

Remarks on species concepts in European Florae of Rust Fungi

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Abstract: In the Florae of rust fungi of the 20th century, basic differences can be found with respect to definition and delimitation of species. Two diverging taxonomic concepts exist due to the use of different characters or the omission of factors, a “biological species concept” on the one hand and a “morphological species concept” on the other. Resulting differences in species delimitation and interpretation is shown for *Melampsora epitea*, *Puccinia dioicae*, *P. recondita*, *Coleosporium tussilaginis* and *P. pazschkei*. Knowledge of these and many other taxa of rust fungi is still fragmentary and the potential of morphological and experimental analyses is still not fully exploited. The overcoming of antithetic species concepts of rust fungi asks for even better knowledge of characters.

1. Introduction

As a list of species names of a delimited area, a Flora describes the plants of an area, either of a geographical region or a political entity. Usually, the species names are supplemented by a more or less detailed diagnosis of the taxa listed. For the term “Flora”, other descriptive names like “Checklist” or “Catalogus”, or others are used as well.

The term “Flora” is not restricted to flowering plants, but is applied to fungi or lichens as well, sometimes even for microorganisms of a specific occurrence as in “gut microflora”. Here, we will concentrate on the rust fungi.

A basic requirement of each Flora is an unquestionable discrimination of the species contained. In rust fungi, this often is exceptionally difficult. In particular, host range and an extensive synonymy due to different spore states cause major problems in species delineation.

As in many groups of organisms, molecular data have proven to eminently stimulate our knowledge of the phylogeny of rust fungi. However, while ample data are available already for the taxonomy of higher taxa, there mostly are still not sufficient molecular data to solve problems within species complexes as the ones addressed here. Together with classical data, molecular data, however, will definitely help to unveil the relationships of species complexes one day.

Some problems of species delimitation in rust fungi and the way in which various authors dealt with them will be addressed here. We comment on a subjective selection of major Florae of rust fungi in Europe, on their key aspects in species delimitation, and on the interdependence of various authors and their Florae.

2. Selected Florae of rust fungi of the 20th century

In 1959, Ernst GÄUMANN published “Die Rostpilze Mitteleuropas” (The Rust Fungi of Central Europe), a voluminous opus of about 1400 pages, more a monograph than a Flora of the rust fungi of Central Europe. Josef POELT (1985) characterized it as a monumental opus which will influence research on rust fungi in the middle of our continent for long. The impact of GÄUMANN’s book can also be seen from its influence on subsequent manuals, for example that of Wolfgang BRANDENBURGER (1985) or that of Friedemann KLENKE and Markus SCHOLLER (2015) both widely used to get the right names for parasitic fungi collected.

In order to understand GÄUMANN’s species concept, where the host specialization is more significant than usually applied morphological characters are, it is indispensable to first study his scientific roots.

IN 1904, Eduard FISCHER published his “Rostpilzflora der Schweiz” (Flora of rust fungi from Switzerland), a comprehensive opus focusing on the alpine area, influenced by the experimental methodology of his master Anton DE BARY. GÄUMANN, in turn, was a student of FISCHER. In his Flora, he followed FISCHER in many descriptions. He did highly valued experiments for defining and delimiting species of parasitic fungi. Another specific approach in FISCHER’s Flora is the linking of rust fungi to plant associations and the influence of the alpine sites to rust life cycles, an approach which later on has not really been carried forward by other authors.

Heinrich KLEBAHN released in 1914 “Die Rostpilzflora der Mark Brandenburg”. Despite covering a rather small area, this opus is comprehensive, and characterized by especially accurate and detailed morphological analyses and the effort to delimit difficult rust taxa by inoculation experiments. He has influenced GÄUMANN a lot, especially with his experimental approach.

An example for the exactness of KLEBAHN’s morphological analyses is the first record of dehiscent platelets of aeciospore walls, which afterwards have been overlooked for half a century until Lennart HOLM (1964, 1967) and especially Douglas B.O. SAVILE (1972, 1973a) reused them, but called them “granules” (HOLM) or “plugs” (SAVILE), respectively.

KLEBAHN (1914) demonstrated the regular occurrence of platelets in aeciospore walls of some species and their absence in others. He took already notes on size and arrangement of warts and platelets and denoted these structures in his drawings with “own observation”. For species of the *Puccinia dioicae* complex, HOLM (1966) showed that the diameters of platelets differ in size, 4.5 μm in *P. extensicola* var. *linosyridi-caricis*, 3 μm in *P. arenariicola* var. *caricis-montanae*, and 1.5 μm in *P. aecidii-leucanthemi*. SAVILE’s (1973a) comment on these structures will be discussed later on.

