Aeciospore types in rusts on *Ranunculus* and allied genera

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Abstract: Aeciospore surface structures in *Puccinia* and *Uromyces* on *Ranunculus* and allied genera have been examined with the scanning electron microscope (SEM). All in all, we could distinguish five morphologically different groups of aeciospores. The pattern of surface zonation is of the same kind in group A, B, C and D: First a finely and densely verrucose, circular, apical zone, then a broad belt with larger and more diverse surface sculptures and again a finely and densely verrucose, basal zone. Group E spores are azonate, their warts tend to enlarge on the whole spore surface. The use of SEM enables us to observe the apex of the uppermost spore of each chain inside open, cup-shaped aecia. The apical spore region is characterized by conspicuous features, i.e. a smooth, round cap or a hole surrounded by an annulus. These features help to define the position of the surface zones and to characterize the ornamentation of the spore wall. Implications for diagnosis and taxonomy have been discussed.

Zusammenfassung: Die Oberflächenstrukturen von Aecidiosporen wurden mit dem Rasterelektronenmikroskop untersucht. Ausgwählt wurden Aecidien der Rostpilzgattungen *Puccinia* und *Uromyces* auf *Ranunculus* und verwandten Wirtsgattungen. Anhand morphologischer Merkmale konnten fünf unterschiedliche Sporengruppen festgestellt werden. In vier dieser Gruppen (A, B, C und D) entspricht die Zonierung der Wandornamente dem selben Grundschema: Auf eine feinwarzige apikale Zone folgt ein breiter Gürtel mit größeren und in der Form unterschiedlichen Wandskulpturen. Während fast die ganze basale Sporenhalbkugel gleichmäßig mit feinen, dicht stehenden Warzen bedeckt ist. In der Sporengruppe E konnten keine derartigen Zonierungen, jedoch zwischen verschiedenen Proben deutliche Unterschiede in der Größe der Warzen festgestellt werden. Das Rasterelektronenmikroskop ermöglichte uns in offene Aecidienbecher zu blicken und den Apex der letzten Spore jeder Kette zu sehen. Den Sporenscheitel zeichnen besondere Merkmale aus – entweder ein von einem ringförmigen Wulst umgebenes Loch, oder eine glatte, Polkappen-ähnliche Auflagerung. Diese besonderen Merkmale helfen, die Position der Zonen mit unterschiedlichen Wandornamenten zu bestimmen. Implikationen für die Taxonomie und Diagnose werden diskutiert.

Key words: Rust fungi, aecia, aeciospore types, surface ornamentation, *Ranunculus*, determination, taxonomy.

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INTRODUCTION

Production of aecia is one of the most spectacular phenomena in the world of phytoparasitic fungi. Some rusts induce formation of pseudoflowers that resemble true flowers in colour and shape (Pfunder et al. 2001). Usually, aecia are produced on bright yellow, reddish or purple-red, leaf spots and swellings, often also on deformed petioles and stems in crowded groups of various size. They can easily be found on many diverse host plants. In many instances, however, their use for diagnosing the parasite is rather limited. A better understanding of morphological criteria in aecia and aeciospore structure may help to separate species better.

In his comprehensive study on rust fungi in central Europe, Gäumann (1959) recorded as many as 13 host-alternating species producing aecia on *Ra-*

nunculus and supposed that it will be more. This group includes rusts with uredinial and telial stages on Polygonaceae (*Uromyces alpinus*, *U. rumicis*) and on Poaceae (*Puccinia magnusiana*, *P. recondita* species complex, *U. dactylidis* species complex). The taxonomy of the different species in the *U. dactylidis* complex is based on the choice of the telial host as well as on morphology of telia and uredinia. Each of the rust species in this complex occurs on a different Poaceae host. Hence, these rusts are more or less recognizable, when uredinia and telia are known. When we find aecia in spring, and no old telia are present, we are in trouble. The aecial host range of these rust species is overlapping. It remains uncertain to what extent results of inoculation experiments reflect the ability of the corresponding rust fungi to infect host plants in nature.

Two separate groups exist in the *P. recondita* species complex: The *P. triticina* group attacking wild and cultivated wheat, and its aecial host *Thalictrum speciosissimum,* and a second group, that form the *P. recondita* complex in a narrow sense, with rye, durum wheat, and *Aegilops* spp. as telial hosts and Boraginaceae as aecial hosts. These two groups appear to be separate biological entities. Each group is further divisible into subgroups slightly differing in their range of telial and aecial hosts and in morphological traits (Anikster et al. 1997, Ben-Ze'ev et al. 2005). In central Europe several subgroups or species, respectively, with aecia on Ranunculaceae occur. However, only one species, *P. perplexans,* produces aecia on *Ranunculus.* A second species with aecia on *Ranunculus* has been reported by Savulescu (1953) and Gäumann (1959) from Europe. But the ability of this species to infect *Ranunculus* has never been proven experimentally (Marková & Urban 1998). Though *Ranunculus* as aecial host of *P. magnusiana, U. alpinus* and *U. rumicis* has been verified in inoculation experiments, the aecial host range of these rusts in nature is still not adequately proven.

Based on morphological characters, which are reported by previous authors (Gäumann 1959; Wilson & Henderson 1966, Cummins 1971), rusts on *Ranunculus* are hardly distinguishable in their aecial stage. Gäumann (1959) stated that aeciospores of *U. dactylidis* s.l. and *U. alpinus* (Syn. *Schroeteriaster alpinus*) are nearly identical, only peridial cells slightly differ in wall thickness. Due to wall structure and form of peridial cells, their wall thickness is often difficult to be measured escpecially by overlapping numbers with other species. For the discrimination of *U. alpinus* from other *Ranunculus* inhabiting rusts, Gäumann (1959) and Majewski (1979) also used size and number of the aecia. The question arises to what extent this character of the aecia is influenced by environmental conditions. Thus rusts with aecia on *Ranunculus* are especially prone to misidentification.

Holm (1964) examined aecia on *Ranunculus ficaria* and found such differential criteria as size of aecial cups and sori of relative value only, not permitting a safe determination. On the other hand, he found the surface ornamentation of aeciospores to be of great diagnostic value. Holm (1967) distinguished three morphological types of aeciospores within *Puccinia* and *Uromyces.* In type 1 the warts are < 1µm; in type 2 they are < 2µm; in type 3 the warts have grown to the status of refractive granules ≥ 2µm.

Savile (1973) examined aeciospore types in *Puccinia* and *Uromyces* species attacking Cyperaceae, Juncaceae and Poaceae. He criticized that »for most species the usual description is a statement of dimensions and wall thickness, with some such indefinite phrase as "finely verrucose"«. Klebahn (1914: 104) first reported ornaments that are different from warts. He described them as "abfallende Plättchen", i.e. deciduous platelets. Savile (1972 and 1973) considered the term platelets inappropriate for a strongly three-dimensional structure. He also criticized the term "refractive granules", because the material, evidently identical with that of warts, is not notably refractive. Savile overworked the term "pore plugs", created by Dodge (1924) for these bodies. He hypothesized that normal warts have enlarged into dehiscent plugs that leave impressed "pores" in the wall.

According to the degree of plug evolution, Savile (1973) distinguished five morphological types of aeciospores. In type 1 the warts are either uniformly small (rarely > 0,5 µm) or a mixture of large and small. He attempted to recognize two groups, uniform and mixed; but the two groups intergrade completely, for there is some variation in even the most uniform warts. In type 2 the walls are bizonately patterned, with more or less abruptly distinct belts of coarse and of fine warts. Type 3 spores resemble type 2 except that some to many warts in the coarse belt have grown to the status of small but definite plugs (1–1,8 µm diam.). The plugs are usually distinguished from warts by the presence of a small tonsure. In mature spores the plugs are freely deciduous. Bodies intermediate between plugs and warts are usually abundant; and occasionally they replace normal warts to such a degree that no tonsure is visible. In type 4 and 5 some warts in the coarse belt have grown to the status of large plugs (about 3 µm diam.). Smaller plugs or intermediate bodies between plugs and warts are abundant in type 4, but scare in type 5, which he considered the most advanced type.

Holm (1967) and Savile (1973) examined a wide range of species in the genera *Puccinia* and *Uromyces*. Nevertheless, aeciospore surface structures of many species are still unknown, and the identification of many rust species in the aecial stage still causes difficulties. Poelt & Zwetko (1997) reported aecia on *Ranunculus repens* from Styria (Austria) with spores characterized by large deciduous plugs, and found uredinia and telia of *U. alpinus* at the same location. The aecia of *U. alpinus* have been usually described as densely and finely verrucose, but the aeciospores on *R. repens* have a zonate surface with a broad, coarsely verrucose band and large deciduous plugs between the coarse warts. These aecia on *R. repens* did not differ morphologically from those of *U. rumicis* on *R. ficaria*.

Tab. 1.: Specimens examined with the scanning electron microscope. Additional specimens (GZU, ZT, M) investigated with the light microscope are not listed.

