities containing the optimal host combination of their monocaryophyte and dicaryophyte. According to FRENZEL (1964), in the last glacial epoch (Würm) there was a prevalence of herbaceous vegetation, which was tundra-like only at the beginning. From the east and southeast there was a migration of plant communities and plant species which gave rise to "a prairie covered with grasses" (*Hordeum*, *Bromus*, *Agropyrum*, *Secale*, *Triticum monococcum*); the occurrence of tundra plants was rather exceptional. According to FRENZEL, grasses were abundant in central Europe because they had already been very common in preceding glacial periods. Thus it is very probable that as members of their plant communities came into central Europe, some heteroecious rusts accompanied them and still persist. It seems that in the last glacial epoch there were in central Europe more frequent and widespread species of *Agropyrum* (*A. repens* included), *Secale*, and *Triticum*. Accord-

ing to TANFILJEV (1925), CAJANDER (1906), DOCHMAN (1954), STEPANOVA (1962), and MORAVEC (1965) *A. repens* seems to be very variable ecologically and probably splits into more infraspecific units. Especially in eastern Europe and the Soviet part of Asia, *Agropyrum repens* represents an important member of various plant communities that may be spread over hundreds of kilometers. It may be that the phytocenosis *Agropyrum-Alopecuretum pratensis*, which MORAVEC described from Bohemia, is related to early Quaternary vegetation with *Agropyrum repens*, which is supposed to have been present (at that time) in central Europe. I suppose that is why rusts on *Agropyrum repens* and *A. intermedium* developed independently, isolated from the evolution of the wheat leaf rust (having aecia also on *Thalictrum*). This suggestion is supported also by physiologic affinity of *Agropyrum* rusts for rye and not for cultivated wheat.

The ancestral form of the wheat leaf rust (*Puccinia persistens* var. *triticultura*) originated in evolutionary centers of hexaploid wheat (subregion Near East and the Mediterranean; see SINŠKAJA 1966, ŽUKOVSKIJ 1969). In these subregions the ancestral form parasitized species of the genus *Thalictrum* and wild *Triticum* and probably also *Secale*, *Aegilops*, and *Agropyrum*. This idea is supported by the fact that in Portugal (Mediterranean subregion) *Thalictrum speciosissimum* is commonly infected in winter, and aeciospores infect wheat. On the contrary, wheat leaf rust from Czechoslovakia does not infect *Th. speciosissimum* in experiments (personal communication of P. BARTOŠ). Further evolution of the wheat leaf rust reflects the same features as described previously in stem rust genealogy.

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Ecology, convergent evolution, and classification in Uredinales

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Abstract

If an important ecological problem has few possible methods of solution, very similar adaptive structures may evolve repeatedly. We must recognize the problems and understand the means by which they are solved in order to distinguish convergence from homology. In the rust fungi critical problems in nutrition, dispersal, and protection from desiccation and from mycophagous animals have induced abundant convergence. Deciduous teliospore pedicels, devices to protect the sori from insects, spores resistant to desiccation, internal basidia, short-cycling, instantly germinating teliospores, and external sori have all arisen repeatedly under appropriate conditions. Some of these topics are amplified. Based partly upon pycnium type, the rusts are disposed in five redefined families: Pucciniastraceae, Melampsoraceae, Phragmidiaceae, Raveneliaceae, and Pucciniaceae.

Introduction

The paper that I gave in the symposium, Taxonomy and Phylogeny of Uredinales at IMC-2 was written without thought of publication. It largely duplicated another symposium paper already in press (SAVILE 1978). I have accordingly changed my text considerably. Its theme is the same but the emphasis is different.

Homology or convergent similarity?

In morphologically simple organisms there can be only limited differences between two structures that evolve to perform similar functions. A classical example is the supposed homology of the ascus hook and the clamp connection. It is now clear not only that the two structures arose independently, as nuclear bypasses at conjugate division, but that the clamp connection has come and gone repeatedly. If we in mycology are to put our evolutionary schemes on as firm a footing as those who work with higher plants or vertebrates, we must make up for the limited number of morphological characters with the fullest possible understanding of the functions of these characters and their causative environmental stimuli. With macroscopic organisms the functions of conspicuous characters are often obvious. With microscopic organisms functions are harder to detect. We must form the habit of thinking in terms of the microecology of the organisms, doing as much as possible of our own field work, and taking notes on the total ecology of each specimen. With the rusts, hosts and host associations are part of that ecology. The total ecology is

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part of the description of each specimen; and that of all the specimens is part of the description of the species.

Some of these similar structures began to disturb me about 40 years ago; but their significance largely escaped me until after 1949, when I started on an extensive program of botanical field work that eventually involved all major climatic regimes of Canada. As I acquired clearer pictures of the ecological limits of many rusts, the functions of their morphological changes also became clearer. Repeatedly I had to qualify the taxonomic value of favored characters.

Examples of convergence in Uredinales

I have recently documented (SAVILE 1976) numerous examples of convergent evolution in the following: deciduous teliospore pedicels, devices to protect the sori from mycophagous animals, resistance to spore desiccation, internal basidia, short-cycling, instantly germinating teliospores, and superstomatal sori. Such devices evolve repeatedly in appropriate conditions. We shall examine a few examples in greater detail.