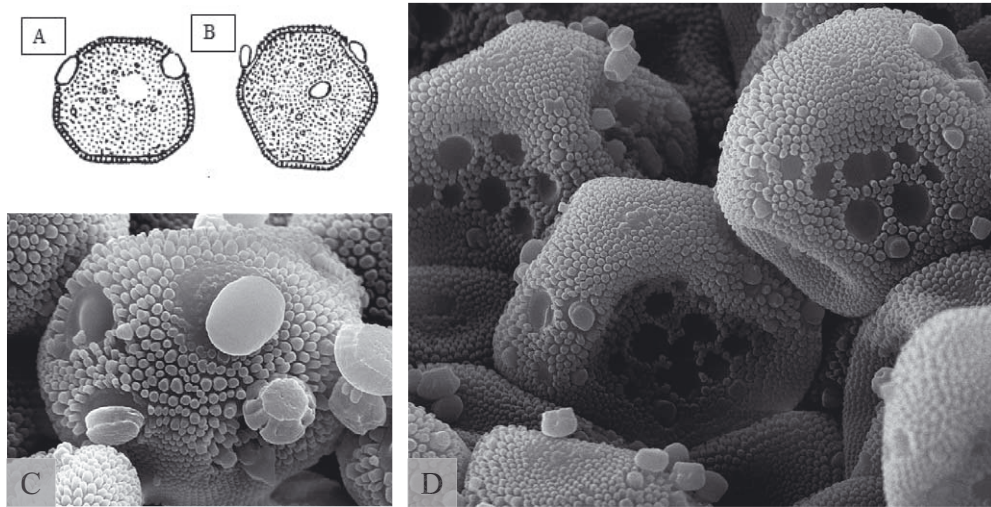


Fig. 1: A) and B) Drawings by KLEBAHN (1914): A) Aeciospore of *Aecidium centaureae* on *Centaurea stoebe* subsp. *maculosa* with verrucose wall ornamentation and with large dehiscant platelets; B) Verrucose ornamented cell wall of aeciospore of *Puccinia dioicae* on *Cirsium oleraceum* showing dehiscant platelets of smaller size than in Fig. 1A; C) Aeciospore of *Aecidium inulae-helenii* on *Inula helenium* with verrucose wall ornamentation and dehiscant platelets. Before dropping off, the platelets stick with their broad, pulvinate side to the spore wall; D) *Puccinia aecidii-leucanthemi* on *Leucanthemum vulgare*; verrucose wall ornamentation of aeciospores with platelets clearly smaller than in Fig. 1C and less distinctly divided in a pulvinate part and a cylindrical upper part; platelets more numerous and crowded compared to Fig. 1C.

Besides studying carefully morphological characters by light microscopy as shown above, KLEBAHN also implemented extensive infection experiments. This is another important aspect of his Flora aimed to species delimitation in especially difficult groups as rusts on *Carex* and on *Salix*. In these groups, KLEBAHN ended up with a separation into many species with a narrow host range in both aecial and telial states.

Paul and Hans SYDOW (1904: 651) commented in their world monograph of rust fungi (1904–1924) on KLEBAHN’s approach to species delimitation with a pointed remark:

P. & H. SYDOW's original quotation:

“In neuester Zeit sind nun namentlich von KLEBAHN von der *Pucc. caricis* noch weitere Formen ausgewiesen worden, deren Aecidien sich nur auf *Ribes*-Arten entwickeln. [.....] Wir ziehen es daher vor, um so mehr, da die von KLEBAHN angegebenen unterscheidenden Merkmale so minimaler Natur sind, hier vorläufig nur unter Anführung dieser Arten auf dieselben hinzuweisen. Ob es aber zweckmäßig ist, eine so weitgehende Teilung vorzunehmen, lassen wir hier unerörtert, doch wäre unseres Erachtens wohl nur eine einzige Art anzunehmen, deren Aecidien sich auf *Ribes* Arten entwickeln. Will man dann innerhalb dieser Art noch weitere biologische Formen unterscheiden, so möge man dies thun, ohne aber dieselben noch mit neuen Namen zu belegen.”

Translation of P. & H. SYDOW's quotation:

More recently, especially by KLEBAHN, further new species of *Puccinia caricis* have been installed, the aecia of which only grow on species of *Ribes*. [.....] Because the discriminating characters mentioned by KLEBAHN are of such inconspicuous nature, we therefore prefer to point out these species by only preliminarily quoting them. It will not be discussed here if it is appropriate to undertake such an extensive splitting. In our opinion, only one species should be accepted with aecia on species of *Ribes*. If one wants to separate more biological entities within this species, one may do so, but without applying new names for them.

The different approaches of how to define species, which had already become clear in the dispute of KLEBAHN and the SYDOWS, have further on developed into two diverse schools. GÄUMANN (1959), Alaine Lucien GUYOT (1938, 1951, 1957) as well as others followed a narrower “biological species concept” as KLEBAHN did, while Ivar JØRSTAD (1940), Nils HYLANDER, Ivar JØRSTAD and John Axel NANNFELDT (1953), Malcolm WILSON and Douglas Mackay HENDERSON (1966) and George Baker CUMMINS (1962, 1971) and others did not join in such a narrow species delimitation.

In order to describe species, GÄUMANN (1959) summarized in his Rust Flora of Central Europe all the available data of inoculation experiments carried out by himself or by others. GÄUMANN grouped closely related species according to their host specificity into “Formenkreise” within which he grouped narrowly defined species. He put special emphasis on statistical measurements of spore sizes in order to characterize biological species, but unlike KLEBAHN he has paid less attention to other morphological features.

POELT (1985: 11) decided to follow generally GÄUMANN's concept of species delimitation – in spite of some given modern tendencies. (“*Der Verfasser [POELT] hat sich in wesentlichen Zügen, gewissen modernen Tendenzen zum*

Trotz, an Ernst Gäumann ... gehalten”). Being aware of the fact that many species complexes cannot be differentiated on the basis of their morphology, he explained the usefulness of the “biological species concept” in the following way:

POELT's original quotation (1985: 15): *Translation of POELT's quotation:*

“Der Versuch, die Art rein morphologisch zu definieren, mußte allerdings in der Konsequenz einen Artbegriff ergeben, der sich selber ad absurdum führt: Die Art wird zur Schublade für biologisch oft sehr heterogene Anhäufungen von Sippen, die z.B. in der Struktur von Teleutosporen und Uredosporen ± übereinstimmen; irgendein spezieller Informationswert biologischer Richtung haftet solchen “species” kaum an. Man vergleiche etwa *Puccinia recondita* im Sinne von CUMMINS (1971: 320), die Rostsippen umfaßt, die von Balsaminaceen, Boraginaceen (und Hydrophyllaceen), Ranunculaceen auf zahlreiche Gräser überwechselt und bei GÄUMANN (1959) auf zahlreiche Formenkreise verteilt werden. In der Natur sind sie auf ganz verschiedene Vegetationsformationen, Höhenstufen, geographische Bereiche verteilt. Dies mag für eine erste vergleichende Übersicht über die Grasrostpilze der ganzen Welt vertretbar sein [gemeint ist CUMMINS Weltmonographie]. Für eine geographisch begrenzte Bearbeitung ist solch ein Artbegriff zweifellos nicht brauchbar”.

The attempt to describe a species exclusively on the basis of morphology, had consequently to end up in a species concept which made itself useless: The species becomes a drawer for a biologically often quite heterogeneous accumulation of taxa, which more or less coincide for example, in the structure of teliospores and urediniospores; there is hardly any special biological information linked to such “species”. Comparing, for example, *Puccinia recondita* sensu CUMMINS (1971: 320) with rust fungi alternating between Poaceae and Balsaminaceae or Boraginaceae or Ranunculaceae, GÄUMANN (1959) splits them up into many Formenkreise. In nature, they are allotted to completely different formations of vegetation, altitude, and geographical area. While this may be acceptable for a preliminary study of grass rust fungi worldwide [refers to CUMMINS' world monography], such a species concept can definitely not be applied to a study which is geographically narrowed down.”