Aecidium indet. on *Ranunculus alpestris*, Austria, Styria, Polster über Präbichl, leg. Ch. Scheidegger, 1981.05.31; GZU.
Ae. indet. on *R. lanuginosus*, Lower Austria, Voralpen, Würflach, ESE of Grünbach am Schneeberg, W of Johannesbachklamm, in close vicinity to the brookside, leg T. Barta, 1998.05.23; GZU.
Puccinia aecidii-leucanthemi on *Leucanthemum vulgare* (*P. dioicae* s.l.), Austria, Styria, Kalkleiten N of Graz, meadow in about 700m, leg. J. Poelt, 1982.05;GZU.
P. borealis (*P. recondita* s.l.) on *Thalictrum alpinum*, Austria, Styria, Wölzer Tauern, in about 2100m, leg. H. Melzer, 1991.07.17; GZU.
P. bromina ssp. *symphyti-bromorum*, on *Pulmonaria australis* (*P. recondita* s.l.), Slovenia, Čičarija, N of Rakitovec, below the high karst edge between the summits Lipnik and Kavčič, meadows with Bromus erectus, leg. Ch. Scheuer, 2006.06.08; GZU; Dupla Graecensia Fungorum (2006).
P. magnusiana on *Ranunculus bulbosus,* Switzerland, E. Gäumann, 1934.04.10 (inoculation experiment); ZT.
P. magnusiana on *R. bulbosus,* Switzerland, E. Gäumann, 1940 (inoculation experiment with telia on *Phragmites* collected in Germany, Bavaria); ZT.
P. magnusiana on *R. montanus,* Switzerland, E. Gäumann, 1934.05.02 (inoculation experiment); ZT.
P. magnusiana on *R. repens*, Ungarn, pr. Nagy Györ, leg. A. Magocsy-Dietz, m. Aug.; Cryptogamae exsiccatae Museo Hist. Natur. Vindobonensi 1305.
P.magnusiana on *R. repens* cult., England, Kings-Lynn, leg. Ch.B. Plowright, 1890; Sydow, Uredineen 402.
P. magnusiana on *R. repens*, Czech Republic, Moravia, Hohenstadt, leg. F. Bubak, 1898.04.03; Sydow, Uredineen 1215.
P. magnusiana on *R. repens*, Czech Republic, Moravia, Sternberg, leg. J. Piskor, 1926.05; GZU.
P. magnusiana on *R. repens,* Switzerland, E. Gäumann, 1934.04.10 (inoculation experiment); ZT.
P. magnusiana on *R. repens*, Austria, Styria, Ennstal near Trautenfels, in close vicinity to reed, leg. P. Zwetko, 1984.06.17; GZU.
P. magnusiana on *R. repens*, Austria, Burgenland, between Neusiedl am See and Jois, marsh area in about 120m, leg. T. Barta, 1994.05.14; GZU (Dupla Fungorum).
P. poae-aposeridis on *Aposeris foetida*, Germany, Bavaria, Schleching, wood in the montane zone, leg. H.& H. Doppelbaur, 1967.05.28; M.
P. recondita s.l. on *Aconitum napellus*, Austria, Styria, Hochschwabgebiet, Dürrsee, leg. P. Zwetko & P. Blanz, 2007.06.04; Herb. P. Blanz.
P. recondita s.l. on *A. vulgaris*, Austria, Lower Austria, ESE of Grünbach am Schneeberg, meadow, leg. T. Barta, 1998.05.23; GZU (Dupla Fungorum).
P. recondita s.l. on *Thalictrum aquilegifolium*, Austria, Styria, Koralpe, Seekar, leg. F. Widder, 1939.07.27; GZU.
P. recondita s.l. on *Th. flavum*, Finnland, Oulu, Kontinkangas, fallow area, leg. E. Ohenoja, 1975.06.30; GZU.
P. recondita s.l. on *Th. flavum*, Germany, Bavaria, Oberbayern, bank of the river Amper, S of Herbertshausen, river wood, leg. D. Podlech, 1980, 06.15; GZU.
P. recondita s.l. on *Th. minus*, Switzerland, Valais, E of Hohtenn, Lötschberg-Südrampe, in about 700-750m, leg. J. Hafellner, 1975.07.15; GZU.
(*P. recondita* s.l. on *Th. minus*, Slovenia, Ternowaner Wood, Čavin, in about 700 m, leg. H. Melzer, 1981.06.26; GZU.
P. c.f. *scarlensis* (*P. recondita* s.l.) on *Aquilegia atrata*, Austria, Upper Austria, Steyrdurchbruch SW of Molln, river wood in about 430 m, Leg. S. Wagner, 1993.06.01; GZU:
Uromyces alpinus on *Ranunculus* cf. *montanus*, Switzerland, Valais, Chemin du Rawil, Praz Jean - Les Ravins, leg. Ch.Terrier, 1947.06.01; ZT.
U. alpinus on *R. montanus*, Switzerland, Valais, Val Ferret; La Sassa sur Praz-de-Fort, leg. Ch. Terrier, 1948.06.27; ZT
U. alpinus on *R. montanus*, Switzerland, Terrassenversuch, leg. Ch. Terrier, 1954.04, (inoculation experiment with telia on *Rumex alpinus*), ZT.
U. cf. *alpinus* on *R. ficaria*, Austria, Styria, "Niedere Tauern, Stumeralm", nutrient rich pasture with *Rumex alpinus*, in ca. 1400 m, leg. H. Mayrhofer & P. Remler, 1975.06.14; GZU.
U. cf. *alpinus* on *R. repens*, Austria, Styria, "Eisenerzer Reichenstein, Grübl", nutrient rich pasture with *Rumex alpinus*, in about 1400 m, leg. H. Köckinger, 1992.06.29; GZU.
U. dactylidis f. sp. *platanifolii-dactylidis* on *Ranunculus platanifolius*, Switzerland, in silvis pr. Neuchatel, leg. E. Mayor, 1911.06.18; Sydow, Uredineen 2453.
U. dactylidis s.l.on *R. aconitifolius*, Austria, Upper Austria, near Windischgarsten, N of Gunst, litter meadow in about 620m, leg. S. Wagner, 1993.06.08; GZU.
U. cf. *dactylidis* s.l. on *R. bulbosus*, Austria, Kärnten, Lavanttal SE of Wolfsberg, in Weißenbach, grassy slope, leg. H. Melzer, 1988.05.10; GZU.
U. cf. *dactylidis* s.l. on *R. nemorosus*, Austria, Tirol, Karwendel, Rontal near Hinterriß, towards Tortalscharte, leg. J. Poelt, 1962.08.12; GZU
U. poae f. sp. *auricomi-pratensis* on *R. auricomus*, Germany, Bavaria, Oberpfalz, Regensburg, Mintraching, leg. E. Eichhorn, 1948.05.01; Plantae Graecenses Fungi 787.
U. cf. *poae* (*U. dactylidis* s.l.) on *R. ficaria*, Austria, Styria, near Mariazell, Rechengraben, leg. Ch. Scheuer, 1988.05.23; GZU.
U. cf. *poae* (*U. dactylidis* s.l.) on *R. ficaria*, Austria, Styria, Botanischer Garten Graz, leg Ch. Scheuer, 2002.04.02; GZU.
U. rumicis on *R. ficaria*, Austria, Upper Austria, St. Pankraz SW of Windischgarsten, leg. F. Grims, 1987.05.19; GZU.

The authors of the Austrian rust catalogue also studied aecia on *Ranunculus*, which have been collected in close vicinity to *Phragmites*. These aecia probably belong to the life cycle of *Puccinia magnusiana*, but the ornamentation of their spore walls did not fit to the spore type described by Savile (1973) for this rust species. That is why we examined aecia on further species of *Ranunculus* and allied genera. The objectives of this study are twofold: First, to improve the analysis of these surface ornaments and ornamentation patterns by means of scanning electron microscopy and second, to verify to what extent surface structures of aeciospores can be used as diagnostic criteria in identifying rust fungi on *Ranunculus* and allied genera.

MATERIAL AND METHODS

For the study on aecidiospore surface ornamentation, airdried specimens have been used. Most of them are deposits of the GZU herbarium of our institute. Further specimens have been loans from the herbaria of the ETH Zürich and Munich (Bayerische Staatssammlung); some specimens were collected by the authors. Details are shown in Tab. 1.

For SEM analyses, airdried aecia on corresponding hosts have been mounted and sputtered with gold first. A Philips XL30 ESEM was used for examining aecidiospore surface structures. The resulting images had been evaluated with Olympus' Cell A software.

In some instances, young, not yet opened aecia had been prepared in such a way that their covering peridia has been cut off in order to get access to young spores.

RESULTS AND DISCUSSION

In our study, the advantages of the scanning electron microscope (SEM) have been employed as aid in three-dimensional description of wall ornamentation at high resolution. Usually, mature aeciospores are not observed in native spore chains but in an assemmblage of scattered spores and fragments of chains. When we know their localisation within the aecium or within the spore chains, we may be able to more reliably interprete their morphological characters. The use of SEM not only enables us to see inside an open, cup-shaped aecium an irregulary scattered mass of spores. Especially in young aecia with spores regularly arranged, it also shows the apex of the uppermost spore of each chain (Fig. 1).

We have studied aecia on several members of Ranunculaceae and Asteraceae. When focusing on single spores, the apical spore region is characterized by conspicuous features, i.e. a smooth, round cap (Fig. 2) or a hole (Fig. 3), These features are hardly recognizable by light microscopy. Littlefield & Heath (1979: 41) described and illustrated the ultrastructure of the aeciospore wall and its development. In immature aeciospores of *Melampsora lini* a mucilage-like interstitial matrix between warts appears to condense or to break down, exposing ornaments. A similar process occurs in *P. recondita,* although the interstitial matrix lacks the mucilage like appearance of that in *M. lini.* SEM-photos of young aeciospores of *P. recondita* in Littlefield & Heath (1979) show shapeless, interstitial matrix (primary wall) covering wall ornaments. Warts of mature *Puccinia recondita* aeciospores are fully exposed; the interstitial matrix has completely disappeared. In contrast, the apical spore caps do not disappear when spores are mature and plugs have dropped off. Their shape is rather regularly circular. In our specimens, they have always been present when spores possess large plugs.

In all our specimens, an apical hole (Fig. 5) has been observed when no apical cap was present. It is surrounded by an annulus. The size of these holes is about 0,350 µm in diam. We have never observed such holes at the base of the spores. Further studies in spore ontogeny are needed to understand the anatomy of this pore-like feature, which is not mentioned by Gold et al. (1979), Littlefield & Heath (1979), or Lee & Kakishima (1999).

These features help us to recognize the apex and basis of isolated aeciospores. When knowing the position of the apex one may see a small, finely verrucose apical zone, a belt with coarse warts or coarse warts and plugs, respectively, as well as a basal hemisphere even with a light microscope. In order to detect a distinct apical zone, a selective search has to be accomplished.

Savile mentions a »substantial constancy of zones and plug positions« within short spore chains (Savile 1972: 2580). However, he could hardly define the position of the zones. His preparation technique did not support this since he prepared spore mounts in heated lactophenol. Irregularly scattered, isolated spores or short chains (two, three or four spores long) resulted from this procedure. All the more admirable are his detailed analyses on form and zonation of wall ornaments and his typology of the spores.

Savile (1973) found type 1, 2 and 3 aeciospores on *Ranunculus*. Aeciospores of *U. rumicis* have been described and illustrated by Holm (1964); they correspond to Savile´s type 5 spores. According to these authors, four of these types of aeciospores apply on aecia occurring on *Ranunculus*. In our study, only two of Savile´s spore types have been found on this host genus, although 25 specimens on 10 *Ranunculus* species have been investigated. We, therefore, studied also aeciospores on further genera of Ranunculaceae, Asteraceae and Boraginaceae. All in all, we could distinguish five morphologically different groups of aeciospores. One of them could be subdivided into less distinct groups:

Group A: Spores with trizonate surface and large deciduous plugs (up to 3,4 µm in diam.).

