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PUCCINIA POARUM IN CZECHOSLOVAKIA AND EUROPE

Z. URBAN* & J. MARKOVÁ*

ABSTRACT. *Puccinia poarum* Nielsen in Czechoslovakia and Europe is a complex of two obligately heteroecious, ecologically and biologically distinct populations. In one of them teliospores quickly germinate during the season; aecia begin to appear in May, with a second generation being produced from August to November. This population is confined to *Tussilago farfara* and *Poa* sp. div. and is recognized as *P. poarum* var. *poarum*. The other variety, *P. poarum* var. *petasiti-pulchellae* (Lüdi) comb. et stat. nov., produces only overwintering teliospores, the last aecia being produced in August. This variety is currently known on the following hosts: *Petasites* sp. div. (? also *Tussilago farfara*), and *Agrostis alba, Festuca carpatica, F. pulchella, Melica nutans, Milium effusum* subsp. *alpicola, Phleum michelii, Poa alpina, P. nemoralis* and *P. pratensis* subsp. *angustifolia*.

The genetic connection of *Aecidium tussilaginis* Pers. to the rust fungus on *Poa* sp. div. was made by Nielsen (1877) in an experiment with *Poa annua*†, *P. nemoralis, P. palustris* (syn. *P. fertilis*) and *P. trivialis*. Plowright (1889) obtained similar positive, cross-infection results with *Poa annua*. Later, in experiments by Tranzschel (1910), aecia developed on *Tussilago farfara* following inoculations using teliospores from *Poa nemoralis* var. *firmula* Gaud. (near Leningrad); by contrast, *Petasites hybridus* remained free of infection. Spores of *Aecidium tussilaginis* gave rise to infections on *Poa alpina, P. annua, P. nemoralis, P. palustris, P. pratensis* and *P. trivialis* in the studies of Klebahn (1908); the heaviest infections occurring on *P. trivialis*. In Norway, Jørstad (1932) experimentally established the obligatory heteroecism of the rust on *Poa pratensis*, and made many observations about the close connection of *Aecidium tussilaginis* with rust on *Poa alpina, P. nemoralis, P. pratensis* and *P. trivialis* in nature. In Switzerland, Mayor (1940) searched herbaria for host plants of *Puccinia poarum* and listed the following species: *Poa alpina, P. annua, P. bulbosa, P. chaixii, P. nemoralis, P. palustris, P. pratensis* and *P. trivialis*. Simultaneously, Mayor confirmed the absence of uredial capitate, thick-walled paraphyses in *Puccinia poarum*—as had already been reported by Nielsen, Plowright, and Jørstad. Further experiments were published by Dupias (1943) and Guyot (1944); the latter succeeded in obtaining very heavy infections on *Poa annua* and *P. bulbosa* but only light infections on *Poa pratensis, P. compressa* and *P. nemoralis*. The experiments with uredospores by Eriksson (1923) are not reliable, for he mentions numerous clavate paraphyses in the uredia.

Nielsen (1877) noted that in Denmark some teliospores germinate immediately whereas the others, produced later, overwinter, and fresh aecia are produced on *Tussilago farfara* until late in the season. Similarly, Plowright (1889) in Britain characterized this species as unusual in having two aecial generations in the course of one year. The same idea was repeated by Wilson & Henderson (1966) who wrote in more detail: 'The earlier crop [of aecia] begins to appear in May, and is followed by the

*Department of Botany, Charles University, Benátská 2, 128 01 Praha 2, Czechoslovakia.
†For phanerogams, authorities are not cited where they follow *Flora Europaea* (1964–80).

uredo- and teleutospores on the leaves of *Poa*; these germinate quickly and the second crop of aecidia is produced about August, and the second generation of teleutospores may be found on *Poa* from October'. The same features on the life-cycle of this rust were also observed by Lagerheim (see Vestergren, *Microm. rar. sel.* no. 685; Lind, 1913). In Finland, aecia appear in June and July, or later (as in Helsinki) and continue to occur until October (Liro, 1908; Rauhala, 1959). In Norway, aecia were collected from mid-May to mid-October; most collections being made between June and August (Jørstad, 1936, 1940, 1951, 1964 p. 36). In Estonia and Latvia, aecia were gathered even in mid-September (Bucholtz, 1905; Arefjev, 1916); according to these authors, teliospores germinate directly, throughout the season.