Thus, some authors used ordinary binomial species names for taxa, which other authors regarded either as species sensu lato or sensu stricto, or “Formenkreis”, variatio, “formae speciales”, or other sub-divisions to delineate taxa of rust fungi. This does not only complicate the comparison of species lists in different Florae, but, beyond that, may even reflect a dissimilar understanding of the evolution of particular rust taxa.

The diverse species concepts, which by some authors are mixed due to different markers and discerning interpretation, will be outlined in the species complexes *Melampsora epitea* s.l., *Puccinia dioicae* s.l., *Puccinia recondita* s.l., *Coleosporium tussilaginis* s.l. and *Puccinia pazschkei* s.l.

The *Melampsora epitea* complex

In their Florae, the Scandinavian and British authors JØRSTAD (1940), HYLANDER et al. (1953), WILSON and HENDERSON (1966), Halvor B. GJÆRUM (1974) and HENDERSON (2000, 2004) defined collective species like *Melampsora epitea* and *M. populnea* on the basis of urediniospore and teliospore morphology while still having in mind narrower “biological” taxa.

WILSON and HENDERSON (1966) segregated most British rust fungi on willows according to their aecial hosts without formally naming narrow species. Within *Melampsora epitea* sensu lato, they accepted a number of races or specialized forms, in part with a special host alternation, in part without such one. They reported only seven species of *Melampsora* on *Salix* from Great Britain. In contrast, 17 species have been recorded by GÄUMANN (1959) in Central Europe. KLEBAHN (1914) and GÄUMANN (1959) have demonstrated that “cryptic species” within the *Melampsora epitea* complex are separable. Based on inoculations of aecial hosts and urediniospore morphology, GÄUMANN identified at least eight species within this complex, but not all species examined differ in urediniospore morphology. Due to their difficult identification and often overlapping *Salix* host ranges, most of the species cannot be defined purely from their occurrence on a particular *Salix* host, but each has a distinctive host specialisation pattern in both aecial and telial stage.

One can hardly imagine that a species or a group of closely related species has such a wide aecial host range as *M. epitea* s.l. Its range includes conifers (*Abies*, *Larix*), and monocotyledonous genera (*Dactylorhiza*, *Gymnadenia*, *Listera*, *Ophrys*, *Orchis*, *Platanthera*, *Pseudorchis*), and dicotyledonous genera (*Euonymus*, *Ribes*, *Saxifraga*, *Viola* and others). Using molecular data Nicolas FEAU et al. (2009) showed that within the comparable *M. populnea* species complex, taxa with aecia on conifers are clearly distinct from taxa with aecia on dicotyledonous hosts. However, JØRSTAD (1940) and HENDERSON (1957) have emphasized that classification should be based on morphological characters as far as possible. But they have found only few characters for segregating taxa within the *M. epitea* group. The only morphological character that has been extensively used by JØRSTAD (1940, 1953) and HENDERSON (1957) is the comparison of dimensions of the more or less capitate uredinial paraphyses. John A. PARMELEE (1989) has emphasized that *M. epitea*, as treated in his paper, certainly contains more than one species, but until abundant cross-inoculations will be made and combined with detailed measurements, realistic treatment of American collections is impossible.

The *Puccinia dioicae* complex

This cosmopolitan species complex occurs in the uredinial and telial states on *Carex* species. It is mainly characterized by laterally flattened urediniospores with two supra-equatorial germ pores, one on each flattened face, and a tonsure devoid of spines below or around each pore as can be seen in KLEBAHN'S (1914) drawings of e.g. *Puccinia silvatica*, *P. extensicola* s.str. and *P. schoeleriana* (Fig. 2A–C). In his key to *Carex* rusts, he placed species with this combination of characters to the species group which he named “Artengruppe *P. silvatica*”.

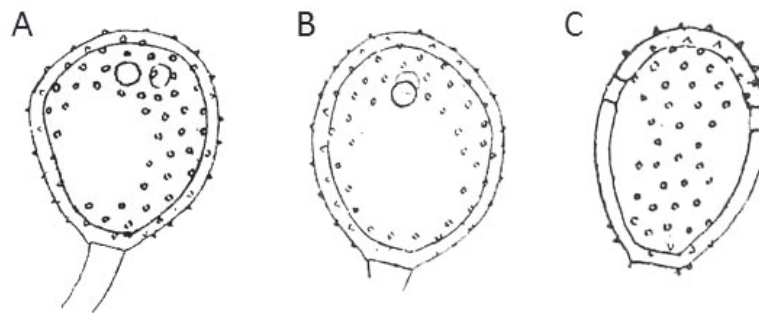


Fig. 2: Drawings by KLEBAHN (1914) of laterally flattened urediniospores in the *P. dioicae* species complex: A) *Puccinia silvatica*, and B) *P. schoeleriana* in face view; C) *P. extensicola* in lateral view. The position of the germ pores and an area devoid of spines below or around each pore characterizes this species complex.

Infection experiments have shown that, in their uredinial and telial stage, most of the rust fungi studied are specialized to one species of *Carex* or to a group of closely related Carices as host species. GÄUMANN (1959) usually treated these as species grouped into “Formenkreise”. These Formenkreise are defined by the aecial host which mostly refers to a genus of Asteraceae.

Because of the peculiarity of its urediniospore morphology (see above) and its aecial host range (mainly Asteraceae), the species complex shows up as a natural group. Corresponding to the evolution of genera and tribus in the Asteraceae, the host ranges of the European taxa of the *P. dioicae* complex conspicuously differ from those of the North American and East Asian taxa. These differences reflect evolutionary splitting of rust taxa within the species complex. In Europe, members of the Cardueae are the most important hosts, while in North America these are members of the Astereae.