Group B: Spores with trizonate surface and small deciduous plugs (up to 1,8 (-2,5) µm in diam.).

Group C: Spores with trizonate surface and no deciduous plugs. Zones are

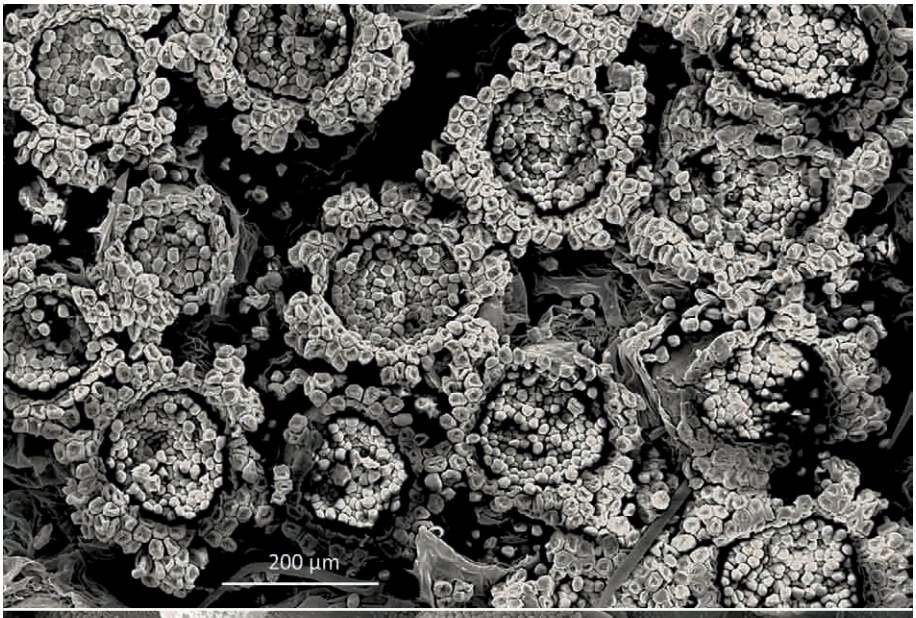

Fig. 1: Open aecial cups of *Puccinia magnusiana* on *Ranunculus bulbosus* with spores and peridia. The peridia are recurved.

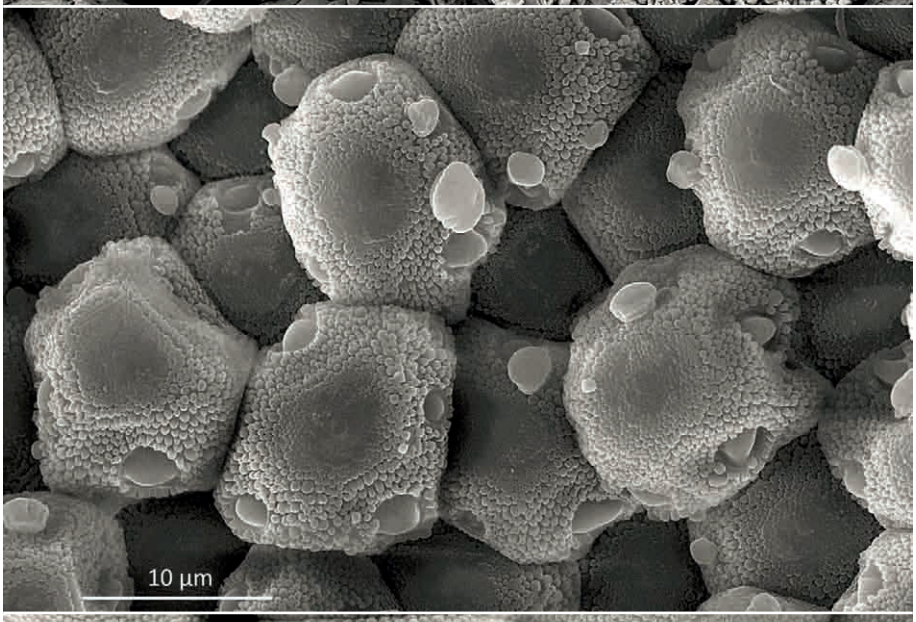

Fig. 2: Aecidiospores of *Puccinia poae-aposeridis* on *Aposeris foetida* with smooth apical caps and large deciduous plugs. Sleek bulges are scars after plugs have left.

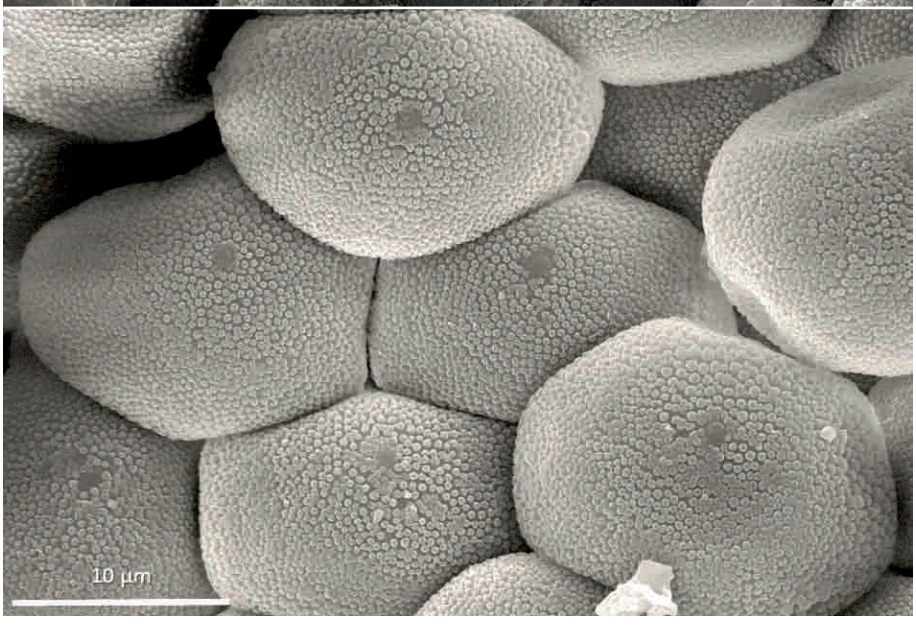

Fig. 3: *Puccinia magnusiana* on *Ranunculus bulbosus* showing young angular spores with apical holes and with compact warts. The warts are partly covered by remains of the primary spore wall. The spores will round up when becoming mature and the warts will not stand this close anymore.

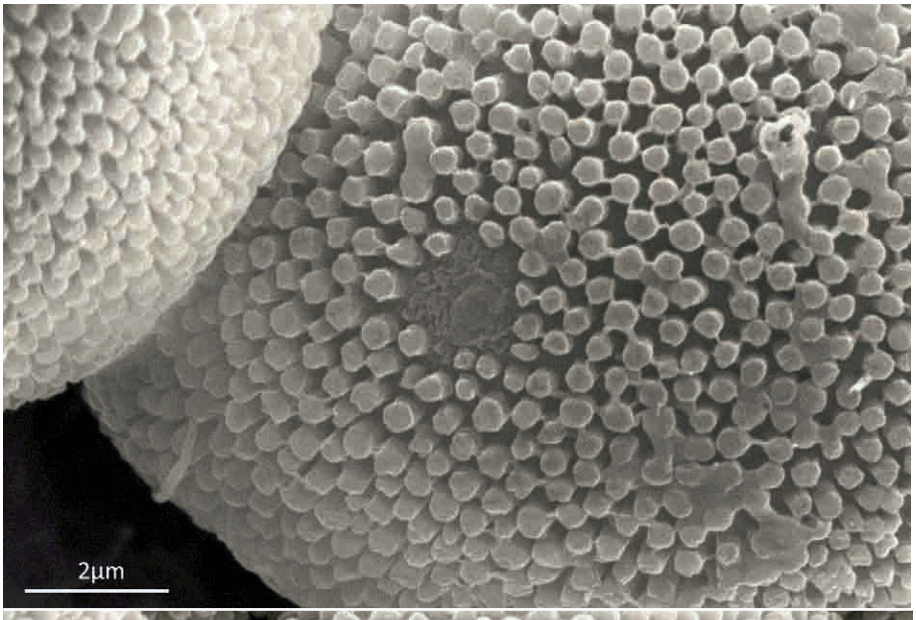

Fig. 4: *Puccinia scarlensis* on *Aquilegia atrata* with irregular layer of the remains of the primary spore wall on and in between the warts.

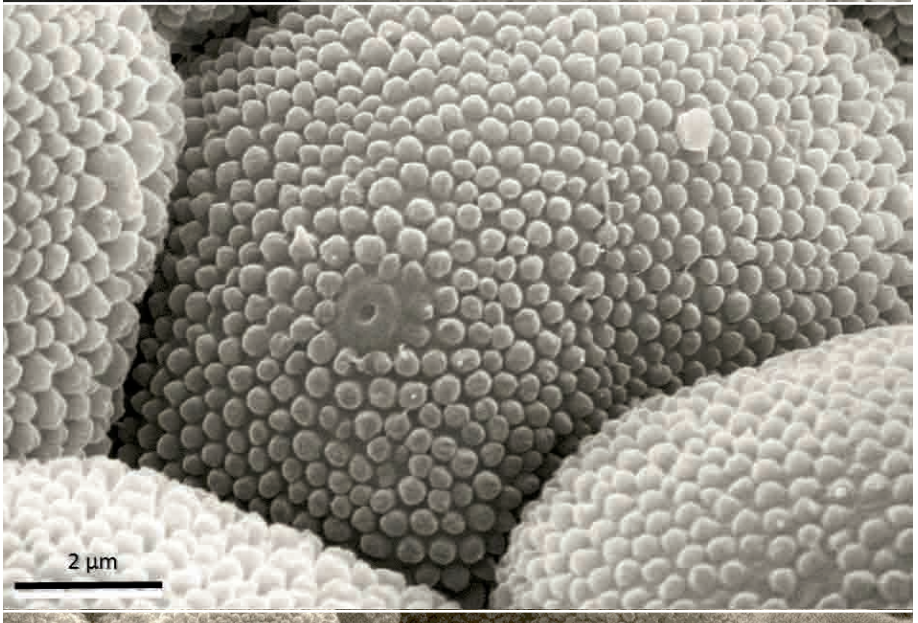

Fig. 5: *Puccinia magnusiana* on *Ranunculus repens*: Apical hole with annulus surrounded by small warts.