From Poland there are numerous records of aecia collected in September and October: Wysokie Tatry Mts, Pieniny Mts (Wróblewski, 1922; Rouppert, 1912), near Rzeszów (Stec-Rouppertowa, 1935), near Jaslo (Wodziczko, 1911), near Sandomierz (Romaszewska-Sałata, 1981), Wyżyna Lubelska and Lublin (Romaszewska-Sałata, 1974, 1977), near Warszawa (Majewski, 1965, 1967), and near Poznań (Dominik, 1935). The records of Wróblewski (1922) from Zaleščiki in the Ternopol region and the region of Lvov now pertain to the USSR.

In the German Democratic Republic, aecia were collected in September and October in Mecklenburg and Thüringen (Buhr, 1958). In the German Federal Republic, aecia were found as late as mid-November in Oldenburg (Niedersachsen) and Bavaria (Buhr, 1958; Paul, 1917, 1919; Poeverlain & Schoenau, 1929). In Rheinland, aecia were found from June to late September (Brandenburger, 1972). In Rumania, many collections were made from mid-May to mid-October (Săvulescu, 1953). In the Mecsek Mts of Hungary, aecia were found in September (Vass & Tóth, 1958). Collections of fresh aecia are recorded from May to late September in Switzerland (canton Neuchâtel) and France (Isère, Haute Garonne, Hautes Pyrénées, Puy-De-Dôme, Normandie: Mayor, 1958; Kuhnholtz-Lordat, 1937; Rayss, 1933; Dupias, 1951, 1962; Buhr, 1958).

According to the collecting dates of herbarium specimens and to the literature, *Aecidium tussilaginis* in Czechoslovakia occurs with the following frequency per half-month:

	May		June		July		August		Sept.		Oct.		Nov.	
half:	1.	2.	1.	2.	1.	2.	1.	2.	1.	2.	1.	2.	1.	2.
	2	11	15	16	4	8	9	4	9	13	11	1	6	–
total:	13		31		12		13		22		12		6	

According to approximate heights of localities, *Aecidium tussilaginis* predominates in lowland and hilly districts (to 500m). Twenty records derive from the submontane belt (880–1100m; Stratenská hornatina Mts, Slovenské rudohorie Mts, Vysoké and Nízké Tatry Mts, Malá Fatra Mts, Slavkovský les Mts, Šumava Mts, Brdy Mts, Českomoravská vrchovina highland) and seven records from the montane–supramontane belts (1000–1500m; Vysoké and Nízké Tatry Mts, Belianské Tatry Mts, Hrubý

Jeseník Mts). The only record from the subalpine belt (1400–1800m) is from Kežmarská chata chalet in Vysoké Tatry Mts.

Puccinia poarum was originally described as a heteroecious rust on *Tussilago farfara* and *Poa* sp. div. However, early cross-infection experiments showed that in nature other genetic connections can occur (Lüdi, 1917; Mayor, 1918; Gäumann, 1941). For example in the Alps, the rust fungus on *Festuca pulchella* alternating with *Petasites* sp. div. can also infect some species of *Poa*. In experiments this rust produced only spermogonia on *Tussilago farfara*. Gäumann (loc. cit.) described several new rust species having their monokaryotic phase on various Swiss species of *Petasites* and their dikaryotic phase on various grass genera: *Puccinia petasiti-poarum* on *Poa nemoralis* and *P. palustris*; *Puccinia petasiti-melicae* on *Melica nutans*; *Puccinia taminensis* on *Phleum michelii*; *Puccinia kummeri* on *Agrostis stolonifera*.

In Czechoslovakia there are records of a rust fungus similar to *Puccinia poarum* on *Festuca carpatica* from Vysoké and Belianské Tatry Mts, and on *Milium effusum* subsp. *alpicola* from Nízké Tatry Mts (Urban, 1966a). All known localities are situated in the montane–subalpine belt (1000–1800m) and the alternating host was not experimentally confirmed. The rust on *Festuca carpatica*, II+III, in Belianské Tatry Mts was gathered together with *Aecidium tussilaginis* on 7 July 1959; two other collections from the same valley (31 vii 1959 and 7 viii 1960) could be connected with either *Petasites* sp. div. or *Tussilago farfara*. *Petasites albus* is very probably the alternate host for the rust on *Milium effusum* in the Nízké Tatry Mts; after a thorough search at the *locus classicus* on 14 August 1986 the first author discovered remnants of two aecial groups on a well-rotted leaf, and other aecial remnants were found on the periphery of two perforations in a still green leaf.