The attempt to subdivide the *P. dioicae* species complex by only morphological characters has still not succeeded, but not all options of morphological analyses have been applied so far. As additional character, HOLM (1966) pointed out different sizes of “granulae” in the aeciospore walls, as mentioned before. Comparative studies on aecial wall ornamentation by scanning electron microscopy are available for only few taxa of this complex until now.

SAVILE (1973a) had found that five different patterns (“types”) of size, shape and arrangement of aeciospore ornamentation can be differentiated and are species-specific. He pointed out that “*P. dioicae* with type 5 aeciospores [with large dehiscent platelets, 3 µm diam. and more], occurs on various genera of Asteraceae, but apparently never on *Artemisia* or other Anthemideae.” Therefore, based on type 3 aeciospores (with small dehiscent platelets about 1.5 µm diam.) and the aecial host *Leucanthemum*, SAVILE separated *P. aecidii-leucanthemi* as a species distinct from *P. dioicae*.

JØRSTAD (1964a, 1964b) treated various collections of the *Puccinia dioicae* complex on *Carex* species on the basis of life cycle and host specificity data. His lists sum up data of field observations of more than forty years in Norway. Besides many other results, he found that a race of *Puccinia dioicae* s.l. is obligatorily alternating between *Carex disticha* and *Achillea ptarmica*. Despite many efforts, this author stated that he could still not gather enough data with markers established until then for separating *Puccinia dioicae* into narrow species.

However, Peter ZWETKO † (1993) described *P. ptarmicae-caricis*, which is obligately alternating between *Achillea ptarmica* and *Carex disticha*, as distinct species within the *P. dioicae* complex. He found that this new species has type 3 aeciospores which are different from those typical for *P. dioicae* as SAVILE (l.c.) had shown before. This separation of *P. ptarmicae-caricis* and *P. aecidii-leucanthemi* is also reflected by the position of the germ pores in the upper cells of teliospores, which differ in this respect from typical *P. dioicae* (ZWETKO l.c.).

Puccinia atrofusca is another rust species with Anthemideae as aecial hosts and *Carex* species as telial hosts. It also has type 3 aeciospores (SAVILE 1973a). Its urediniospores are laterally flattened with two equatorial pores, one on each flattened face and a tonsure devoid of spines below or round each pore. They differ only in the position of the pore from urediniospores of the *P. dioicae* complex (Fig. 3).

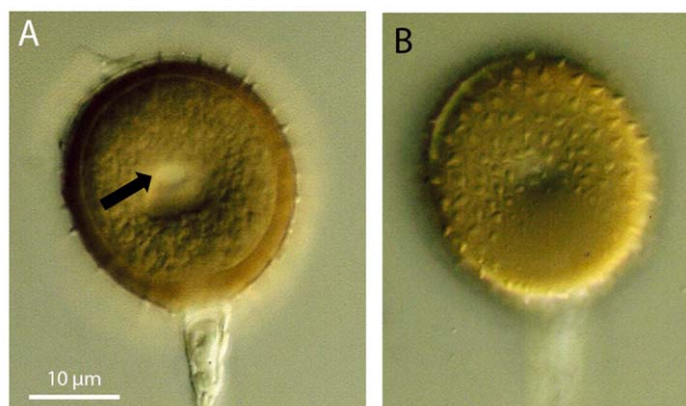


Fig. 3: Flattened face of urediniospores of *Puccinia* aff. *atrofusca* on *Carex curvula* with an equatorial germ pore (arrow) and a tonsure: A) optical section; B) surface view with the tonsure below the germ pore.

Puccinia atrofusca is not known from Europe, but a rust on *Carex curvula* has urediniospores with the same combination of characters as *P. atrofusca*. This rust has been reported by ZWETKO (2000) and ZWETKO et al. (2004). The distribution of *C. curvula* is restricted to the mountains of Europe. Although the sedge is not rare in the Alps, only few collections of its rust are known from Switzerland and Austria. The affinity of the rust on *C. curvula* to *P. atrofusca*, which has similar urediniospores, remains unclear. But its urediniospore morphology might point to its potential aecial host range in the Anthemideae.

The three rusts with aecia on members of the tribus Anthemideae have so far been assigned to different species complexes by various authors. However, these rusts and the still unnamed rust on *Carex curvula* show conformity within several morphological characters of aecio-, uredinio- and teliospores and within the aecial host range, and are therefore probably closely related. Until now, there are not sufficient molecular data available to confirm this.

It is a paradox that morphologically defined species complexes are often based on incomplete morphological analyses. This becomes apparent when using aecia as an example. SAVILE (1973a) already criticized that “for most species the usual description of aeciospores is a statement of dimensions and wall thickness, with some such indefinite phrase as ‘finely verrucose’”. SAVILE’s criticism fits many comprehensive European rust floras still used today, e.g. GÄUMANN (1959), WILSON and HENDERSON (1966), GJÆRUM (1974), TOMASZ MAJEWSKI (1977, 1979). This applies also to GUYOT’s monographs (1938, 1951, 1957) on *Uromyces*, and to the monograph on “Rust Fungi of Cereals, Grasses and Bamboos” of CUMMINS (1971). The latter noted that in his monograph “most descriptions of aecial stages are adopted from other sources. Only minimal original study was devoted to the aecia, and their hosts are indexed only by genera and families”.

SAVILE (1970, 1972, 1973a, 1973b) demonstrated that critical use of morphological data and more detailed morphological analyses help to overcome the antagonism between morphological and biological species concepts. He showed that morphology alone is a bad guide to delimitate rust taxa: “In the heteroecious *Carex*, rusts evolutionary splitting has been done partly according to host relationship and partly to host habitat. The latter is an inevitable phenomenon, but it tends to be overlooked. When, however, the morphological entity embraces hosts of widely different habitats as well as different sections of *Carex* we must suspect that the taxonomy is inadequate” (SAVILE 1965). His papers strongly influenced ZWETKO’s (1993) studies on *Carex* rusts in the Alps which was not only adopted by his master POELT in the second edition of the Catalogus of the Austrian Rust Fungi (POELT & ZWETKO 1997) but also by HENDERSON (2004) in his guide to identify the rust fungi of the British Isles by their host plants. The latter author is a well-respected representative of a morphological species concept.