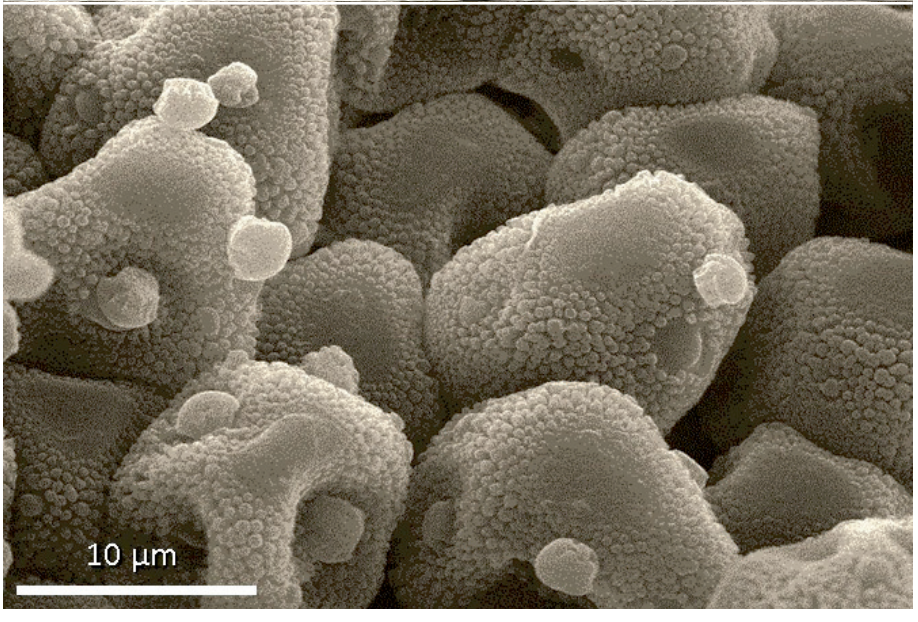

Fig. 6: Aeciospores of *Uromyces alpinus on Ranunculus* cf. *montanus* with smooth apical caps and large deciduous plugs. — **Aeciospore group A.**

Tab. 2: Aeciospore groups on host plants investigated in this study.

Host-species	Spore group						
	A	B	C1	C2	C3	D	E
Ranunculus							
R. aconitifolius	-	-	-	+	-	-	-
R. alpestris	-	-	+	-	-	-	-
R. auricomus	-	-	+	-	-	-	-
R. bulbosus	-	-	-	+	-	-	-
R. ficaria	+	-	+	-	-	-	-
R. lanuginosus	-	-	+	-	-	-	-
R. montanus	+	-	-	+	-	-	-
R. nemorosus	-	-	-	+	-	-	-
R. platanifolius	-	-	-	-	+	-	-
R. repens	+	-	+	+	-	-	-
Aconitum							
A. napellus	-	-	-	-	-	-	+
Aquilegia							
A. areata	-	-	-	-	-	-	+
A. vulgaris	-	-	-	-	-	-	+
Thalictrum							
Th. alpinum	-	-	-	-	-	-	+
Th. aquilegifolium	-	-	-	-	-	+	-
Th. flavum	-	-	-	-	-	+	-
Th. minus	-	-	-	-	-	-	+
Leucanthemum							
L. vulgare	-	+	-	-	-	-	-
Pulmonaria							
P. australis	-	+	-	-	-	-	-

visible in examination with the light microscope.

In group **C1**, the warts are rather large (up to 1,5 µm in diam.).

In group **C2**, the warts are smaller (up to 0,75 µm in diam.).

In group **C3**, the warts are similar to that in group C2, but the spores are slightly lager and the walls slightly thicker.

Group D: Spores with indistinctly zonate surface. Zones are nearly invisible in examination with the light microscope. Deciduous plugs are lacking.

Group E: Spores with azonate surface. Deciduous plugs are lacking.

Group A: Spore surface ornamentation trizonately patterned. *Zone 1* apically positioned, for the most part covered by a circular, smooth cap (Fig. 6 and 8). In a narrow band around the apical cap, fine warts are exposed. *Warts* about 0,3 µm in diam. *Zone 2* superequatorially positioned, broadly belt-shaped, more or less sharply distinguished from the apical zone by coarse warts and large plugs (Fig. 7 and 8). In contrast to the basal hemisphere, *warts* in this broad belt are not uniform in size and shape; besides small warts also warts up to 0,8 µm in diam. occur. *Plugs* have a hemispherical basis and a short, more or less cylindrical shank. They are inserted with the hemispherical basis in the spore wall. The shank is narrower than the hemispherical basis; its surface is ridged towards the basis (Fig. 8). The size of the plugs is (2,3) 3,0-3,4 µm in diam. Smaller plugs or intermediate bodies between plugs and large warts are scare. In mature spores the plugs are freely deciduous. Smooth, circular buldges are scars after plugs have dropped off. Plugs inserted in the wall show a narrow, dark ring around them. *Zone 3* more or less covering the whole basal hemisphere of the spore, uniformly, densely and finely verrucose (Fig. 7 and 8). *Warts* in this zone are similar to those in the apical zone.

Group A spores correspond to Savile´s type 5 spores. In this group, the surface structures of aeciospores can be used as good diagnostic criteria in identifying rust fungi with aecia on *Ranunculus*. Only the aeciospores of *Uromyces alpinus* and *U. rumicis* have walls with large freely deciduous plugs. It is remarkable that Gäumann (1959: 425) described the surface ornamentation of the aeciospores of *U. alpinus* as "finely and densely verrucose", but did not mention plugs. We examined material from Switzerland (ZT), which was tested by Gäumann and Terrier in inoculation experiments, and found in all specimens large plugs. Poelt & Zwetko

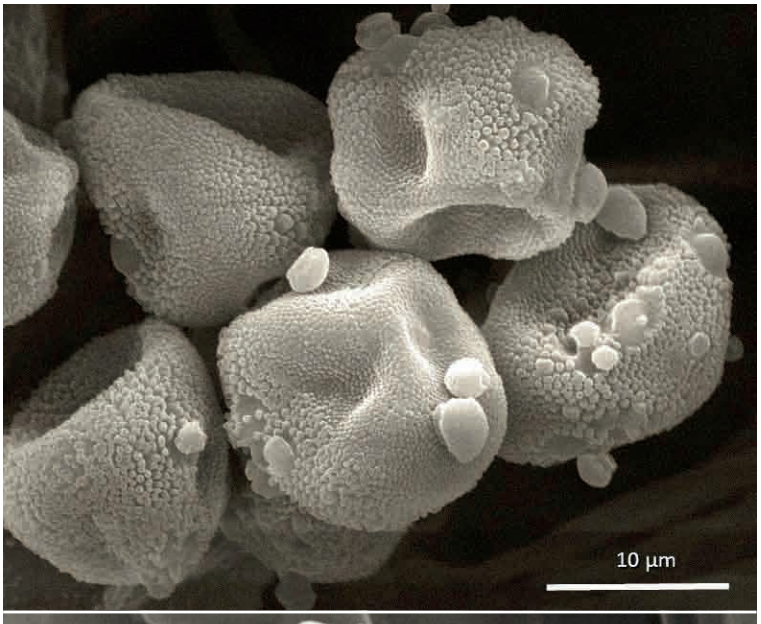

Fig. 7: *Uromyces* cf *alpinus* on *Ranunculus ficaria* showing scattered aeciospores. In spores with deciduous plugs and coarse warts, wall ornamentation of the basal spore hemisphere is distinctly different from that of the upper zones. — **Aeciospore group A.**

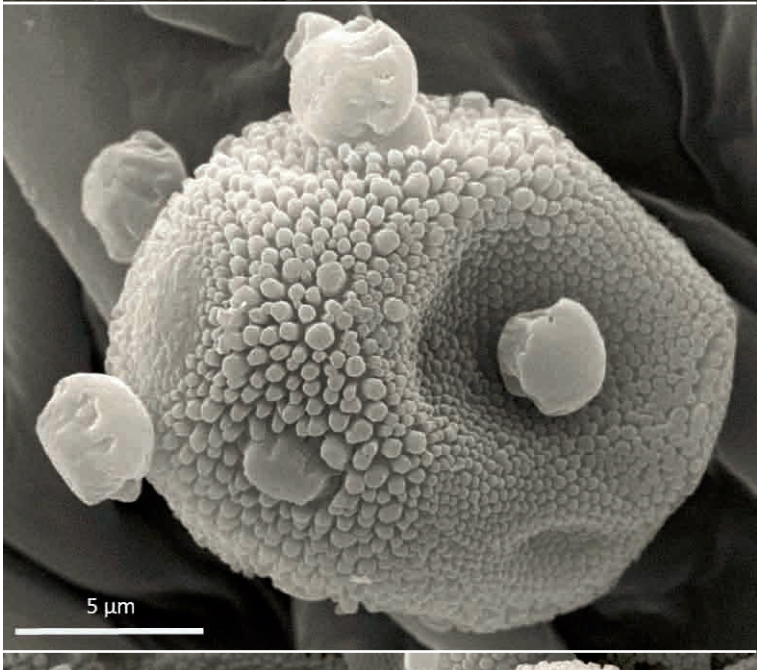

Fig. 8: Isolated aeciospore of *Uromyces alpinus* with a smooth apical cap, a broad belt with coarse warts and deciduous plugs and a finely verrucose basal spore hemisphere. — **Aeciospore group A.**