Aecidium petasitis P. & H. Sydow seems to occur, by comparison with *A. tussilaginis*, with more sporadic occurrence. According to the literature it is known from S Sakhalin on *Petasites amplus* Kitam. (Hiratsuka, 1931) and from Kamchatka on *P. frigidus* (Azbukina, 1963). *A. petasitis* is further reported on the last mentioned and other species, such as *Petasites tomentosum* (Ehrh.) DC., *P. laevigatus* (Willd.) Reichenb. and *P. hybridus* (syn. *P. officinalis* Moench), from: Karelo-Finnish SSR, lower Yenisei River, Tartar, Bashkir and Komi ASSR; the regions of Omsk, Sverdlovsk, Kirov, Gorki, Voronezh and Stanislav; Latvian SSR; the crimean Krasnodar region and Georgian SSR (Tranzschel, 1939; Uljaniščev, 1960; Voronichin, 1927; Wróblewski, 1913; Bucholtz, 1905; Arefjev, 1916). It is, as yet, unknown in Scandinavia. On the Baltic coast its occurrence seems to be scarce: aecia were found in Mecklenburg on *Petasites spurius*, and in Schleswig-Holstein on *P. hybridus* (Klebahn, 1914). From Denmark there are records on *P. albus* (Lind, 1913, p. 309) and *P. hybridus*, but Nielsen (1877) considered this *Aecidium* to be rare. It seems that in Germany the occurrence of aecia increases in the hilly and higher altitudinal belts: Saxen and Rheinland (on *Petasites hybridus*), Bavaria (on *P. albus, P. hybridus, P. niveus* Baumg.); see Klebahn (1914), Paul (1917, 1919), Poeverlein & Schoenau (1929), and Poeverlein (1940). Similarly, in Switzerland this *Aecidium* is relatively frequent on *P. albus* and *P. niveus*;

on both hosts it ascends to relatively high altitudes, e.g. Berner Oberland 1900m (Ivanoff, 1907; Lüdi, 1917; Mayor, 1918, 1963; Oefelein, 1969). From France we have only one record, from the Massif Central, Puy-De-Dôme, lake Pavin, on *Petasites albus,* 25 vii 1928 (Rayss, 1933). From the same locality *Aecidium tussilaginis* is also recorded, but four years later on 30 August 1932 (Rayss, 1933). *Aecidium petasitis* is relatively common in the Polish Wysokie Tatry Mts on *Petasites hybridus* and *P. albus* (Wróblewski, 1922; Stec-Rouppertowa, 1935). In Rumania, aecia are common on *P. albus, P. kablikianus, P. niveus* and *P. hybridus* in the submontane and montane belts of the Transylvanian Alps (Săvulescu, 1953). In Bulgaria, Chinkova (1959, p. 59) considered *Aecidium petasitis* on *P. albus, P. hybridus* and *P. kablikianus* to be one of the most frequent rusts in the altitudinal belt of beech forest (800–1100m; see also Chinkova, 1978), although it has now been found up to 1600m. In Yugoslavia the rust occurs on *Petasites albus, P. hybridus* and *P. kablikianus* (Ranojević, 1899; Picbauer, 1930, 1932) in similar montane to submontane conditions. Concerning the dates from the SE countries, Henderson (1963, sub *P. poarum*) recorded *Aecidium petasitis* on *P.*