1. *Deciduous teliospore pedicels* The introduction of an additional diaspore into the life cycle of any non-motile organism must be strongly adaptive under almost all circumstances. In the three advanced rust families, with pedicellate teliospores, Phragmidiaceae, Pucciniaceae s. str., and Raveneliaceae, reliable pedicel breakage has been achieved at least 49 times in 15 genera by nine distinct methods. One method has evolved in all three families and four other methods in two families. These methods and their occurrence are illustrated and discussed in detail in SAVILE (1976, 1978). In summary, we find the following: forcible discharge by breakage at the middle lamella between spore and pedicel, through elongation of the thin apex of a septate pedicel (*Trachyspora*); breakage near the top of a very thin pedicel through upthrust by younger spores (in at least 20 *Puccinia*–*Uromyces* lineages, and in *Ravenelia*, *Prospodium*, *Triphragmium*, *Sphaerophragmium*, *Xenodochus*, *Cleptomyces*), which occurs frequently because any abrupt angle or change in thickness of a structure is a point of weakness where cracks easily start; breakage as in the last, but powered by swelling of gelatinous cells (*Ravenelia*, *Uromycladium*); separation at base of simple pedicel (three lineages of *Puccinia*, and in *Prospodium*, *Uropyxis*, *Phragmopyxis*, *Dipyxis*, *Cumminsella*, *Ravenelia*); separation by localized pedicel gelatinization (few *Puccinia*, *Uropyxis*, *Phragmopyxis*); separation at lysis-pitted fracture zone in pedicel (*Uropyxis*, *Ravenelia*, *Phragmidium*); jet propulsion by rupture at base of swollen pedicel (*Puccinia*); break at pedicel base through swelling of pedicel, causing lifting (*Puccinia*, *Phragmidium*). Finally, passive release through separation at the middle lamella in the spore hilum, the method universal in urediniospores, has been recorded, imperfectly developed, only in *Uromyces intricatus* var. *intricatus* and the related *U. bisbyi*, both on *Eriogonum* (SAVILE 1966). The meager development of this last method of teliospore release emphasizes the fact that the elaboration of pedicellate teliospores came very much later in the history of the rusts than did the evolution of urediniospores.

2. *Correlated changes in diasporic teliospores* Teliospores that germinate in the sorus generally have the wall thin at the sides but markedly thickened above, for maximum protection from desiccation and from mycophagous animals. The germ pore is typically apical, or near the septum in lower cells, providing the shortest route through the enveloping water film at germination (Fig. 1, left). The spore wall is smooth.

Once the teliospore is freely released it is subjected to new adaptive pressures. It now germinates lying free at an air-water interface (Fig. 1, right). With relaxation of ancestral selection pressures, wall thickening tends to become uniform, and the germ pores tend to drift from apical and septal positions. The spore wall often becomes verrucose or otherwise sculptured, which allows a thick boundary layer of air to be maintained, increasing the effective size of the spore and decreasing its rate of fall. There is also a common tendency for the spores to become wider than in the ancestral species, in which close packing of spores in the sorus encouraged both genetic and phenotypic narrowing. These changes are especially clear in various lineages of *Puccinia* and *Uromyces*, but the same trend is occasionally seen in Phragmidiaceae and Raveneliaceae.

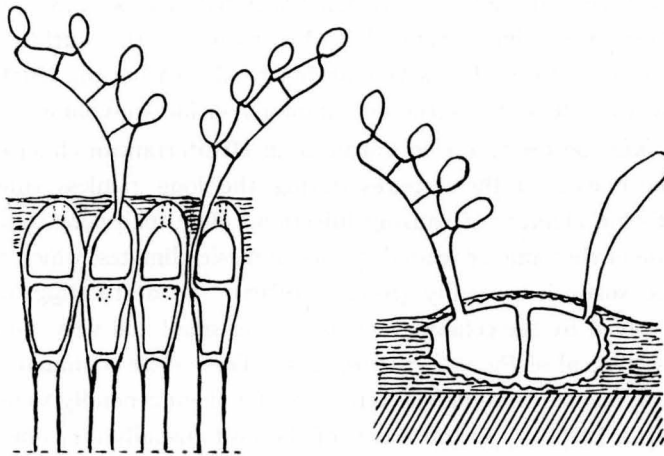


Fig. 1. Teliospore evolution in *Puccinia*. Left, teliospores of primitive species germinating in sorus. Right, spore of advanced species, germinating detached; correlated changes in wall thickness, wall surface, and pore positions follow initiation of function as diaspore.

These correlated changes all result from the initiation of dispersal, before which all would have been inadapative. Thus correlation does not indicate phylogenetic relationship in this instance, but merely the direction and extent of evolutionary advance. The action of ARTHUR (1934) in recognizing two subgenera of *Puccinia* based on these characters was completely unrealistic, for it often separated closely related species on, for example, Alliaceae, Polygonaceae, Saxifragaceae, Fabaceae, Onagraceae, and Heliantheae. Species with intermediate morphology were forced arbitrarily into either subgenus. Some species were completely misplaced; for example, *Uromyces hedydari-paniculati*, with fully diasporic verrucose teliospores, was placed in *Eupuccinia* because the pedicels break at the base and

remain on the spore. Such "long" pedicels were a character of *Eupuccinia*, whereas those in *Bulleromyces* were "short and fragile" (i.e. they break near the spore); but actually they are on average longer than those of the more primitive species, being often 60 to 110 μm long. Arthur's subdivisions are merely evolutionary *grades*, not phylogenetic clades.

3. *Adaptations against water loss* Water loss from exposure to dry air limits the scope of all terrestrial fungi. The mycelium of most rusts is protected by the host tissues, but the spores are seriously exposed to desiccation in dry weather. Rust spores undergo a series of correlated changes in Mediterranean and other seasonally arid climates. The most conspicuous changes are increased wall thickness, increased wall pigmentation, and increased spore size (SAVILE 1970a). It is often stated that wall pigment protects from ultraviolet radiation, and so it may; but its intensity correlates with aridity rather than radiation. In almost all temperate *Puccinia*, *Uromyces*, and *Phragmidium* species pigment is much more intense in over-wintering teliospores than in urediniospores, which are exposed to substantial ultraviolet radiation. About the darkest urediniospores known to me (as black as any teliospores) are those of *Puccinia poae-nemoralis* ssp. *hyparctica* (SAVILE & PARMELEE 1964), which occurs at 81°50'N, where ultraviolet intensity is negligible, but the spores must survive nearly a year in Hazen Valley with ca. 30 mm annual precipitation.

Increased spore size reduces water loss by reducing the surface-to-volume ratio. *Puccinia* teliospores tend to react to severe aridity by decreasing the length-to-width ratio; they thus approach a sphere, the form with minimal surface-to-volume ratio.

Several *Puccinia* species attacking Cardueae in Mediterranean climates have modifications to delay the release of their spores during the long rainless summer, when shed spores have negligible chances of causing infection. The teliospores have slightly firmer pedicels than those of the same or related species in mesic climates, which causes them to be released from the sorus less readily (SAVILE 1970a). In aestivating urediniospores the same problem is solved by the echinulations becoming small and very closely spaced, often approaching those typical of *Puccinia* aeciospores. These close echinulations must provide, as with aeciospores, enough friction between spores for them generally to be held indefinitely in the sorus (SAVILE 1970b). As the leaves of the hosts usually die completely during the summer, the mechanism for the ultimate release is not clear. Perhaps release by wind agitation is so gradual that many are not shed until after the renewal of growth in autumn.