The *Puccinia recondita* complex

The *P. recondita* complex is characterized by urediniospores with several scattered germ pores, and by telia often with fused brown paraphyses, and teliospores with very short pedicels on various Poaceae.

CUMMINS (1971) defined *P. recondita* as species complex with an explicit statement: “This is not unique nor is it particularly satisfactory, but on a world basis, the variability in morphological features is continuous from extreme to extreme. Distinctive segments of the population may exist regionally and will, undoubtedly, receive separate names. Fifty-one such names are listed above as synonyms; there can hardly be need for more.”

For the *P. recondita* complex, SAVILE (1973a) found three morphologically different types of aeciospore surface ornamentation which he did assign to three groups parasitizing on different aecial host families. The first type characterizes *P. triticina* and related taxa with aecia on various genera of Ranunculaceae, among them *Aquilegia*, *Clematis*, *Ranuncunculus* and *Thalictrum*. The second type marks *P. recondita* sensu stricto with a host alternation from *Anchusa*, *Lithospermum* and *Onosmodium* to *Secale*. The third type distinguishes *P. symphyti-bromorum* with a host alternation expressed in the species epitheton.

By use of scanning electron microscopy, ZWETKO and BLANZ (2012) could confirm SAVILE’S conclusion, but split SAVILE’S type 1 into two groups of aeciospore wall ornamentations. One of these groups parasitizes on *Thalictrum aquilegifolium*, *Th. flavum* and *Th. speciosissimum*; the other group on *Th. alpinum*, *Th. minus*, *Aconitum napellus*, *Aquilegia atrata* and *A. vulgaris*. *Thalictrum speciosissimum* has been found as aecial host of the important wheat leaf rust, *P. triticina* (s.str.). In inoculation experiments, *P. triticina* produced aecia on more than 30 *Thalictrum* species (GÄUMANN 1959), including *Th. aquilegifolium*, *Th. flavum*, *Th. alpinum* and *Th. minus*, but the aeciospore ornamentation of the rusts on the two first mentioned host species differs from that of the two others (ZWETKO & BLANZ 2012). Based on different techniques, these results indicate that aeciospore ornamentation patterns had not adequately been used for species delimitation within the *P. recondita* complex before but match well with host specificity.

Surprisingly, it is still not completely resolved on which *Thalictrum* species *Puccinia triticina* (s.str.) produces aecia in nature. According to Evsey KOSMAN et al. (2004), *Th. speciosissimum* is the only aecial host in nature and, therefore, sexual reproduction in nature is very rare, and in practice, *P. triticina* reproduces asexually. Samuel BLUMER (1963), Zdeněk URBAN and Jaroslava MARKOVÁ (2009) and others pointed out that host alternation in Central and Eastern Europe has not been detected; however, a number of taxa related to *Puccinia triticina* alternates between wild grasses and *Thalictrum* species.

From Italy, host alternation even between *Clematis vitalba* and *Triticum aestivum* has been reported by Cesare SIBILIA (1956).

Israel S. BEN-ZE'EV et al. (2005) criticize that the “use of the binomial *P. recondita* for the entire complex of cereal leaf rusts does not answer major practical questions: Is there any gene flow among the various rust types within this complex? Are cultivars of wheat and rye susceptible to any of the grass attacking rusts included in the complex?”

Several methods have been applied in order to clarify the question how to distinguish species within the *Puccinia recondita* complex, i.e. isozyme banding patterns of germling urediniospores (Jeremy J. BURDON & Alan P. ROELFS 1985; Charlotte A. SWERTZ 1994), DNA analysis (first results published by Paul J. ZAMBINO & Les J. SZABO 1993), germling morphology of urediniospores (SWERTZ 1994), and crossing experiments combined with various other methods (Yehoshua ANIKSTER et al. 1997, Pnina BEN YEHUDA et al. 2004).

Despite of diverse taxonomic concepts and of the application of many different methods, SZABO, ANIKSTER and MARKOVÁ (2004) agree that the highly complex taxonomic relationship within the *P. recondita* complex is only insufficiently clarified so far. The taxonomic status of many formae speciales and biological species (species in the terminology of GÄUMANN 1959) remains unclear. This can especially be seen in the numerous taxa with Ranunculaceae as aecial hosts and wild grasses as telial hosts, because not all results from inoculation experiments coincide with observations from nature. The wide aecial host range of *P. triticina* (sensu GÄUMANN l.c.) may serve as good example.

The *Coleosporium tussilaginis* complex

The *Coleosporium tussilaginis* complex occurs with primary aecia on two-needle pines, and with secondary aecia (“uredinia”) and telia on various families of angiosperms, especially Asteraceae.

In his treatment of “*Coleosporium* in Europe”, Stephan HELFER (2013) agreed with most authors (HYLANDER et al. 1953, WILSON & HENDERSON 1966, BOERMA & VERHOEVEN 1972) that European taxa of this genus are indistinguishable in their morphology. He concluded “that, morphologically, the taxa are all part of the same species”, but kept formae speciales apart on the basis of discrete host plant ranges. Even GÄUMANN (1959) expresses reservations to treat them as distinct species because of slightly overlapping and sometimes surprising host ranges reported by KLEBAHN (1924).

SEM studies of Naohide HIRATSUKA and Shigeru KANEKO (1975) of surface ornamentation of aeciospores in the genus *Coleosporium* showed great variability and taxonomic relevance of this morphological character. KANEKO (1981) recognized 28 species of *Coleosporium* in the Japanese Archipelago.

He principally treated *C. tussilaginis* as a species complex, but separated only *C. pulsatillae* from *C. tussilaginis* on the basis of different length of teliospores.