TABLE 1

Occurrences of *Aecidium petasitis* in Czechoslovakia

May	June	July	August	Annotation
26 v				*P. albus,* Beskydy Mts, I closed, c.500m
	2 vi			*P. hybridus,* Turnov, c.250m
	6 vi			*P. albus,* Stratenská hornatina, c.700–900m
	9 vi			*P. albus,* Stratenská hornatina, c.550m
	10 vi			*P. albus,* Malá Fatra Mts, 300–600m
	12 vi			*P. albus,* Levočské pohorie Mts, c.700m
	13 vi			*P. hybridus,* Žďár n. Metují, c.400m
	20 vi			*P. albus,* Bukovské vrchy Mts, Riaba skala, c.600m
	26 vi			*P. albus,* Křížová-Štíří důl (Havlíčkův Brod), c.600m
		7 vii		*P. kablikianus,* Protež chalet in Belianské Tatry Mts, c.1300m
		14 vii		*P. kablikianus,* at the same place
		23 vii		*P. albus,* Vysoké Tatry Mts, Tristarský důl valley, c.1000–1500m
		vii		*Petasites* sp., Vysoké Tatry Mts, Malá studená dolina valley, 1500–2000m
		vii		*P. albus,* Králický Sněžník Mt, c.550m
		vii	viii	*P. albus,* Vysoké Tatry Mts, 750–1700m
			6 viii	*Petasites* sp., Nízké Tatry Mts, Vernár, c.900m, I obsolete + (II) + III on *Poa nemoralis*
			7 viii	*P. hybridus,* Vysoké Tatry Mts, Temnosmrečinová dolina valley, c.1500m
			14 viii	*P. albus,* Nízké Tatry Mts, Trangoška chalet, I very obsolete on rotten leaves + (II) + III on *Milium effusum,* 1120m
			20 viii	*P. albus,* Orlické hory Mts, Deštná, c.700m

Number of collections from different altitudinal zones:
- 14 Lowland and hilly districts (to 500m)
- 15 Submontane belt (to 1100m)
- 4 Montane–supramontane belts (to 1500m)
- 1 Subalpine belt (to 1800m)

hybridus in Turkey near Artvin, c.2000m, 3 viii 1960. An *Aecidium* on *Petasites fragrans* was noted in Algeria (N Africa), Djidjelli, i 1913 (see Guyot, 1953, p. 111).

According to the cited collecting dates, *Aecidium petasitis* was most common during May, June and July, but sparse by August, on *Petasites frigidus* in Karelo-Finnish SSR (Liro, 1908), on *P. hybridus* in Wysokie Tatry Mts (Wróblewski, 1922) and in Yugoslavia, Vlasina, E of Vranje (Ranojević, 1899). The record on *P. niveus,* dated 25 ix 1919, from near Grafrath (W of Munich) in Bavaria, c.500m (Poeverlein & Schoenau, 1929) is quite unique.

Ecological Comparison of the Populations

It seems that in Europe and in the European part of the USSR there are two obligately heteroecious populations of *Puccinia poarum.* They may be distinguished by the time of germination of their teliospores. One possesses immediately germinating teliospores, whereas the teliospores of the other overwinter and germinate the following spring.

The obligate heteroecy of the *Tussilago*-alternating population was confirmed by Jørstad (e.g. 1936, 1940, 1951) in Norway, Mayor (1958) in Neuchâtel, Durrieu (1966) in the Pyrénées, Wilson & Henderson (1966) in the British Isles, and Brandenburger (1974) in the Austrian Tirol. Fresh aecia are produced up to October and sometimes even November.

On the other hand, *Aecidium petasitis* has been gathered only once as late as September (near Munich in Bavaria). Its genetical connection to a grass rust was observed in nature and experimentally proved only in Switzerland. Dikaryont hosts in Switzerland are species from the genera *Festuca, Poa, Melica, Phleum* and *Agrostis.* In the Nízké Tatry Mts of Czechoslovakia the rust on *Milium effusum* subsp. *alpicola* has been repeatedly observed at the same locality since 1960; its alternate host is most probably *Petasites albus.* A similar rust on *Poa nemoralis,* together with effete aecia on *Petasites* sp., was gathered in Nízké Tatry Mts near Vernár. A similar rust found on *Festuca carpatica* in the Vysoké and Belianské Tatry Mts probably alternated with either *Petasites* sp. div. or *Tussilago farfara.* Both in Switzerland and Czechoslovakia *Aecidium petasitis* is mainly restricted to mountainous localities: in Switzerland 1000–1600m (*Puccinia petasiti-pulchellae, P. petasiti-melicae, P. taminensis, P. kummeri*), up to 1800m (*P. petasiti-poarum*; see Mayor, 1918, 1963); in Czechoslovakia 900–1700m. The type locality of *P. petasiti-poarum* near Regensburg (FRG), however, is at an altitude of about 340–400m. Therefore, some credence can be given to the idea of Lüdi (1917, pp. 87–88) who wrote concerning *P. petasiti-pulchellae*: when *Festuca pulchella* was not present in the biotope (plant community) a substitution by some species of *Poa* was likely. This idea led Paul (1917, p. 65) to suggest that *Aecidium petasitis* on *P. albus* in Leinbachtal (Bavaria, c.600m) was alternating with some hitherto unknown species of *Poa* because in Bavaria *F. pulchella* was not found below 1600m; the same interpretation was made by Poeverlein & Schoenau (1929).