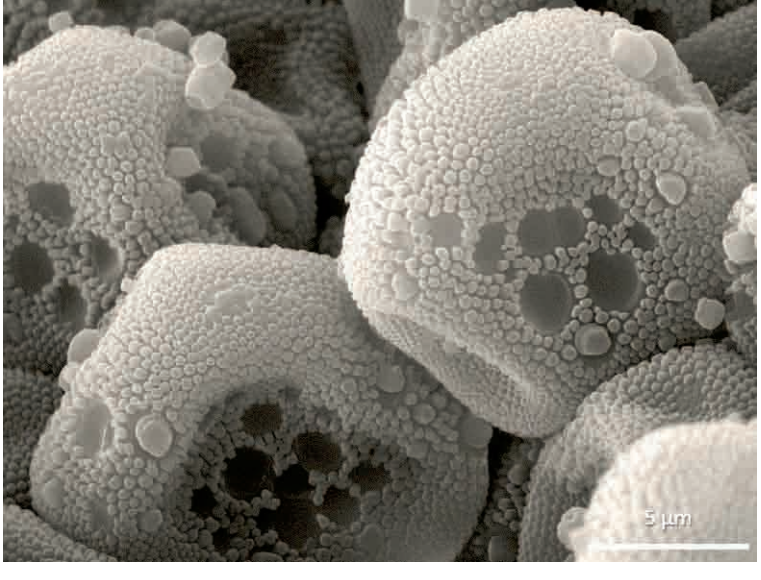

Fig. 9: Mature aeciospores of *Puccinia aecidii-leucanthemi* on *Leucanthemum vulgare* showing an apical hole in the centre of a finely verrucose area and broad belt with coarse warts and abundant deciduous plugs. — **Aeciospore group B.**

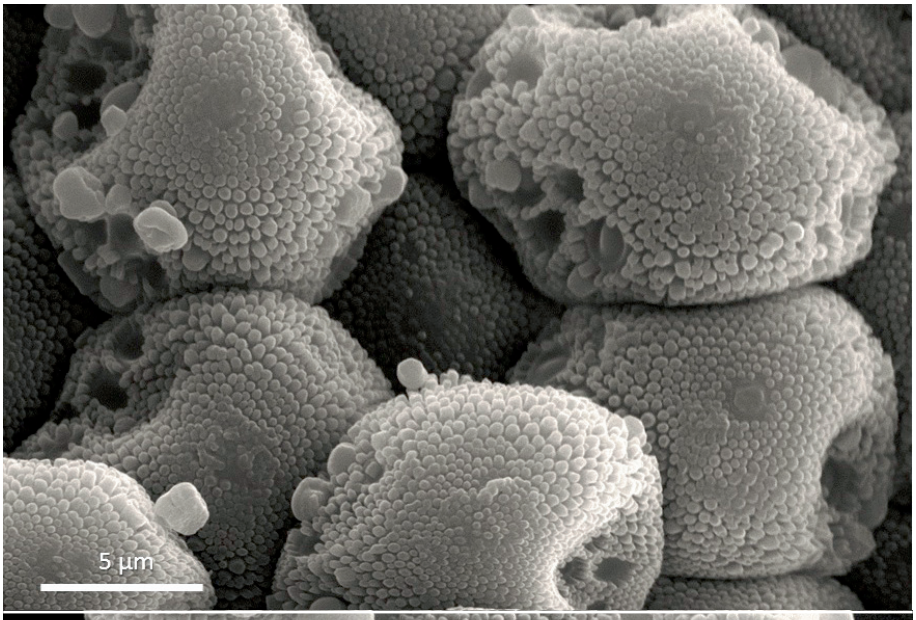

Fig. 10: Young aeciospores of *Puccinia aecidii-leucanthemi* on *Leucanthemum vulgare*. In young group B spores (*P. aecidii-leucanthemi),* the apical cap has a more irregular shape and disappears when spores are mature; then an apical hole becomes visible. — **Aeciospore group B.**

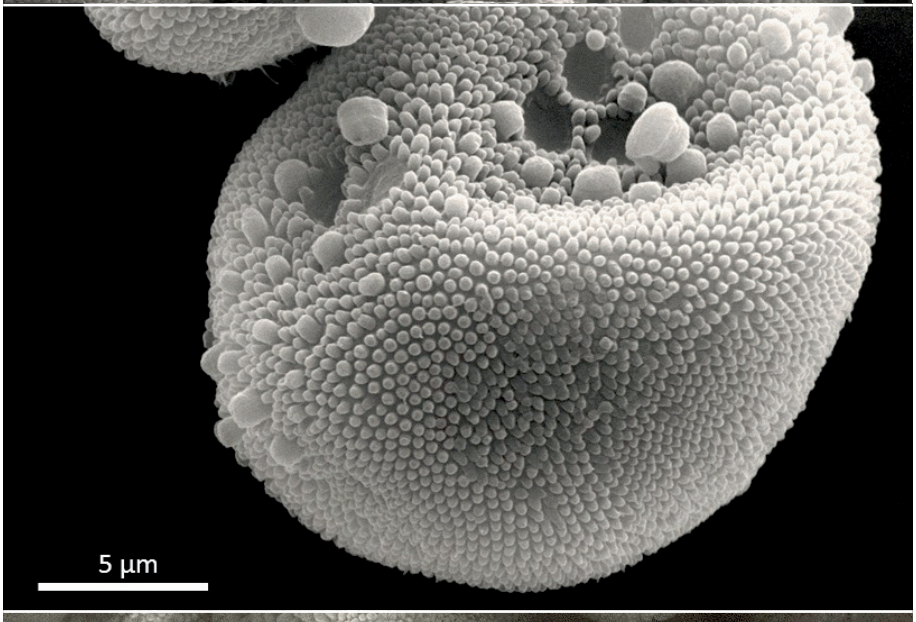

Fig. 11: *Puccinia bromina* ssp. *symphyti-bromorum* on *Pulmonaria australis* showing the uniformely and finely verrucose basal hemisphere and a belt of plugs of different size and shape. — **Aeciospore group B.**

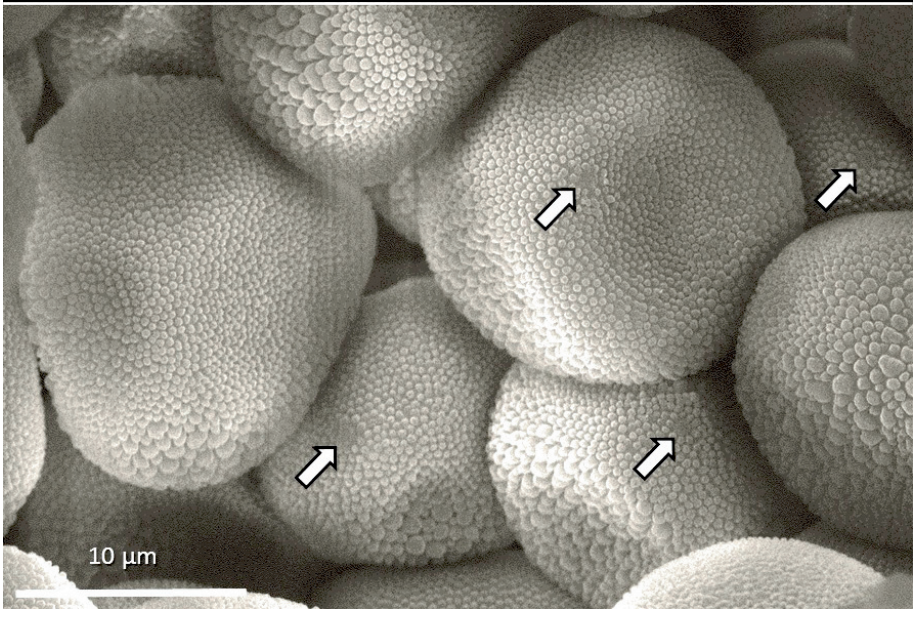

Fig. 12: *Uromyces cf poae* on *Ranunculus ficaria*: Finely verrucose apical zone with hole (arrow) and notedly coarse warts underneath. — **Aeciospore group C1.**

(1997) reported aecia on *Ranunculus repens* from Styria (Austria) with spores characterized by large deciduous plugs. They found uredinia and telia of *U. alpinus* at the same location. The aecia on *R. repens* did not differ morphologically from those of *U. alpinus* on *R. montanus* from Switzerland (ZT), which were tested by Gäumann and Terrier in inoculation experiments. Therefore, these aecia on *R. repens* can possibly be assigned to *U. alpinus*.

We also suppose that aecia on *R. ficaria* found on a typical *U. alpinus* site in Styria (Niedere Tauern, nutrient rich pasture wih *Rumex alpinus,* in about 1400 m) belong into the life cycle of this rust species. Teliospores of *U. alpinus* need moist conditions for eight days to germinate (Gäumann 1959: 429). That is why this rust occurs mainly on nutrient rich, moist sites in the (montane-)subalpine cloud belt of the Alps. *U. rumicis* occurs frequently on sites in the planar-colline-submontane altitudinal zone, but has rarely been found at greater altitudes (Poelt & Zwetko 1997). *R. ficaria* and *R. repens* have not been recorded as hosts of *U. alpinus* till now.

Group B: Spore surface ornamentation trizonately patterned. *Zone 1* positioned apically, finely and densely verrucose. *Warts* 0,3-0,4 µm in diam. A small circular area at the apex is free of warts. In its centre a hole surrounded by an annulus is visible (Fig. 9). The apex of young spores is covered by an irregular and shapeless layer, which disappears when spores are mature (Fig. 10). The layer probably consists of remains of the primary spore wall. *Zone 2* superequatorially positioned, broadly belt-shaped, more or less sharply distinguished from the apical zone by coarse warts and abundant small plugs. In contrast to the basal hemisphere, *warts* in this broad belt are not uniform in size and shape; besides small warts also larger warts occur. *Plugs* generally smaller, more abundant and more variable in size and shape than in group A spores. Plugs (0,65) 0,9-1,8 (2,5) µm diam. Shape of larger plugs is similar to that in group A spores. Smaller plugs are broadly conical to cylindrical and rounded or flattened at the top. Their hemispherical basis is strongly reduced. In mature spores the plugs are freely deciduous. Smooth, circular areas are scars, after plugs have dropped off. Plugs inserted in the wall show a narrow, dark ring around them. *Zone 3* more or less covering the whole basal hemisphere of the spore, uniformly, densely and finely verrucose. *Warts* in this zone are similar to those in the apical zone (Fig. 11).

Group B spores correspond to Savile´s type 3 spores. They are sharply distinguished from all group A and C spores. No specimens on members of Ranunculaceae investigated by us have group B spores, but specimens of *Puccinia aecidii-leucanthemi* on *Leucanthemum* and *P. bromina* ssp. *symphyti-bromorum* (*P. recondita* s.l.) on *Pulmonaria* show all characters of this group. Savile (1973) stated that *P. magnusiana* has type 3 aeciospores. *Ranunculus* has been reported as aecial host of *P. magnusiana* from Europe, Central Asia (Uljaniščev 1978) and China (Wang Yun-Chang & Zhuang Jian-Yun, 1998), but not from North America. Savile studied only two specimens of this rust species. His specimens probably have been collected in Europe. We have investigated aecia of *P. magnusiana*, which have been checked by Gäumann in inoculation experiments. We also studied aecia on *Ranunculus*, which have been found in close vicinity to *Phragmites*, and probably belong to *P. magnusiana.* All specimens examined by us have group C aeciospores, i.e. the spores possess no deciduous plugs. Therefore, reidentification of the specimens used by Savile (1973) will be required to clarify these differences.