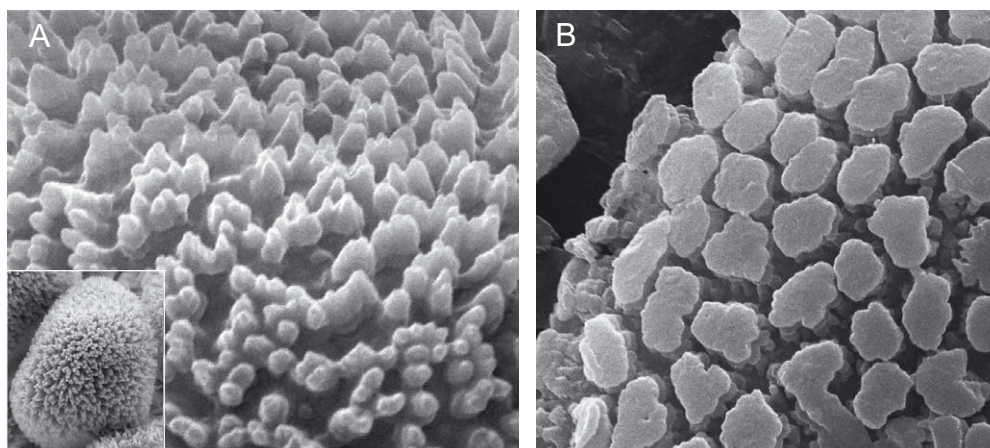


Fig. 4: Aeciospore wall ornamentation of *Coleosporium tussilaginis*: A) on *Pinus sylvestris*, collected in Austria and looking very much alike the specimen collected by HOLM in Sweden and published by HOLM et al. in 1970. Lower left corner: one aeciospore; B) on *Pinus mugo*, warts cylindrical with a flat top, showing an explicit difference compared to Fig. 4A (see text).

When comparing different collections of *C. tussilaginis* by SEM, ZWETKO & BLANZ found two different aeciospore wall ornamentations. Only in one of their collections the warts showed a tapering shape with “rootlike stilts” (Fig. 4A). This form has also been reported by HOFSTEN and HOLM (1968) and HOLM et al. (1970). However, in the majority of collections, warts were found to be cylindrical with a flat top (Fig. 4B). HELFER (2013) published a SEM-photo, which resembles these other collections in spore ornamentation. There can be no doubt that rusts with these two different types of aeciospore wall ornamentation represent at least two distinct species by any realistic species concept. Such still unnamed species have to be examined in order to clarify if they can be grouped with existing biological species or formae speciales. For this purpose, infection and molecular studies are promising; further morphological studies can also be helpful. The genus *Coleosporium* produces secondary aecia instead of true, morphologically defined uredinia. According to KANEKO (1981), the surface ornamentation of the urediniospores (secondary aeciospores) is usually similar to that of the (primary) aeciospores. However, wall ornaments of urediniospores in the *C. tussilaginis* complex have barely been studied.

The *Puccinia pazschkei* complex

The *Puccinia pazschkei* complex contains taxa on *Saxifraga* which are adapted to alpine and arctic climates as their hosts are. As in some other species complexes, its life cycle is microcyclic, i.e. it is strongly reduced; only telia are known. This confronts us with additional aspects. One aspect of microcyclic alpine and arctic taxa is the lack of pycnia and the resulting question if and how sexual reproduction occurs. This is still an open question for these rust taxa. Of the 49 Norwegian microforms, only one has been found with pycnia (JØRSTAD 1964a). More than 90 % of the microcyclic taxa reported from Austria by POELT and ZWETKO (1997) do not have pycnia. All taxa within the *P. paschkei* complex are among these 90 %. SAVILE (1954, 1973b) did not describe pycnia in this group, as well.

The second aspect applies to phylogeny. Assuming that microcyclic rusts originate from macrocyclic forms, knowledge on the ancestors is important. Often, ancestors are unknown or possibly extinct. Microcyclic complexes, which are mainly morphologically circumscribed, are prone to be polyphyletic. This became apparent in the species complex of *Puccinia cnici-oleracei* sensu HYLANDER et al. (1953) that contains many narrow species which originate from different taxa within the *P. dioicae* and *P. atrofusca* complex. This has been shown by morphological data (ZWETKO 1993) as well as by molecular data (J. ENGHANINUM et al. 2005). SAVILE (1975) considered the short cycled (microcyclic) rusts on *Saxifraga* as a coherent group but did not mention where they originate from. However, *P. pazschkei* sensu SAVILE is not necessarily monophyletic; significant molecular data on this group are still lacking.

So far, there are no accounts of inoculation experiments with taxa of the *Puccinia pazschkei* species complex; therefore, discrimination of taxa is mainly based on morphological characters of teliospores. GÄUMANN (1959) accepted several species within this complex not without reservation, HYLANDER et al. (1953) and GJÆRUM (1974) considered *P. pazschkei* as one polymorphous species, and reduced all species to synonyms. SAVILE (1954) considered all previously recognized species as varieties and described even more. He noticed that a main character of the spore wall in *P. pazschkei* presents a “difficult problem, largely because the decorations of the spore walls do not always stand up steeply, but are shallowly sloping, with the result that patterns are difficult to discern.” SAVILE (1971) emphasized that “geography, ecology and host identity is part of the description of every rust specimen, and must often supplement morphology to allow a meaningful taxonomic treatment.” His second study (1973b) on microcyclic *Puccinia* species on Saxifragaceae is based on intensive field studies in the North American Cordillera and the Canadian Arctic, and on use of phase-contrast microscopy; European collections were included only in low numbers. In 1975, SAVILE interpreted the “evolution and biogeography of Saxifragaceae with guidance from their rust parasites”.

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He concluded “that the most recent radiations in *Saxifraga* and its parasites have been in Cordilleran North America and the [European] Alps”. The host-parasite combinations reported from North America conspicuously differ from those reported from Scandinavia and from the European Alps.

Tab. 1: Comparison of host-parasite combinations in different geographical regions.

<i>Saxifraga aizoides</i> :	<i>P. pazschkei</i> var. <i>jueliana</i> : European Alps, Scandinavia, Greenland and Canada (SAVILE 1954, 1973b) <i>P. fischeri</i> : Svalbard (SAVILE 1954)
<i>Saxifraga mutata</i> :	<i>P. pazschkei</i> var. <i>huteri</i> : European Alps (SAVILE 1954, 1973b) <i>P. pazschkei</i> var. <i>pazschkei</i> : European Alps (MAYOR 1975)
<i>Saxifraga oppositifolia</i> :	<i>P. pazschkei</i> var. <i>jueliana</i> : Scotland (WILSON & HENDERSON 1966) <i>P. pazschkei</i> var. <i>oppositifoliae</i> : Scandinavia (SAVILE 1954), Greenland and eastern Canada (SAVILE 1973b) <i>P. fischeri</i> : North American Arctic, islands and northern coast (?) of Siberia (SAVILE 1954, 1973b). <i>P. fischeri</i> has been reported from the European Alps on <i>Saxifraga biflora</i> – a species closely related to <i>S. oppositifolia</i> – by SAVILE (1954) <i>P. joerstadii</i> : European Alps and Carpathians (SAVILE 1954)
<i>Saxifraga paniculata</i> :	<i>P. pazschkei</i> var. <i>pazschkei</i> : European Alps, Scandinavia (SAVILE 1954) <i>P. pazschkei</i> var. <i>huteri</i> : Germany (BRANDENBURGER 1994) <i>P. fischeri</i> ?