According to the above evidence it seems that *Aecidium petasitis* in the European submontane to supramontane belts (Switzerland, Tatry Mts in

Czechoslovakia and Poland, Rumanian and Bulgarian Carpathians, Serbian, Bosnian and Hercegovian mountains) is connected with a rust-fungus like *Puccinia poarum* but diverging from it in the following characteristics:

1. aecia on *Petasites* sp. div. (? also *Tussilago*);
2. aecia from May to mid-August;
3. all teliospores overwintering, before germinating;
4. known dikaryont hosts from the genera: *Agrostis, Festuca, Melica, Milium, Phleum* and *Poa*.

At present it is difficult to determine more accurately the dikaryont hosts in the lowland and hilly belts. One must consider such rusts as *Puccinia petasiti-pendulae* Gäum. (1943) from Switzerland (I on *Petasites* sp. div. and *Tussilago,* II+III on *Carex pendula*) and *Puccinia ruttneri* R. Fisher (1952) from Austria (I on *Petasites hybridus,* II+III on *Carex gracilis* Curtis).

The species concept in rust fungi as demonstrated by Gaümann (1941, 1959) implies that: when there is a new combination of a hitherto unrecognized alternate host with a dikaryont-host a new rust species should be distinguished. A more recent view is based on the statement that distinct morphologic identity implies specific identity (Greene & Cummins, 1967; Cummins, 1971). The forma specialis was often recognized as the lowest infraspecific unit. However, some authorities gave the rank of variety to formae speciales, but this is not appropriate. Urban (1968) published a rather different view on the species concept in obligately parasitic fungi, especially rusts: stating that every taxonomic problem should be solved individually, irrespective of the existence of a previously constructed, universal, schematic hierarchy of intraspecific units. This is why we suggest a new approach to *Puccinia poarum*.

Puccinia poarum Nielsen in Bot. Tidsskr. ser. 3, 2: 34 (1877), var. **poarum**. Fig. 1A.

Syn.: *P. poae-trivialis* Bub. in Ann. Mycol. 3: 220 (1905).
P. poae-alpinae Eriks. in Ark. Bot. 18 (19): 1 (1923).

Spermogonia epiphyllous, sometimes numerous. *Aecia* hypophyllous, in dense clusters on circular, yellowish or reddish bordered spots; first generation from May, the second one from (July) August to November. Pseudoperidium short, whitish, margin revolute and dentate. Outer cell-wall to 11μm thick, punctate, inner wall 3–4μm thick, minutely verrucose. Fresh aeciospores orange. *Aeciospores* (18–)20–27(–31) × (15–)18–24(–27)μm, wall colourless c.1μm thick, verrucose or verrucose-echinulate, with some refractive granules 2·5–3μm in diam., without pores (see Holm, 1967; Henderson, Prentice & Eudall, 1972; Savile, 1973). *Uredia* mostly adaxial, a few abaxial or on sheath, bright orange yellow when fresh, then whitish, long covered, usually without paraphyses; occasionally with short single, peripheral, thin-walled, clavate paraphyses. *Uredospores* (19–)22–30(–34) × (16–)19–25(–27)μm, wall c.1·5μm thick, colourless or pale yellowish, spine spacing 2–2·5(–3)μm, pores (7–)8–9(–11), very indistinct, ± bizonate, without visible caps, without wall depression around pore. *Telia* mostly abaxial, blackish, permanently covered, narrow