Ranunculus has been reported as aecial host of *U. dactylidis* s.str. from Europe and North America. Savile (1973) studied six specimens of this rust species, all of them has type 3 aeciospores. Hence, *U. dactylidis* s.str. should be distinguishable from all other rust species producing aecia on *Ranunculus*. In contrast to Savile, Urban & Marková (2009: 244) stated that isolated findings of aecia on *R. bulbosus* and *R. repens* are rather abundant in central Europe, but it is not possible to say whether they really belong to the life cycle of *U. dactylidis* s.str, *U. festucae, U. poae* and *P. magnusiana*. Usually, the analyses of Savile are very exact, so we have to suppose that one rust species on *Ranunculus* has group B spores, and that it is *U. dactylidis* s.str.

Urban & Marková (2009) assigned following literature records to *U. dactylidis* s.str.: *Aecia* on *R. acris, R. aconitifolius, R. lanuginosus, R. polyanthemos* and *R. scleratus*. Based on observations in nature and experiments, *R. ficaria* and *R. auricomus* are no aecial hosts of *U. dactylidis* s.str.

Group C: Spore surface ornamentation trizonately patterned. *Zone 1* positioned apically, finely and densely verrucose. A small circular area at the apex is free of warts. In its centre a hole surrounded by an annulus is visible. *Zone 2* superequatorially positioned, broadly belt-shaped, more or less sharply distinguished from the apical zone by coarse warts. In contrast to the basal hemisphere, *warts* in this broad belt are not uniform in size and shape; besides small warts also warts up to 1,5 µm in diam. occur. Enlarged warts are broad conical to hemispherical and rounded or flattened at the top. *Zone 3* more or less covering the whole basal hemisphere of the spore, uniformly, densely and finely verrucose. *Warts* in this zone are similar to those in the apical zone.

Group C spores correspond to Savile´s type 2 spores. Most specimens on *Ranunculus* investigated in this study have group C spores, among them all specimens of *P. magnusiana*. The wall ornamentation of this rust species appears to vary between Group C1 and 2.

Group C1: Coarse warts (0,6) 0,7-1,5 µm in diam. (Fig. 12). One has to be careful. Sometimes, warts of immature spores are coarser in appearance than warts of mature spores (Fig. 13 and 14).

Two specimens on *Ranunculus repens* (Cryptogamae exsiccatae Museo Hist. Natur. Vindobonensi 1305;

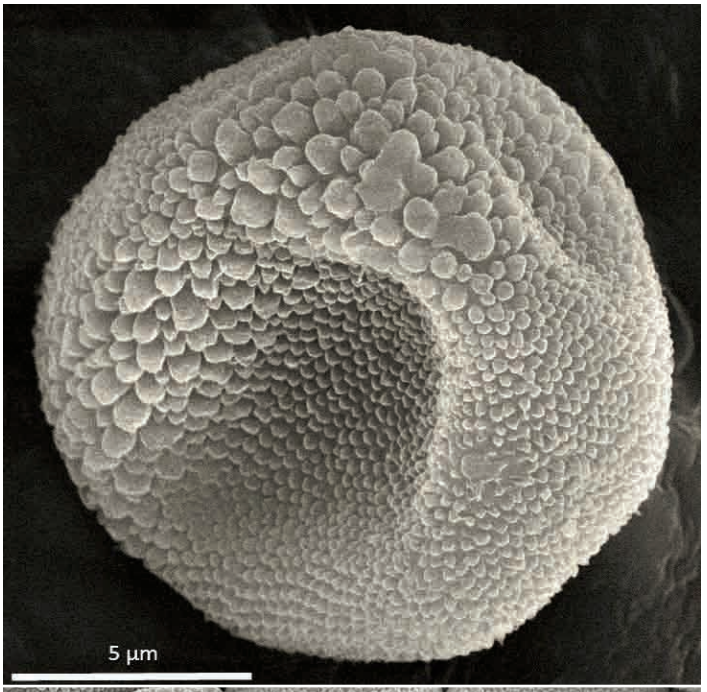

Fig. 13 : *Uromyces* cf *poae* on *Ranunculus ficaria*: Warts of immature spores are coarser in appearance, because the parts of the primary wall are spread over the larger warts. — **Aeciospore group C1.**

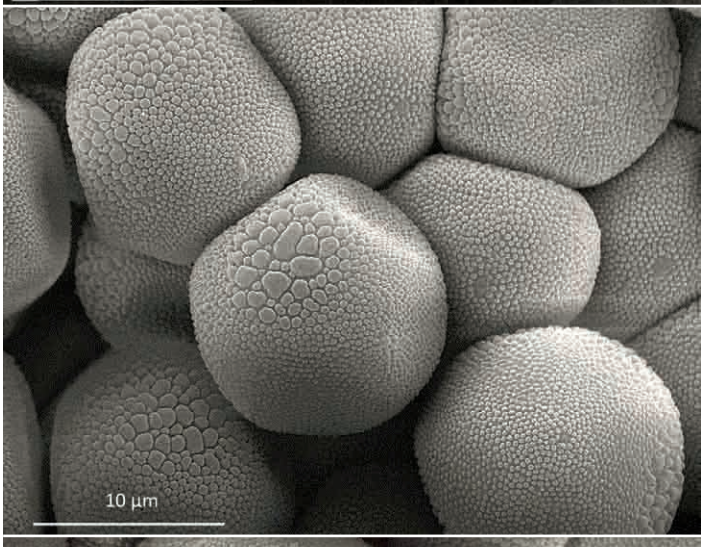

Fig. 14: *Uromyces* cf *poae* on *Ranunculus ficaria*: Young, angular spores showing compact warts and crusts. — **Aeciospore group C1.**

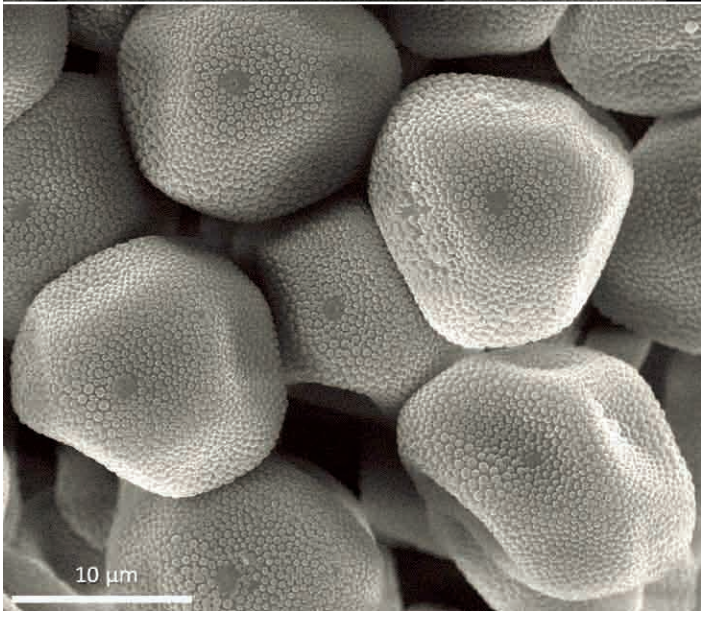

Fig. 15: *Puccinia magnusiana* on *Ranunculus repens*: Young, angular spores showing apical zone with hole and a belt with coarse warts. — **Aeciospore group C2.**

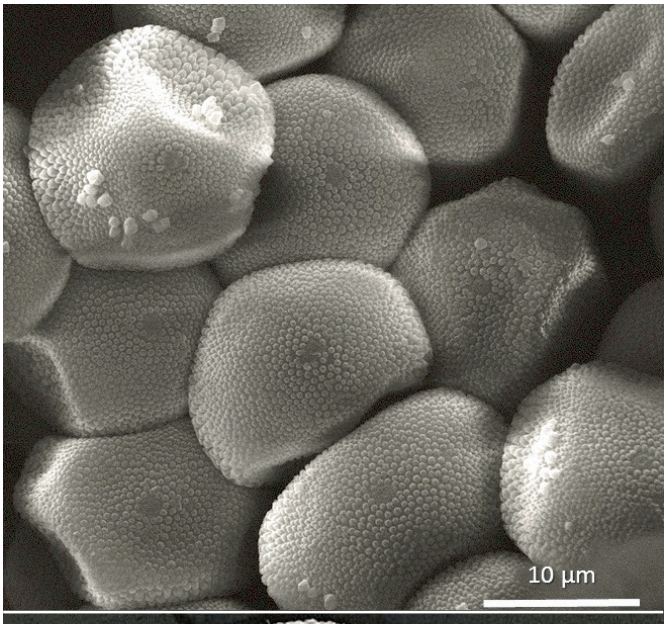

Fig. 16: *Uromyces dactylidis* f.sp. *platanifolii-dactylidis* on *Ranunculus platanifolius*: Spores with uniformly small warts in the apical zone and coarse warts underneath. Several warts have been detached by the preparation. — **Aeciospore group C3.**

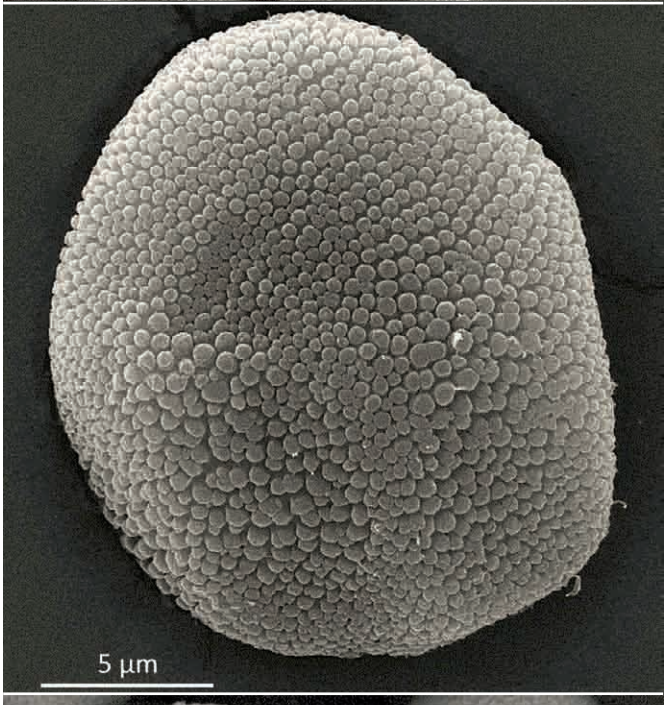

Fig. 17: *Puccinia recondita* s.l. on *Thalictrum aquilegifolium*: Upper und lower zones with fine warts, middle zone with coarse warts, but less distinct when compared to group C. — **Aeciospore group D.**