Teliospores of aridity-adapted rusts often look extremely similar, although stable characters such as urediniospore germ pore patterns may show them to belong to quite distinct lineages.

4. *Adaptations to tropical rain forest* Comparative morphology of the rusts, strengthened by a growing understanding of patterns in flowering plant evolution (STEBBINS 1974), makes it clear that many rusts are secondarily adapted to tropical rain forest. In this regime the air is essentially saturated even in rainless weather, and teliospores can germinate throughout the year. Germination inhibitors, thick spore walls, and wall pigment all become superfluous and tend to be eliminated. Regardless of the appearance

of the ancestral teliospores, their rainforest descendants all tend to have pale, thin walls and to germinate instantly. Unless we have pycnia, distinctive paraphyses, or unusual urediniospores to guide us, we run a serious risk of putting together rusts that are quite unrelated.

Another reaction to the tropical rain forest is discussed in the next section.

5. *Superstomatal sori* It has occasionally been suggested that rusts with superstomatal sori are a natural group, and even that they are close to being "living ancestors" of the rusts. One or more spore states of the following genera are superstomatal, i.e. the spores and their supporting structures form outside the leaf on hyphae that emerge through nearly unaltered stomata: *Olivea*, *Hemileia*, *Gerwasia*, *Blastospora*, *Stomatisora*, *Cystopsora*, *Desmella*, *Edythea*, *Prospodium*, and *Dasyspora*.

Pycnia are known in five of these genera, and are of types 4, 5, 6, and 7 in the system of HIRATSUKA & CUMMINS (1963). Types 5 and 7 are closely related, but 4 and 6 are very different from them and from each other. The pycnium is a very stable organ, protected from the external environment by the host tissues and its nectar drop, and diverse types do not occur in closely related genera. The superstomatal genera are clearly polyphyletic, which is further emphasized by correlations between superstomatal and subepidermal genera in morphology and often in hosts.

Olivea (type 7) is plainly related to the erumpent *Sorataea* (7).

Cystopsora (4) is the superstomatal equivalent of *Zaghouania* and both are on Oleaceae.

Desmella, on ferns, evidently arose from the mainly temperate fern rust *Hyalopsora*, and an intermediate species is known.

Edythea, on *Berberis*, seems to derive from *Diorchidium* (7), with a species on *Berberis*, or from its immediate ancestor.

In *Prospodium* (7) the uredinia are, in different species, subepidermal or superstomatal.

Gerwasia (6) on *Rosa* and *Rubus*, has telia subepidermal, intraepidermal, or superstomatal.

Hemileia, with pycnia and aecia apparently lacking, has peculiar "hedgehog" urediniospores, reniform and half smooth as the name implies, which strongly resemble those of *Dipyxis* (7); but the teliospores, greatly modified for instant germination, are inevitably unlike those of *Dipyxis*.

No affinities are known for *Dasyspora* (5) or *Blastospora* and *Stomatisora* (pycnia unknown). However, pycnia or correlations with orthodox rusts show the superstomatal rusts to have sprung from Pucciniastraceae, Phragmidiaceae, Pucciniaceae, and especially Raveneliaceae, which is strongly represented in tropical rain forest. All except *Desmella* are on moderately advanced flowering plants, which further disqualified them as ancestral rusts.

Except for *Cystopsora*, which is manifestly a refugee from tropical rain forest and secondarily adapted to a monsoon climate by such drastic means as thick-walled basidia and basidiospores (SAVILLE 1976, pp. 178, 183), the superstomatal rusts are essentially

confined to tropical rain forest. The anomalous occurrence of *Hemileia vastatrix* on *Coffea arabica* is discussed in SAVILE (1978). In the rain forest the ambient air is always about as moist as the air within the leaf, and this is the one regime in which the exposure of so much fungal tissue to the air is readily tolerated. In fact, with perpetual high humidity the superstomatal habit, which damages less host tissue than orthodox erumpent sori, is probably adaptive, for the rusts can use only healthy cells for their nutrition.

The tropical rain forest is also the one climate in which heteroecism can never be significantly adaptive. If fresh foliage of the telial host is always available, host alternation, with its serious population drop (SAVILE 1976, p. 155), must be inadapative. If a telial host, entering the rain forest with its rust, loses association with the aecial host, autoecism or indefinite survival in the uredinial state are the only alternatives to extinction, and mutations favoring self-fertility and reinfection of the telial host by basidiospores will be selective. (Recombination can still occur by the exchange of nuclei between genetically dissimilar mycelia.) *Desmella* clearly arose by this means when *Hyalopsora* penetrated South America, where *Abies*, its aecial host, does not occur. Probably *Hemileia* originated similarly.

Evolution of *Ravenelia*

I have presented (SAVILE 1976, sect. 15) a preliminary explanation of the evolution of the complex teliospores of *Ravenelia* by mimicry of the increasingly compound pollen grains of *Acacia* and some other Mimosoideae. The developing picture of the co-evolution of the rusts, their hosts, and bees that both pollinate the hosts and effect long-range dispersal of the teliospores is one more example of the need to understand the total natural history of the host plants of our parasites. The inter-relationship is still poorly understood, but a few facts are emerging. First, at least two species of *Trigona*, the most widespread genus of the stingless bees (meliponine), are markedly modified for raking up shed pollen; but they have not yet been seen collecting mimosoid pollen. Second, I find that in arid savanna the deep-rooted acacias flower in the rainless season, when they have no competition for pollinators; and I suspect that *Ravenelia* teliospores (before flowering) and shed pollen (after flowering) may be important dry-season protein sources for what ever bees are concerned.

Conclusion

Disregarding the numerous convergent resemblances presented here and in SAVILE (1976), and relying considerably on pycnium type, I assign Uredinales to five families, circumscribed in SAVILE (1976, pp. 188~192): Pucciniastraceae, with pycnium types 1, 2, and 3; Melamosporaceae, with pycnium types 2, 3, 4, 5, 7, 8, 9, and the newly established 12 (HIRATSUKA & HIRATSUKA 1977); Pucciniaceae, with pycnium type 4; Phragmidiaceae, with pycnium types 6, 8, and especially 10 and 11; Raveneliaceae, with pycnium types 5 and 7.