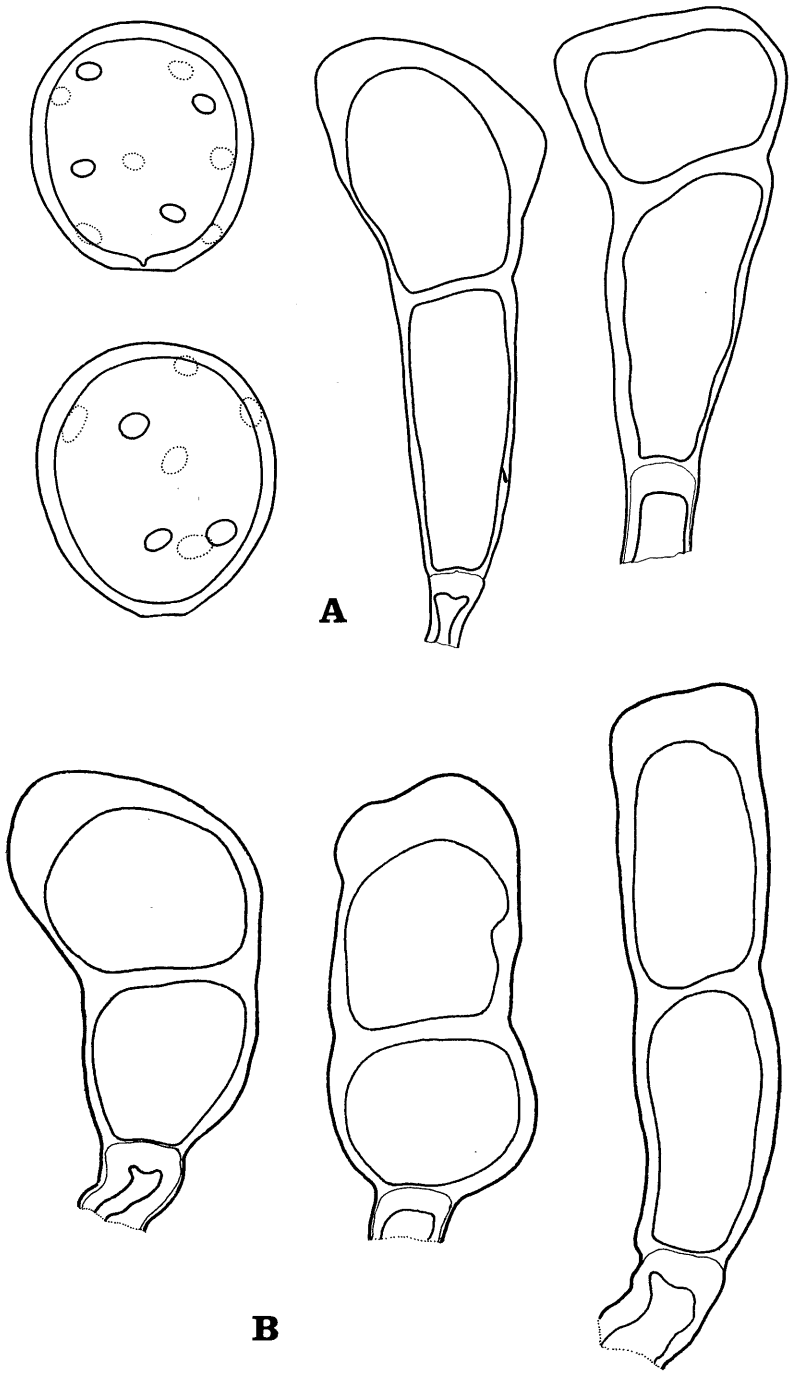


FIG. 1. A, *Puccinia poarum* var. *poarum*, II, III from *Poa pratensis*, Mariánské Lázně, 11 viii 1960, *Urban*; B, *Puccinia poarum* var. *petasiti-pulchellae*, III from *Milium effusum* subsp. *alpicola*, Trangoška chalet, 6 ix 1960, *Urban*.