When comparing different collections of *P. pazschkei* s.l. from the Alps and Scandinavia by SEM, ZWETKO and BLANZ found two different teliospore wall ornamentations (Fig. 5). In the collection of *P. pazschkei* var. *pazschkei* on *S. paniculata* from the Alps, the spore wall has been described as “conspicuously rugose ... with irregular warts and broken labyrinthiform ridges” by SAVILE (1973b). In SEM, the ridges are irregularly interwoven and form coarse knots which more or less resemble warts (Fig. 5A). In a collection of *P. pazschkei* s.l. on *S. aizoides* from Finland, wall ornamentation is similar but the ridges are less striking and the knots are more conspicuous (Fig. 5B) than in the specimens of *P. pazschkei* var. *pazschkei*. This collection on *S. aizoides* from Finland distinctly differs from a collection of *P. pazschkei* var. *jueliana* on *S. aizoides* from the Austrian Alps. In the Austrian collection the ridges are finer, and structures which resemble thickened knots or coarse warts are lacking

(Fig. 5C). Its wall ornamentation is similar to that of *P. pazschkei* var. *huteri* on *S. mutata* from the Austrian Alps but the ridges of the latter are “tending to run longitudinally” (SAVILE 1954) (Fig. 5D). The collection on *S. aizoides* from Finland cannot be assigned to any variety described by SAVILE (l.c.).

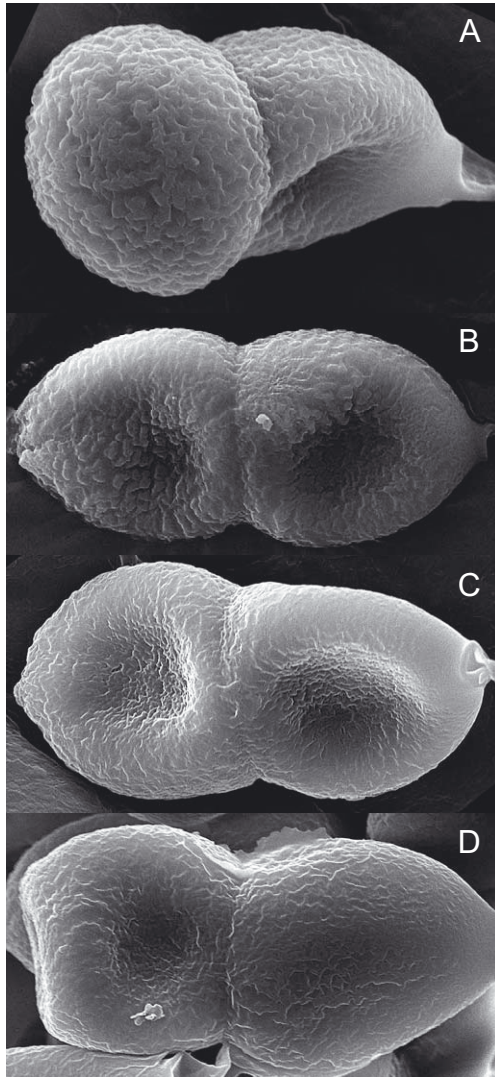


Fig. 5: Teliospores with different pattern of wall ornamentation: (for details see text).

A) *Puccinia pazschkei* var. *pazschkei* on *Saxifraga paniculata* with spore ornamentation showing ridges irregularly interwoven and coarse knots which more or less resemble warts;

B) *Puccinia pazschkei* s.l. on *Saxifraga aizoides* with similar wall ornamentation as in fig. 5A, but with ridges less striking and knots more conspicuous;

C) *Puccinia pazschkei* var. *jueliana* on *Saxifraga aizoides* with finer ridges and without structures, which resemble thickened knots or coarse warts;

D) *Puccinia pazschkei* var. *huteri* on *Saxifraga mutata* with similar spore ornamentation as in fig. 5C, but ridges “tending to run longitudinally” (SAVILE 1954).

Both major types of wall ornamentation have been found in Scandinavia and in the Alps. The hosts of both belong to *Saxifraga* sect. *Xanthizoon* (*S. aizoides*) as well as to *S. sect. Ligulatae* (*S. paniculata* and *S. mutata*). These types of wall ornamentation are most likely appropriate to characterize single varieties or narrow species, but it remains unclear if they do indicate how closely these rusts are related. Especially in microcyclic groups without pyc-

nia, importance of sexual reproduction is unclear. It is also unclear to what extent the phylogeny of the hosts reflects the phylogeny of their parasites. On the basis of molecular studies, Douglas E. SOLTIS et al. (1996) suggested a very close relationship between members of the *Saxifraga* sections *Porphyrion*, *Ligulatae* and *Xanthizoon*. Reliable intersectional hybrids have been reported to exist between members of sections *Porphyrion* and *Xanthizoon* (*S. oppositifolia* and *S. aizoides*) on the one hand, and *Ligulatae* and *Xanthizoon* on the other. *S. aizoides* is closely related to species of the section *Porphyrion*.