Acknowledgement

I thank Dr. Bernard R. BAUM for pertinent information on growth patterns in Mediterranean plants.

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Phylogeny of Uredinales on Pinaceae

Guy DURRIEU*

Abstract

Comparison of host range of rusts on Pinaceae with the phylogeny of this tree family indicates possible relationships between the different rust genera. A phyletic system is proposed, based also on morphologic criteria. *Melampsora*, common to nearly all members of Pinaceae, is probably closely related to the ancestor of a rust group that includes *Pucciniastrum*, *Melampsorella*, *Hyalopsora*, *Uredinopsis*, and *Milesina*. *Coleosporium*, *Cronartium*, and *Chrysomyxa* seem to be separate from the former group.

Résumé

La répartition sur les Pinacées des Rouilles qui les parasitent examinée en comparaison avec la phylogénie de ces arbres donne des indications sur les relations possibles entre les divers genres d'Urédinales. Un tableau phylétique est proposé, qui tient compte aussi de caractères morphologiques. *Melampsora*, qui se trouve sur presque toutes les Pinacées, est certainement très voisin de l'ancêtre commun au groupe constitué des genres suivants: *Pucciniastrum*, *Melampsorella*, *Hyalopsora*, *Uredinopsis* et *Milesina*. *Coleosporium*, *Cronartium* et *Chrysomyxa* semblent se situer à part du groupe précédent.

Introduction

One of the basic phylogenetic studies of rusts is to look at the species parasitizing the most ancient of living plants *i.e.* ferns and gymnosperms. Several rust genera are hosted by Pinaceae (=Abietaceae), some of them using ferns as secondary hosts. Their study should provide valuable information about what could have been primitive Uredinales, since they probably are the most ancient living types.

For many authors the genera *Hyalopsora*, *Milesina*, and *Uredinopsis* are the most primitive of living Uredinales because they attack *Abies* (aecia) and ferns (uredia and telia). Some authors (KUPREVICH & TRANZSCHER 1957, LEPPIK 1967) also consider the lack of pigment in *Milesina* and *Uredinopsis* as an additional primitive character, but there are objections: FAULL (1938) and SAVILE (1976) pointed out that discoloration has happened several times during evolution of the rusts. Nevertheless, according to SAVILE (1976), *Uredinopsis* should be the most primitive of present genera. He describes a phylogeny in which the starting point is individual teliospores buried in the leaf tissues. LEPPIK (1973) tried to draw a parallel between the phylogeny of conifers and that of their rust parasites. But it seems that he misinterpreted the data of botanists, who generally consider that *Pinus* is the most primitive of living Pinaceae; LEPPIK puts it as the most advanced. Hence, it appeared to me that it was necessary to study again the question. However, I would like first to make some preliminary remarks.

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Phylogenetic studies of other plant groups have shown that the different organs do not always evolve at the same rate: why may we not think that the same has also happened for rusts? Then the evolutionary rank of a fungus cannot be settled at the sight of only one of its spore forms; it is not impossible to find, on the same species, primitive spermogonia and advanced telia.

We must also consider the phylogenic conclusions drawn from the presence of the same parasite on different hosts. If several plant species A, B, C... support the same parasite p (or closely related forms p, p', p'') it is highly probable that the parasitic combination Ap, Bp, Cp.... (or Ap, Bp', Cp''....) happened with a common host ancestor, and p is at least as old as this ancestor. But if among several related plants A, B, C...., only one is attacked by the parasite p, it can mean that p appeared only after the splitting of the different host species from a common ancestor.

These remarks should not be considered as absolute rules but only as indicative. Other phenomena such as migrations, loss of alternating host, or gene selection for resistance could also be involved.

Phylogeny of Pinaceae

What is known about phylogeny of Pinaceae? Figure 1 shows, as established by GAUSSEN (1970), relationships among different genera, based on morphology, anatomy, ontogeny, and palynology. *Pinus* is indubitably the oldest. Several genera probably derived from ancestors of living pines: *Cedrus* and *Abies*, *Larix* and *Pseudotsuga*, *Pityites*

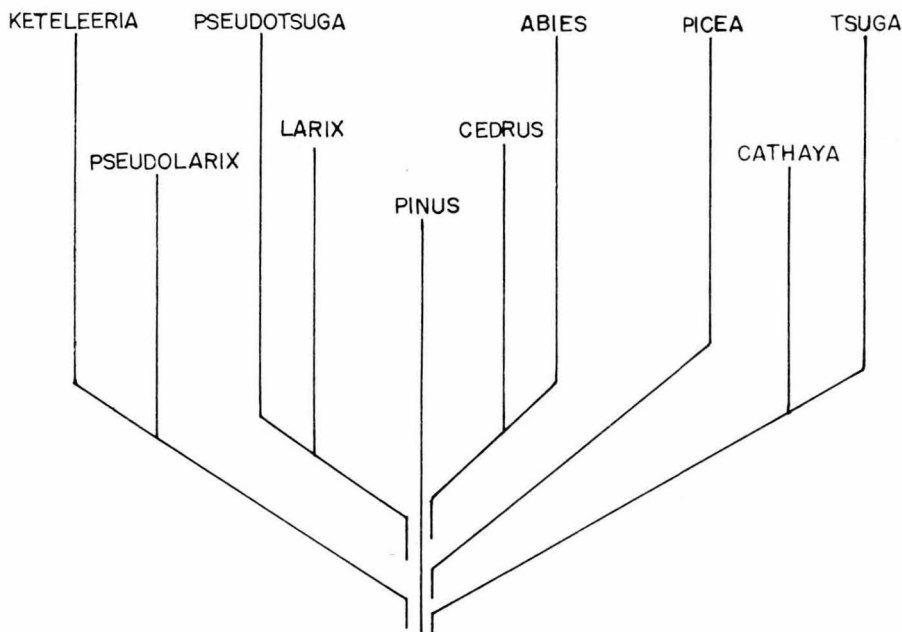


Fig. 1. Phylogeny of Pinaceae (after GAUSSEN 1970).

(only fossil) and *Picea*, *Pseudolarix* and *Keteleeria*, *Cathaya* and *Tsuga*. The splitting of these genera is probably anterior to Cretaceous. It is noteworthy that in a recent paper PRAGER *et al.* (1976) have, in a serological study, found very similar results; the difference is that *Tsuga* derived early from the genera *Cedrus-Abies*.