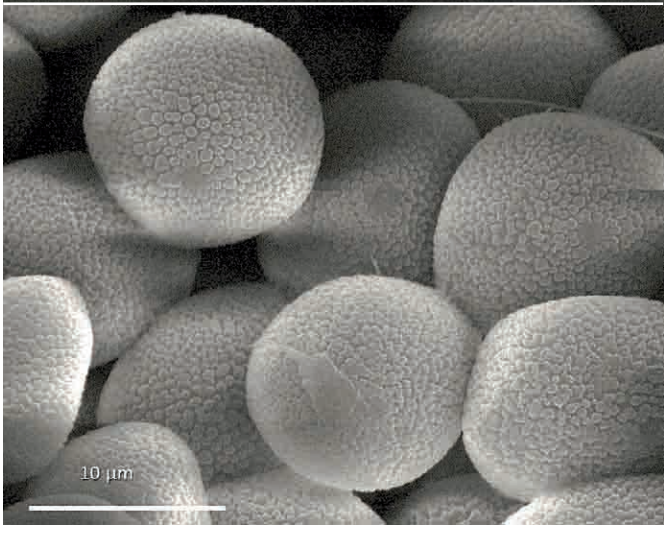

Fig. 18: *Puccinia recondita* s.l. on *Aquilegia vulgaris* with notedly coarse warts all over the spore surface. — **Aeciospore group E.**

Sydow, Uredineen 402) and two on *R. ficaria* investigated in this study have group C1 spores. The aecia on *R. repens* probably belong to the life cycle of *Puccinia magnusiana*, that on *R. ficaria* to the life cycle of *Uromyces poae*. Photos produced in examinations with the light microscope are published by Holm (1964: 106-107). They show aeciospores of *U. poae* on *R. ficaria* with belts of rather coarse warts. Holm (1967) was placing aeciospores of *P. poae* in his type 2 (warts ≥ 1 µm, < 2µm). His results fit to our observations. In the Czech and Slovak Republics *U. poae* has been reported on *R. auricomus, R. bulbosus, R. ficaria* and *R. repens* in lower altitudinal belts (Urban & Marková 2009:). According to infection experiments and observations in nature in Europe, *R. auricomus* seems to serve as aecial host only for *U. poae* (Urban & Marková 2009: 266). The spores in the specimen on *R. auricomus* investigated in this study have rather coarse warts. This rust has been determinated as *U. poae* f. sp. *auricomi-pratensis*. Our results confirm this identification.

The specimens on *R. alpestris* and *R. lanuginosus*, both having group C1 spores, could not be assigned to any perfect rust taxon with certainty.

Group C2: Coarse warts 0,5-0,75 µm (Fig 15).

Within group C2, the surface structures of aeciospores can not be used as good diagnostic criteria in identifying rust species. Savile (1973) reported type 2 aeciospores on *Ranunculus* for *P. perplexans* (*P. recondita* s.l.), *U. alopecuri* (*U. dactylidis* s.l.), *U. festucae* (*U. dactylidis* s.l.) and some rusts that appear to be *U. poae* (*U. dactylidis* s.l.), which has type (1–) 2 spores.

Most specimens of *P. magnusiana* investigated by us have group C2 spores. In the Czech and Slovak Republics aecia of *P. magnusiana* on *R. bulbosa* and *R. repens* occur rather late, mostly in May and during June (Urban & Marková 2009: 159). Aecia of *U. festucae* appear in May on *R. bulbosus* and *R. illyricus*. Marková& Urban (1998) have reported only one *Ranunculus*-species, *R. acer* and its subspecies *stevenii*, as an aecial host of *P. perplexans* (*P. recondita* s.l.) from Europe. In the Czech and Slovak Republics aecia appear from the end of April and are still present in the first mid-June. (Urban & Marková 2009: 172).

Group C3: Wall ornamentation resembling that of group C2 spores, but spores slightly larger and walls slightly thicker (Fig. 16).

U. dactylidis s.str. is reported to show six formae speciales (Gäumann 1959), one of them, f. sp. *platanifolii-dactylidis* occur only on white-flowering *Ranunculus*-species. This f. sp. has group C3 aeciospores, i.e. rather large (24-30 µm long) and thick-walled (1,5 µm thick) spores without deciduous plugs. The aeciospores of forma typica are distinctly smaller (18-22 µm long) and thin-walled (less than 1 µm thick). According to Gäumann (1959), *R. platanifolius* does not serve as host of any other taxon than *U. dactylidis* f. sp. *platanifolii-dactylidis*. The taxonomic status of this specialised form has to be reinvestigated.

Group D: Spores resembling those of group C except that the zones are nearly invisible in examination with the light microscope. The warts in the coarse belt are less enlarged and less diverse than in group C. Nevertheless, the pattern of surface zonation is of the same kind in group A, B, C and D: First a finely and densely verrucose, circular, apical zone, then a broad belt with larger and more diverse surface sculptures and again a finely and densely verrucose, basal zone. A small circular area at the apex is free of warts. In its centre a hole is visible.

Group D spores do not wholly correspond to Savile´s type 1 spores. In our investigation, no specimen on *Ranunculus* has group D spores. In contrast to our results, McCain et al. (on-line specimen documentation) listed several specimens of *P. recondita* s.l. on *Ranunculus* from North America all having type 1 spores.

In specimens on *Thalictrum aquilegifolium* and *Th. flavum* investigated by us, the spores are less conspicuously zonate than in specimens of group C spores, but still zonate (Fig 17). Group D spores resemble indistinctly zonate group C spores. Savile (1973) assigned them all to type 1, but SEM analyses show that they are intermediate between type 1 and 2. Gold et al. (1979: 79, fig.17) published SEM-photos of aeciospores of *P. triticina* s.str. on *Th. speciosissimum*. A circular, finely verrucose area at the apex of the spores surrounded by a broad belt with distinctly larger warts is recognizeable.

Wall ornamentation of aeciospores on *Th. aquilegifolium*, *Th. flavum* and *Th. speciosissimum* appears to be very similar. The latter is the aecial host of the important wheat leaf rust, *P. triticina* (s.str.). In inoculation experiments, *P. triticina* produces aecia on more than 30 *Thalictrum* species (Gäumann 1959), e.g. *Th. alpinum*, *Th. aquilegifolium*, *Th. flavum* and *Th. minus,* but in central and eastern Europe host alternation does not occur (Blumer 1963, Urban & Marková 2009). Aeciospores of *P. borealis* (*P. recondita* s.l.) on *Th. alpinum* and *P. recondita* s.l. on *Th. minus* investigated by us differ from those of *P. triticina* on *Th. speciosissimum* by azonate spore surface.

Group E: Spores azonate, more or less uniformly verrucose. The warts tend to enlarge on the whole spore surface (Fig. 18 and 19). In the specimen on *Aquilegia vulgaris*, rather coarse warts are predominant on the whole surface. Warts 0,5-0,6 µm in diam. In the other specimen, the warts are smaller, slightly smaller on *A. atrata* (0,4-0,5 µm in diam), distinctly smaller on *Aconitum* and *Thalictrum* (Fig. 20 and 21). In the specimen on *Th. alpinum* the warts are 0,3-0,4 µm in diam. A small circular area at the apex is free of warts. In its centre a hole is visible.

We found group E spores on the genera *Aconitum, Aquilegia* and *Thalictrum*, but not on *Ranunculus*. All specimens investigated by us belong to the *P. recondita* species complex. Group E spores are the fourth morphologically different group of aeciospores within this broad species complex.

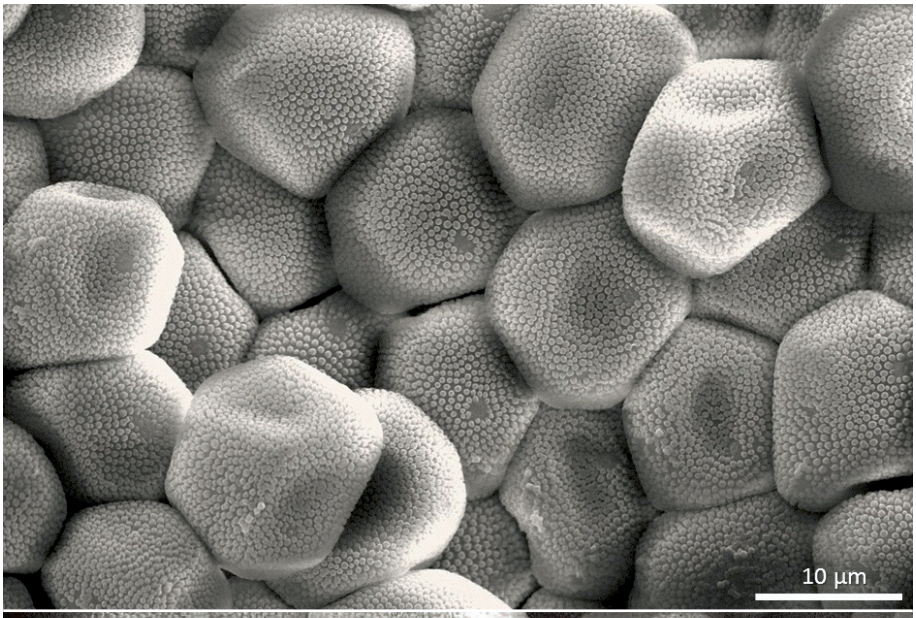

Fig. 19: *Puccinia* c.f. *scarlensis* on *Aquilegia atrata* with coarse warts all over the spore surface. — **Aeciospore group E.**