Saxifraga oppositifolia has been reported as host for four different rust taxa, *P. pazschkei* var. *jueliana*, *P. pazschkei* var. *oppositifoliae*, *P. fischeri* and *P. joerstadii*. Rolf HOLDEREGGER and Richard J. ABBOTT (2003) studied the phylogeography of the arctic-alpine *S. oppositifolia* by the use of molecular data. Two major clades have been detected, a Eurasian and an East Asian-North American clade. Molecular data support the occurrence of two major evolutionary lineages of *S. oppositifolia*, which most likely have been geographically isolated from each other during the Pleistocene. We assume a correlation between the two major evolutionary lineages of the host plant and its rust parasites. According to SAVILE (1973b), *P. pazschkei* var. *jueliana*, *P. pazschkei* var. *oppositifoliae* and *P. fischeri* occur in both the Alps and the Arctic, while *P. pazschkei* var. *pazschkei*, *P. pazschkei* var. *huteri* and *P. joerstadii* are restricted to the European Alps. *P. pazschkei* var. *pazschkei* occurs naturally in the mountains of Europe but it has appreciably been spread with horticultural material. Meanwhile, it has been found even outside of the Alps. Eugène MAYOR (1975) reported this variety from the botanical garden in Champex (Valais, Switzerland) on *Saxifraga mutata*, as a new host for the variety. The host has been transplanted together with *S. hostii* from the Italian Alps. The rusts on both plants are morphologically identical. But based on the diagnosis given by GÄUMANN (1959), MAYOR (1975) could not assign them to *P. pazschkei* var. *huteri*, despite the fact that this rust was unknown from *S. mutata* until then. Such untypical host range data can also be observed in *Uromyces apiosporus* which parasitizes *Primula minima* but usually not *P. glutinosa*, on which it has nevertheless been found in close vicinity to a heavily infected *P. minima* (POELT & ZWETKO 1997).

The assignment of Scottish collections on *Saxifraga aizoides* and *S. oppositifolia* to *P. pazschkei* var. *jueliana* by WILSON and HENDERSON (1966) is based on the morphological diagnosis of SAVILE (1954) although this author did not list *S. oppositifolia* as host of *P. pazschkei* var. *jueliana*.

As can be seen from the examples discussed before, further morphological as well as experimental studies will provide a more solid basis for separating at least some still unclear species complexes. This should result in species delineations which best reflect their phylogeny.

Perspective

Denomination of species is the primary information in a written Flora. Due to different species concepts, corresponding taxa may be named differently. It may therefore be tedious work to figure out which taxa of one Flora correspond to which taxa of another. The availability of new markers and techniques will lead us to new connections of data and new ways how to deal with these differences. By this, we learn more about the phylogenetic relationships and evolution of rust fungi and their host plants. It is therefore important to keep compiling data in Florae of many areas. Here, only few European Florae have been used. However, even in the newest European Florae, manuals, checklists or catalogues, the controversy in species delimitation does still exist (MAJEWSKI & RUSZKIEWICZ-MICHALSKA 2008, URBAN & MARKOVÁ 2009, TERMORSHUIZEN & SWERTZ 2011, KLENKE & SCHOLLER 2015). It is therefore important to keep the discussion going.

Of course, it is in a way discreditory to restrict the discussion on species concepts to few European Florae. However, for the purpose to line out the basic differences in species concepts, this reduction may be excusable.

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5. Appendix

To study the aeciospore surface ornamentation, specimens have been sputtered with gold. A Philips XL30 ESEM was used for examining aeciospore walls. Images have been calibrated with Olympus' Cell A software. Deposits of the GZU herbarium and collections of the authors have been studied.

List of taxa in figures

- Aecidium centaureae* (DC.) in KLEBAHN (1914: 877) on *Centaurea stoebe* L. subsp. *maculosa* (LAM.) HAY. (syn. *C. maculosa* LAM.), Drawing from KLEBAHN (l.c.); Fig. 1A.
- Aecidium inulae-helenii* CONST. on *Inula helenium* L., Romania (Distr. Vaslui), prope Grajduri, leg. J. CONSTANTINEANU; Fig. 1C
- Coleosporium tussilaginis* (PERS.) LÉV. s.l. on *Pinus mugo* TURRA, Austria, Styria, Hochschwab, Lamingsattel, 1650 m, 01.07.2000, leg. P. ZWETKO; Fig. 4B.
- Coleosporium tussilaginis* (PERS.) LÉV. s.l. on *Pinus silvestris* L., Austria, Lower Austria, near Klosterneuburg, leg. E. RATHAY; Fig. 4A.
- Puccinia aecidii-leucanthemi* ED. FISCH. on *Leucanthemum vulgare* LAM.; leg. J. POELT, 04.07.1982; Fig. 1C.
- Puccinia dioicae* MAGN. on *Cirsium oleraceum* (L.) SCOP. (from KLEBAHN 1914); Fig. 1B.
- Puccinia extensicola* PLOWR. on *Carex extensa* GOOD. (from KLEBAHN 1914); Fig. 2C.
- Puccinia pazschkei* DIET. s.l. on *Saxifraga aizoides* L., Finland, Ks, Kuusamo, Jauma, Kitkajoki, 175–240 m, 25.08.1978, leg. P. ALANKO; Fig. 5B.

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Puccinia pazschkei DIET. var. *huteri* (SYD. & P. SYD.) SAVILE on *Saxifraga mutata* L., Austria, Tyrol, Tuxer Voralpe, Navistal near Matrei, 1350–1450 m, 20.08.1981, leg. J. POELT; Fig. 5D.

Puccinia pazschkei DIET. var. *jueliana* (DIET.) SAVILE on *Saxifraga aizoides* L., Austria, Styria, Wölzer Tauern, Planneralm, 1700 m, 29.07.1978, leg. J. HAFELLNER & ZICH; Fig. 5C.

Puccinia pazschkei DIET. var. *pazschkei* sensu SAVILE on *Saxifraga paniculata* MILL., Austria, Salzburg, Kitzbühler Alps, Geißstein, 29.08.1985, leg. F. GRIMS; Fig. 5A.

Puccinia schoeleriana PLOWR. & MAGN. on *Carex ligerica* GAY (from KLEBAHN 1914); Fig. 2B.

Puccinia silvatica J. SCHROET. on *Carex praecox* SCHREB. (from KLEBAHN 1914); Fig. 2A.

Puccinia aff. *atrofusca* HOLWAY on *Carex curvula* ALL., Austria, Tyrol, Öztaler Alps, Hohe Mut south of Obergurgl, 2450 m, 14.07.1994, leg. W. DIETRICH; Fig. 3.

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