On the other hand, from paleontological data, *Pinus* known since late Jurassic (and perhaps since Lias) is unquestionably the oldest. For most of the other genera, oldest fossils are either Eocene (*Abies*, *Tsuga*) or Miocene (*Larix*, *Pseudotsuga*), with some late Cretaceous fossils doubtfully identified as *Picea* and *Cedrus*.

Range and origin of conifer rusts

From the range of Uredinales on Pinaceae (Fig. 2), it is obvious that each genus hosts a characteristic flora of parasites. I have withdrawn from this sketch *Cathaya*, *Pseudolarix*, and *Keteleeria*, which do not have known parasites. However, as these trees live in countries where mycological flora has not yet been studied in detail, it is possible that further discoveries may allow us to complete the diagram.

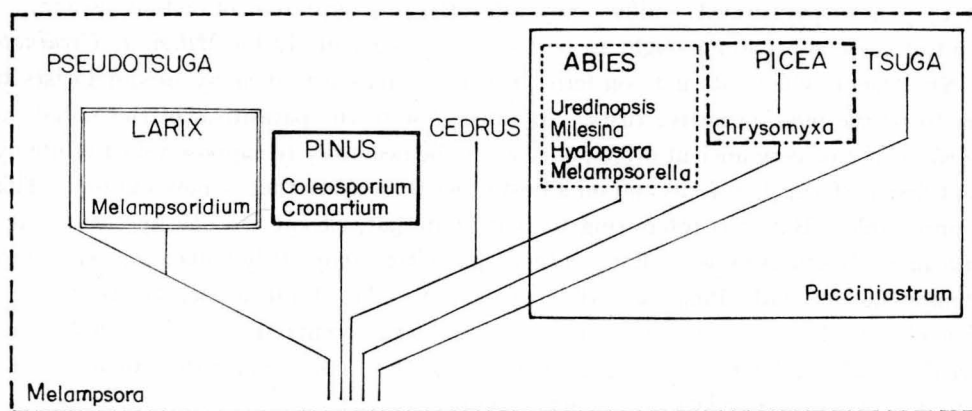


Fig. 2. Host range of rust genera on Pinaceae.

Every genus bears one or several species of *Melampsora*. Then it appears highly probable that this genus is the oldest which attacked the family. Its origin should be older than the differentiation of the different genera of Pinaceae. This assumption requires that the first *Melampsora* had alternating host plants that are today extinct (ferns or prephanerogamic groups of gymnosperms); indeed Pinaceae are only aecial hosts (but for a microcyclic species on *Pinus excelsa*, see BAGCHEE 1950). With the rise of angiosperms, the dicaryotic mycelium passed to Salicaceae, which in turn became aecial hosts and were used as source for infection of more advanced families: Liliaceae, Saxifragaceae etc. (LEPPIK 1953, 1967). It is interesting to note that botanists do not usually consider Salicaceae as one of the most primitive families. Nevertheless, there are known fossils for these trees dating from middle Cretaceous, when they probably were already abundant.

It can be supposed that *Melampsora* did not pass to the most primitive species of angiosperms, which perhaps have never formed crowded populations, but rather when some groups, expanding widely, gathered in large communities superseding the gymnosperms. So these populations offered to rust spores an adequate target to allow development of new strains. But it must be added that origin of the Pucciniaceae, the most widespread rusts on angiosperms, is not to be searched in this way.

The other rust genera have a more restricted range: *Pucciniastrum* (including *Thekopsora* and *Calyptospora*) lives on *Abies*, *Tsuga*, and *Picea*. This must be an ancient association, since, according to GAUSSEN, these trees are distributed among different genera that branched off before the Cretaceous. If today these fungi are widespread on several angiosperm families in their dicaryotic stage, it must be the result of their ability to persist without host alternation.

Each of the other genera are restricted to one host only: *Melampsoridium* on *Larix*; *Chrysomyxa* on *Picea*; *Cronartium* and *Coleosporium* on *Pinus*; *Milesina*, *Uredinopsis*, *Hyalopsora*, and *Melampsorella* on *Abies*.

It can be thought that most of these fungi appeared rather recently or, at least, that they have parasitized conifers only after the differentiation of actual genera. The second of these conceptions ought to be considered particularly for *Milesina*, *Uredinopsis*, and *Hyalopsora*, which alternate on ferns; this is the reason that many uredinologists take them to be the most primitive rusts. As already seen, the parasitism of the aecial stage on *Abies* is not of very ancient origin, or it would be necessary to suppose that the life cycle was at first performed on ferns and on a host other than *Abies* that is now extinct. This is not impossible. But it is interesting to point out that, except for one species living on *Osmunda* in North America, all the others parasitize only Polypodiaceae, ferns nearly contemporaneous with Pinaceae, while older ferns like Marattiaceae, Schizeaceae, and Gleicheniaceae do not host rusts. Moreover, fir – fern communities, which offer the most convenient habitat for these fungi, grow under mild to cold temperate climates and are certainly biocenoses of relatively modern origin.

One could expect to find some related fungi on *Cedrus*. We must consider that new discoveries are still possible, but, on the other hand, that the different species of *Cedrus* live under dry climates which are not very favourable to rusts, especially if alternating hosts should be ferns or Ericaceae. In the same manner, it may not be impossible that *Melampsoridium*, or something related, should be found on *Pseudotsuga*, but the Asiatic area of these trees is yet poorly known from a mycological point of view.

Pines bear two other genera in addition to *Melampsora*: *Coleosporium* and *Cronartium*. Their relationships to the other conifer rusts are not obvious, except perhaps with *Chrysomyxa* on *Picea*. This may be the mark of an early disjunction between *Pinus* (or *Protopinus*) and the genera leading to the other Pinaceae. Or, when this disjunction took place, the parasitic flora did not spread as a whole over the new taxa.