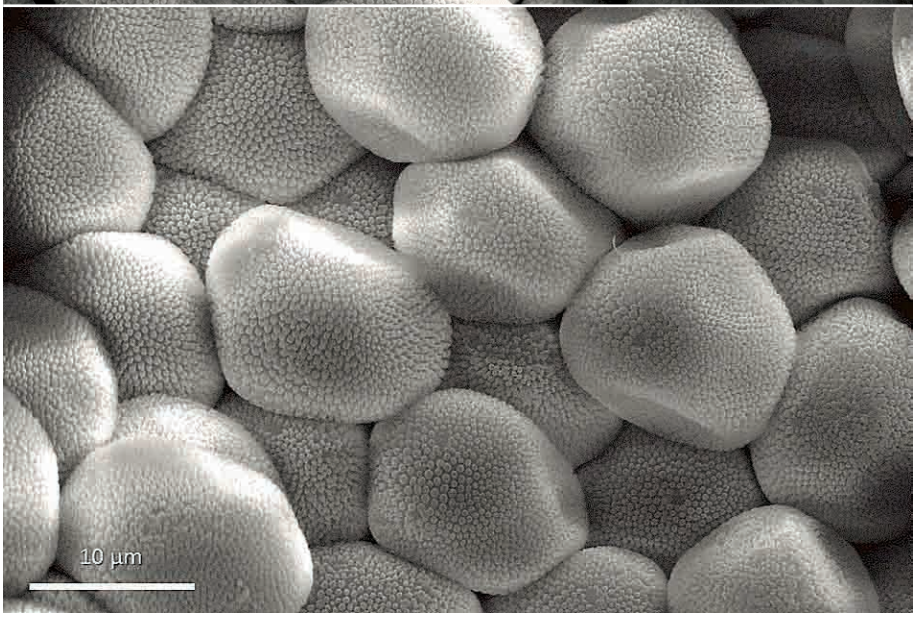

Fig. 20: *Puccinia borealis* on *Thalictrum alpinum*: Aeciospores with azonate surface corresponding to Savile´s type 1 spores. — **Aeciospore group E.**

In the specimen on *Aquilegia vulgaris* investigated in this study, spores correspond neither to Savile´s type 1 nor to type 2 spores, because rather coarse warts are predominant on the whole surface, even close to the apical hole. Savile (1973: 233) drew an illustration of type 1 spores of *Puccinia andropogonis*; the warts in his illustration are rather dense and fine; they are similar to those on the basal hemisphere of group A, B and C spores. He noted that in type 1, the warts are either uniformly small or a mixture of large and small. The warts in spores on *Aquilegia vulgaris* are rather uniformly coarse in appearance.

Among all specimens investigated by us, those on *Th. alpinum* and *Th. minus* match most closely Savile´s type 1. *Th. minus* has been listed as the aecial host of at least five rust taxa by Marková & Urban (1998): *P. persistens* ssp. *persistens*, *P. persistens* ssp. *agropyri* var. *agropyrina*, var. *bromi-erecti* (= *P. alternans*), var. *thalictri-poarum* and var. *borealis* (= *P. borealis*). *Th. alpinum* has only been recorded as the aecial host of *P. persistens* var. *borealis*. Savile (1973) classified the aeciospores of this taxon as type 2, and separated *P. borealis* from *P. recondita* s.l. While Holm (1967) was placing aeciospores of *P. borealis* in his type 1 (warts < 1µm).

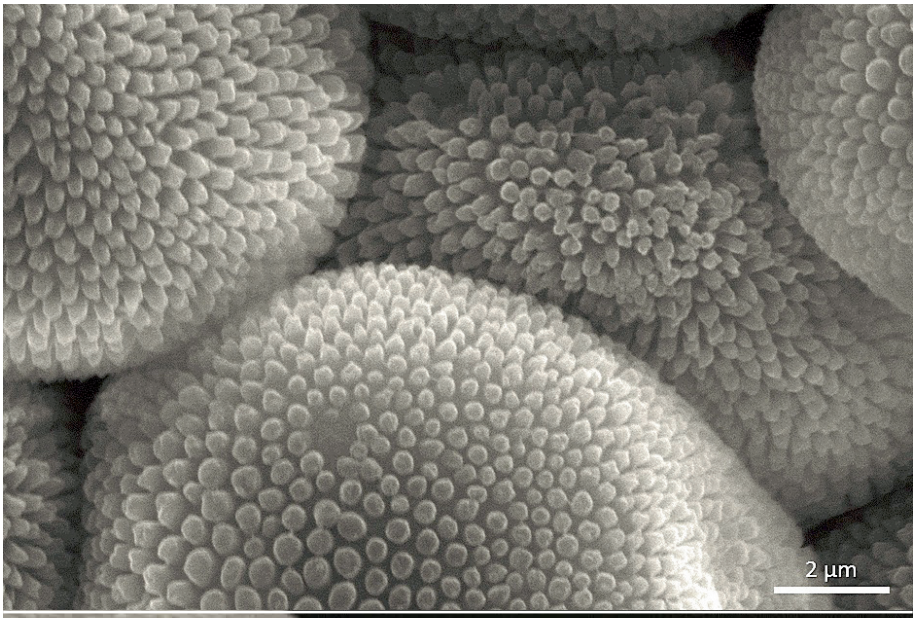

Fig. 21: *Puccinia borealis* on *Thalictrum alpinum*: Warts conical, with truncated tips. — **Aeciospore group E.**

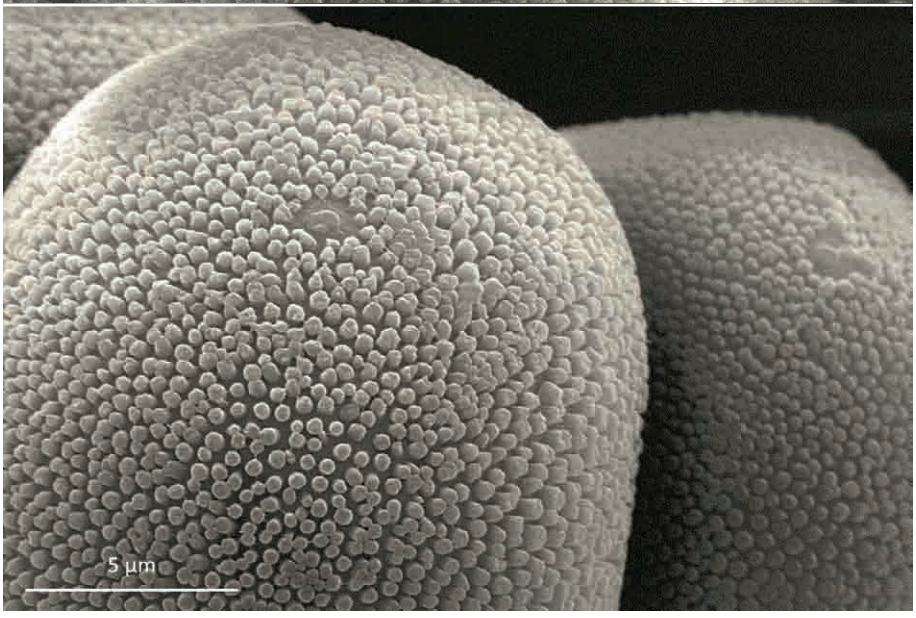

Fig. 22: *Puccinia recondita* s.l. on *Thalictrum minus*: Aeciospores with azonate surface corresponding to Savile´s type 1 spores. — **Aeciospore group E.**

Our results confirm the dimensions observed by Holm.

P. persistens s. Marková & Urban (1998) is a broad rust complex within the *P. recondita* species complex. It includes several rusts with aecia on Ranunculaceae (e.g. *Aconitum, Aquilegia, Ranunculus* and *Thalictrum*) and Boraginaceae. Gäumann (1959) assigned this rusts to different "Formenkreise" and species. Several methodes have been applied to reliably differentiate members of this species complexes, e.g. inoculation experiments, isozyme banding patterns of germling urediniospores (Burdon & Roelfs 1985; Swertz 1994), germling morphology of urediniospores (Swertz 1994), shapes of teliospores stated by dividing the arithmetic mean of spore length by the mean of the lower cell width (Marková & Urban 1998), selfing of individual collections and crossing experiments, flow cytometry to estimate the nuclear DNA content of pycnospores and basidiospores, video image analyses for the measurement of dimensions and of spore areas of the teliospores, basidiospores, aeciospores and urediniospores (Anikster et al. 1997; Ben Yehuda et al. 2004), DNA analysis (first results published by Zambino & Szabo 1993). Nevertheless, the problem »Who´s Who?«

Provisional key to rust species in the aecial stage on *Ranunculus*:

1a Rusts with group A spores ..... ***Uromyces alpinus***, ***U. rumicis***

1b Rusts with group B spores ..... ***Uromyces dactylidis*** s.str.*

1c Rusts with group C spores

2a Spores 18-24 (26) µm in diam., wall thickness 1 µm or less **3**

3a Occurs usually in the early spring ..... ***Puccinia perplexans*****, ***Uromyces alopecuri****, ***U. festucae****, ***U. poae****

3b Occurs usually at the end of spring (in vicinity to *Phragmites*) ..... ***Puccinia magnusiana***

2b Spores (24) 25-26 (30) µm in diam., wall thicker (about 1,5 µm) ..... ***Uromyces dactylidis*** f.sp. ***platanifolii-dactylidis***

1d Ornamentation of spore surface insufficiently known **4**

4a Spores 18-24 µm in diam., wall about 1 µm thick ..... ***U. agrostidis***, ***U. phlei michelii***, ***U. poae-alpinae***

4b Spores 21-28 µm in diam., wall thicker (1,5-2 µm) ..... ***Uromyces ranunculi-distichophylii***

*According to Savile (1973). ** According to Savile (1973) and Marková & Urban (1997 Editum 1998).

(Szabo, Anikster & Marková 2004) remains unsolved for several rust taxa within the species complex.

In the present study four morphologically different groups of aeciospores have been recognized in *P. recondita* s.l. (group B, C, D, and E). These results confirm the expectation that aeciospore ornamentation patterns are an additional character for the taxonomic classification of leaf (brown) rusts.

SEM studies of spore surface structures support the interpretation of what can be seen in the light microscope. They also allow to detect even structures too small to be seen with this instrument. However, to fully understand spore structures even on their outside, detailed knowledge of the spore ontogeny is necessary. For this, analyses of cut material with the aid of a transmission electron microscope are indispensable. Though DNA analyses help escpecially to check the natural relationship of organisms, host specificity and morphological characters as spore ornaments easily accessible by light microscopy and SEM allow to sort and understand rust fungi in the first instance.

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