Phylogeny of rust spore forms

Now it seems necessary to see whether we can correlate these ideas with the lesson we can learn from rust morphology. I have tried to build up a phylogenic sketch (Fig. 3) starting from the remark that the most frequent sporulating method is obviously a catenulate feature. Then it is possible to suppose that most primitive Uredinales produced chains of spores (probably without intercalary cell), these spores being able to operate as vegetative conidia or as probasidia. Or perhaps these fungi produced basidia in chains, and a later transformation gave, on one hand, probasidia by an event similar to that in Auriculariales and, on the other hand, "conidia" by delay of nuclear fusion and increased duration of the vegetative state. An example which recalls this ancestral state is the case of *Caeoma espinosae*, which parasitizes a South American Cupressaceae: it is a form with catenulate spores devoid of intercalary cell and peridium (PETERSON 1974).

Differentiation of the intercalary cell between two spores in the chain gives us the typical structure of aecial spore columns. It can be thought that at the beginning the peridium was lacking (as it is in the "uredia" of *Coleosporium*). The peridium appears in *Melampsora* (*Caeoma* forms), where it remains rudimentary, while it reaches its full development in other genera (*Peridermium* and *Aecidium* forms). It is also necessary to point out the presence of peculiar protective tissues made of several layers of cells in two conifer rusts of the Southern Hemisphere: *Micronegeria fagi* on *Araucaria* (Peterson 1968) and *Caeoma peltatum* on *Agathis* (SHAW 1976).

Uredia seem to be the result of heteroecism, and it can be thought that no morphological differences marked immediately the differences in function of aecia and uredia. Catenulate uredia of *Coleosporium* and *Chrysomyxa* seem to be relicts of this stage.

It is also possible to consider typical uredia, with pedicellate spores, as derived from ancestral forms with catenulate spores like in *Chrysomyxa* or *Coleosporium* (Fig. 4). In fact, spore production processes are not basically different: pedicel or intercalary cell formation follows exactly the same way (Moss 1926, 1929) and in the case of *Cronartium* the intercalary cell elongates as a pedicel. To proceed from one to the other, the sporogenous cell has only to change its acrogenous and monopodial growth, giving "catenulate meristem arthrospores" (HUGHES 1970), into a pleurogenous sympodial growth, leading to "sympodioconidia" (HUGHES) or "spores fasciculées" (KUHNHOLTZ-LORDAT 1943). A peridium somewhat different from the aecial peridium has also developed.

As for sessile teliospores of *Melampsora* or *Melampsoridium*, it is possible to consider a lineage starting with teliospores in chains like those still existing in *Chrysomyxa* or *Cronartium* (catenulate basidia of *Coleosporium* may be a relict of an ancient type, mentioned earlier). These chains are able to shorten to only one spore: *Coleosporium* shows all stages between the many-layered and one-layered sorus (DURRIEU 1977). For SAVILE (1976) the scattered teliospores with unpigmented walls of *Uredinopsis*, *Milesina*, and *Hyalopsora* are the most primitive form, from which a first advance gives the pigmented-wall spores grouped in a tight palisade, as in *Melampsora* or *Melampsoridium*. We can

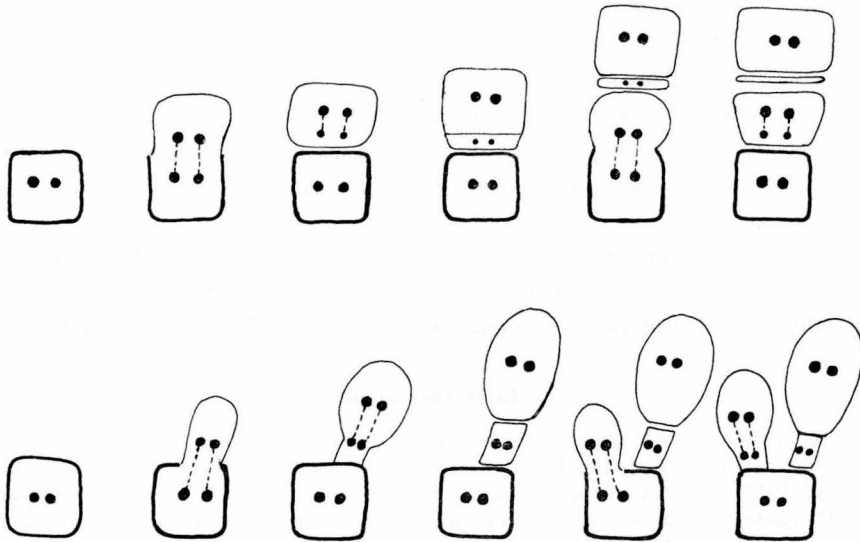


Fig. 4. Sporulation in rusts: above, catenulate sporulation; below, sympodial sporulation. The similarity between intercalary cell and pedicel is obvious.

also propose the reverse direction: the loss of wall pigment and the intracellular position could be considered as signs of a very close adaptation to parasitism and spore protection by host tissues. Then we should have the highly advanced forms which have gone into an evolutionary dead end. *Pucciniastrum* occupies an intermediate position in this way.

If the direction of evolution I propose is right, *Endocronartium* (*Peridermium* with spores looking exactly as aeciospores but giving basidia) is a striking example of what has been called "surévolution" or "pseudo-cyclic evolution" (GAUSSEN 1952). There is an appearance of a return towards an ancestral form with catenulate probasidia but with advanced aecia.

Pycnium structures have not been included in this sketch, but according to the study published by HIRATSUKA & CUMMINS (1963), their phylogenetic sequence is not incompatible with what I propose. I could just suggest, with SAVILE (1976), that type 1 (*Milesina*) is derived from type 2 (*Melampsora*, *Uredinopsis* etc.) by a sinking of hymenium in the host tissues.

A general look at the whole sketch shows that, as already pointed out, the different spore forms of the fungus may have reached different levels of evolution. For example, in *Melampsora*, uredia are more advanced than aecia, while in *Cronartium*, aecia are more advanced than telia.

Conclusion

In conclusion, it seems possible to propose a phylogenic system in which *Melampsora*

is accepted as rather primitive. It was from a closely related form that was derived an important generic complex involving *Pucciniastrum*, *Melampsorella*, *Hyalopsora*, *Milesina*, and *Uredinopsis* living on the most advanced Pinaceae. *Melampsoridium*, which looks somewhat intermediate, lives on *Larix*, an intermediate between *Pinus* and the most evolved conifers. *Chrysomyxa* can only be included with doubt in this lineage because of its primitive features of catenulate urediospores and teliospores. *Coleosporium* and *Cronartium* are obviously apart.

These conceptions represent only a tentative theory. I have tried to locate the phylogeny of parasites in parallel with host phylogeny, an idea that may be different from those generally argued, but not in disagreement with possible lines of evolution.

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The rusts on Rosaceae and their affinities

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The direct impetus for this communication was Dr. SAVILE's recent (1976) admirable article on the evolution of the rust fungi, which stimulates much thought and some contradiction. Among other things I was surprised by his taxonomic treatment of some genera inhabiting the Rosaceae. Table 1 gives a survey of the rosaceous rusts as classified by SAVILE. He recognizes five families, all of which have some members on Rosaceae.

In the Pucciniastraceae there are only a few species of *Pucciniastrum* which infect rosaceous plants, like *P. padi* on *Prunus*, and *P. arcticum* on *Rubus*. Quite obviously they have nothing to do with the other rosaceous rusts and they do not concern us here.

In the Pucciniaceae I will emphasize that the enormous genus *Puccinia* has remarkably few (if any ?) representatives on Rosaceae. I do not know those species, for example, *Puccinia waldsteiniae*, that are reported to occur on members of Rosaceae but with regard to them I will, *mutatis mutandis*, quote a statement by SAVILE, referring to the rusts on Leguminosae: "Any rusts on Fabaceae assigned to *Puccinia* demand scrutiny, for the family takes many species of several genera but few if any true *Puccinia*" (SAVILE 1971, p. 1090). The same holds true for the rusts on Rosaceae, and not only as relates to *Puccinia*, but to *Uromyces* as well.

I question SAVILE's assignment of *Ochropsora* to Melampsoraceae, and of *Tranzschelia* and *Gymnoconia* to Raveneliaceae. Speaking of *Ochropsora*, I confine myself to *O. ariae*; there are two further eastern asiatic species currently referred to *Ochropsora*, but they are incompletely known and of doubtful affinity. Placing *Ochropsora* in the Melampsoraceae is in agreement with an old tradition: the genus has been thought related to *Coleosporium* because of the internal basidia. However, DIETEL (1922, pp. 30~32) has already questioned this taxonomy; he pointed out the striking resemblances between *Ochropsora* and *Tranzschelia* in biology and to some degree also in morphology, and concluded that the two genera are indeed related. I think that the evidence is quite convincing. First, there is great agreement in host spectra (Table 2), which certainly is indicative of relationship; in addition there are morphological similarities. The monocaryotic mycelium is systemic in all three genera. The pycnia are of the same type in *Ochropsora* and *Tranzschelia*; their complete likeness was emphasized by LINDFORS (1924), who investigated their ontogeny and cytology. *Tranzschelia* also has periphysate pycnia, a detail omitted in the survey by Y. HIRATSUKA & CUMMINS (1963). It seems impossible to deny a close affinity between *Ochropsora* and *Tranzschelia*, and apparently *Leucotelium* is related, too. I have not studied the latter genus, but according to TRANZSCHEL (1935, p. 182) the pycnia and aecia

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closely match those of *Tranzschelia*. I think that these three genera can appropriately be grouped together in a tribe Tranzschelieae.

The above conclusion has an interesting corollary. The telia are dissimilar; among other differences the teliospores are sessile in *Ochropsora*, but pedicellate in *Tranzschelia*. Apparently this difference, which has been given much weight in rust taxonomy, is of little importance, at least sometimes.

An interesting problem is that of direction of this telial evolution. In my view, the pedicellate type is the primitive one in this case, because the *Ochropsora* telia are in some other respects quite obviously strongly advanced; for example, the teliospores germinate immediately, with internal basidia. Moreover, *Tranzschelia* also seems to be the less advanced genus with regard to the aecia: the aeciospores have a somewhat coloured, comparatively thick wall with distinct germ pores, whereas *Ochropsora* has quite hyaline, very thin-walled aeciospores with hardly discernible pores. In my opinion the latter type of aeciospores represent an advanced stage (cf. HOLM 1967).

Can anything be said about the origin of the Tranzschelieae? It is my firm belief that we should always consider the host plants. The host combination Ranunculaceae – Rosaceae is peculiar: it must have arisen by a jump of some ancestral rust with one or both generations on either Ranunculaceae or Rosaceae. No rusts are known to occur on Ranunculaceae, which ought to be considered. On the other hand, on Rosaceae we have the vast group of Phragmidieae, all autoecious. As SAVILE (1976) has emphasized, the present Phragmidieae are on the whole an advanced group; for example, the aecia are caeomoid or even replaced by primary uredo.

Table 1. Rusts on Rosaceae (according to SAVILE 1976)

Pucciniastraceae	<i>Pucciniastrum</i> spp. II+III
Melampsoraceae	<i>Ochropsora ariae</i> II+III
Pucciniaceae	<i>Gymnosporangium</i> O+I, <i>Coleopuccinia</i> , ? <i>Puccinia</i> , ? <i>Uromyces</i>
Phragmidieae	<i>Phragmidium</i> and allied genera (all autoecious)
Raveneliaceae	<i>Tranzschelia</i> II+III, <i>Gymnoconia</i> (autoecious)

We can reasonably assume, I think, that the recent Phragmidieae are the descendants of a proto-*Phragmidium* with peridiate aecia. The direct morphological evidence for kinship between Tranzschelieae and proto-*Phragmidium* is not particularly convincing; on the other hand, I can see nothing which makes such an assumption improbable. There are also similarities. The pycnia are subcuticular in the Tranzschelieae, as in most Phragmidieae; they are periphysate not only in the former but also in *Gymnoconia*, and a homologous counterpart may be the pycnial peridium of *Phragmidium*. The uredial paraphyses, which are so prominent in the Phragmidieae, also have a counterpart in *Tranzschelia*. Certainly phylogenetic speculations are particularly risky when relating to the rusts, because of they very widespread parallel evolution within this group; nevertheless, I think that the Tranzschelieae cannot be assigned a better place than in the vicinity of the Phragmidieae.

Accepting or not the hypotheses that the Tranzschelieae are the descendants of some

Table 2. Host spectra of the Tranzschelieae

	O+I	II+III
<i>Ochropsora ariae</i>	<i>Anemone</i>	<i>Sorbus</i>
<i>Tranzschelia</i>	<i>Anemone</i>	<i>Prunus</i>
<i>Leucotelium</i>	<i>Aquilegia</i>	<i>Prunus</i>
	<i>Eranthis</i>	

proto-*Phragmidium*, can we say something about the origin of the Phragmidieae? I think so, and it seems to me that *Gymnosporangium* is a very good candidate for discussion.

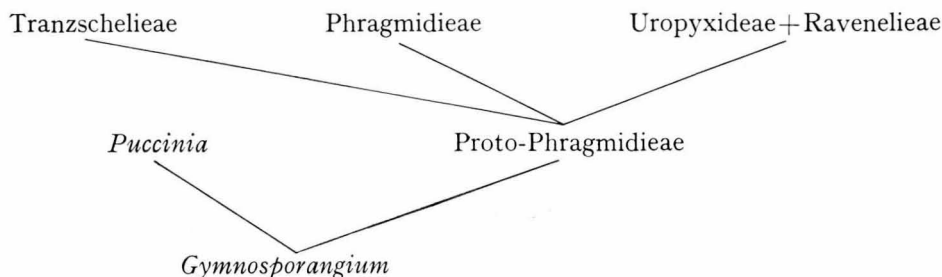
Gymnosporangium is indeed a remarkable genus. Though a comparatively small genus, it presents an unparalleled variation in aecial and telial characters. As Dr. CUMMINS (1959, p. 82) has stated, "the species possess such variable morphology as to make a generic definition almost impossible". As I have tried to demonstrate in my studies of the genus, several apparently primitive traits have survived in *Gymnosporangium* (HOLM 1971). From an evolutionary point of view this plastic group certainly merits attention. Generally admitted are the connections with *Puccinia*, and I will suggest an affinity also with the Phragmidieae, as was done already by DIETEL (1928, p. 73). Is there any positive evidence for such an assumption? Surely there is. First of all, of course, is the biological evidence, i.e. the predilection for the Rosaceae. In the Phragmidieae, the dicaryotic phase also has shifted over to the rosaceous host.

There are morphological similarities, too. The aeciospores of *Gymnosporangium* normally have a thick, dark yellow-brown wall, pierced by several conspicuous pores. Resemblances can be found in some species of *Phragmidium*, e.g. *P. violaceum*, which has aeciospores with a thick, yellowish-brown wall with conspicuous pores.

A characteristic trait of *Gymnosporangium* is the gelatinous teliospore pedicels. I find it significant that the capacity for gelatinization is widespread in the Phragmidieae. This was recognized by CUNNINGHAM (1931, p. 121), who particularly emphasized the resemblance in the telia of *Gymnosporangium* and *Hamaspora*.

The most significant differences between *Gymnosporangium* and the Phragmidieae can perhaps be found in the pycnia. They are flask-shaped and subepidermal in *Gymnosporangium*, but more or less flat and mostly subcuticular in the Phragmidieae. Subepidermal pycnia, however, characterize the genus *Hamaspora*. Moreover, the importance of the pycnial type should not be over-emphasized. I will recall the two, *inter se* closely allied genera *Milesia* and *Uredinopsis*, the former with globose, often subepidermal pycnia, the latter with flat, subcuticular ones.

These considerations are summarized in the following evolutionary scheme.



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Taxonomic significance of teliospore germination types in rust fungi

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Abstract

Teliospores germinate with or without a period of rest depending upon the species but in some genera they germinate intrasorum at maturity as a rule. The promycelium may emerge out through a germ pore or the spore apex may elongate and form the basidium. This has generic significance and genera such as, *Maravalia*, *Chaconia*, *Chrysocelis* and others are recognized by this character. The boundaries between the teliospore and the promycelium are distinct.

In two genera, *Blastospora* and *Acervulopsora*, the teliospores germinate by the prolongation of the spore apex, but the first wall cutting off the basidium from the teliospore is laid to include portion of the teliospore. Thus the basidium is semi-internal. This character is more pronounced in the genus *Zaghouania*, where the first wall is laid almost in the middle of the teliospore. This semi-internal basidium is of generic significance.

In contrast to the external basidium usually met with, several genera have internal basidium. The teliospores are usually thin walled and at maturity the fusion nucleus undergoes two successive divisions followed by septa formation and a four celled basidium is formed. From each cell of the basidium a sterigma is developed bearing a basidiospore. Numerous genera such as *Coleosporium*, *Goplana*, *Chrysospora*, *Ochropsora* and others have this character. Where the sorus is not erumpent, the sterigmata from the basidial cells penetrate through the host matrix developing the basidiospores above the host surface. The lowermost cell of the basidium has the longest sterigma. In *Acervulopsora* the cells of the septate basidium round off and form basidiospores themselves. In *Zaghouania* there are no sterigmata and the basidiospores are sessile.

Abnormal germination types which are characteristic of the species only are found in the telioid aeciospores of *Endophyllum*, *Monosporidium* and few other rust species. In *Scopella echinulata* one of the divisions in the basidium is vertical and the basidiospores are arranged as in a tetrahedron. In *Uromyces aloes* there are no basidiospores formed, and from each cell of the two celled basidium, an infection hypha is formed directly. In *Uromyces setariae-italicae*, the teliospore splits open at the apex from which a large vesicle protrudes out. The promycelium is formed as a branch of this vesicle on the side.

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Teliospore ontogeny as a criteria for rust phylogeny

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Abstract

Principles of rust fungi have been developed through some studies with temperate specimens. Tropical materials have been poorly collected and studied, and none of the theories developed provided a satisfactory explanation of the phenomena which involve tropical individuals. Patterns of life cycles, genera affinity and phylogeny are some of the points where tropical rust do not fit in the general scheme.

Through the studies with teliospore ontogeny it has been possible to determine that the process of basidium production is continuous in all genera and is only delayed by the cell wall desposition, which can be evident in the probasidium or in the metabasidium.

Specialization of the cells which are at the tip of the hypha has given origin to the different forms that are known today. Specialization has been in three ways: metabasidium, pedicel or cyst production.

In the meristematic zone (sporogenous basal cell) are evident all the phenomena involving metabasidium production and differentiation, but no definitive timing is present, because the metabasidium production is continuous.

When the meristematic zone has appeared, a pedicel may be produced rising this meristematic zone, and thus fixing the metabasidium number. All of these phenomena fit in a chain which is continuous, lending to a better understanding in genera relationship.

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