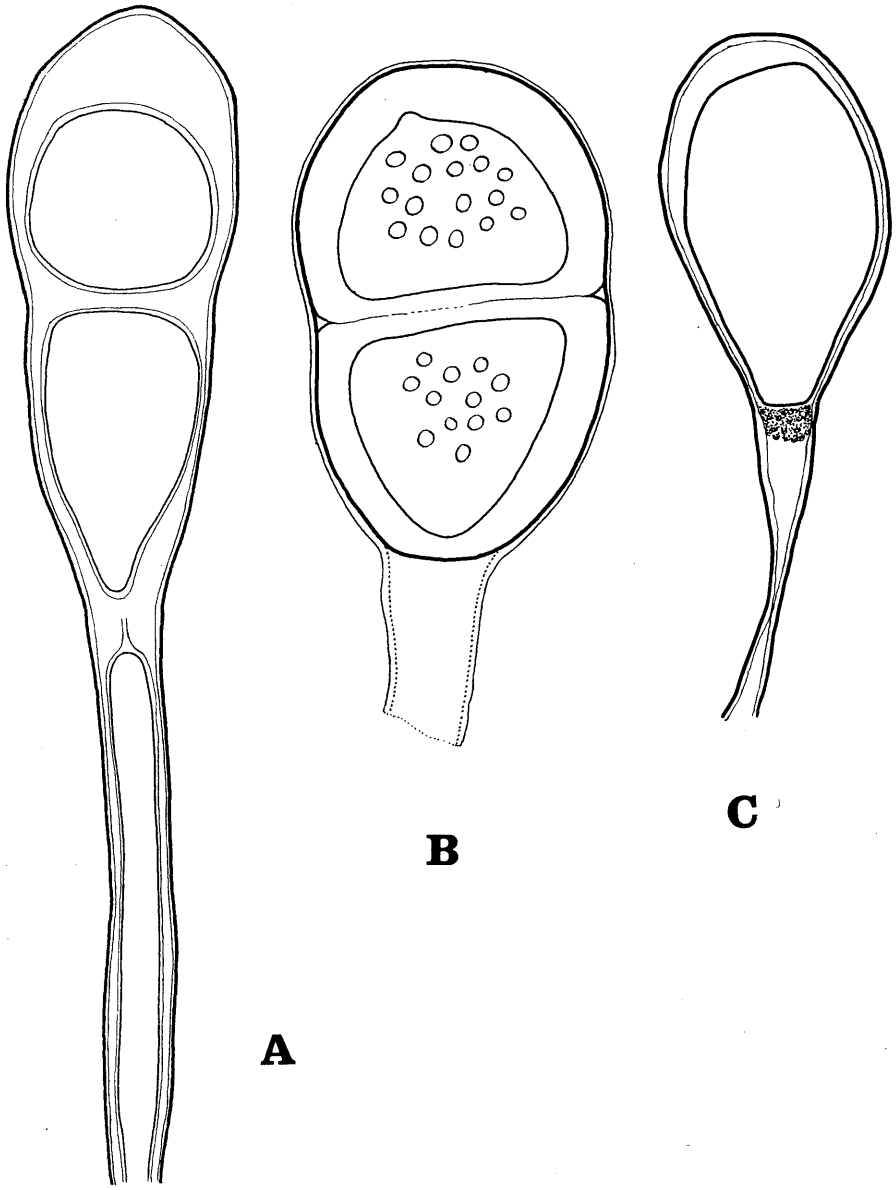
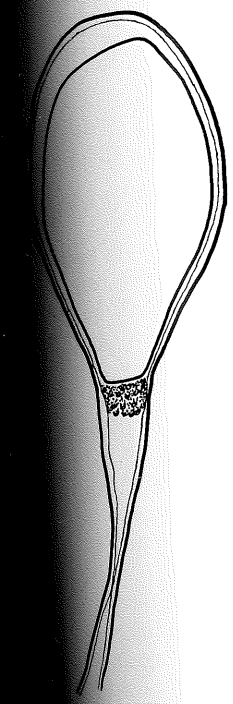


FIG. 2. Teliospore pedicel types: A, Crassipes; B, Tenuipes; C, Semicrassa.

or wide shortly linear, often grouped in an ellipsoid pattern around a uredium, with variable development of brown cylindrical paraphyses forming loculi (c. 2–7 spores wide). *Teliospores* (34–)39–60(–68) × (13–)17–24(–30) × 13–20(–23)μm, variably clavate, wall c.1–1·5μm thick at sides, (2–)3–8(–11)μm apically, smooth, chestnut-brown above, pedicel Crassipes-type (Urban, 1966b; see Fig. 2), short, persistent, apically



(2–)3–5(–7)μm thickened and chestnut-brown; occasionally 1- or 3-celled spores present. Teliospores immediately germinating.

Lectotype: on *Poa trivialis* from inoculation with aeciospores 10 vii 1875, collected 5 viii 1875, *Nielsen* (C): see Greene & Cummins (1967).

Distribution: Temperate to cooler countries of Europe, eastward to the western part of the USSR, Central Siberia, Mongolia (Schmiedeknecht & Puncag, 1967), China (Hsiao-Wu-tai-shan Mts, W of Peking) and Asia Minor (see also Jørstad in Ahmad, 1956, and Jørstad, 1959).

Aecial host: *Tussilago farfara.*

Uredial and telial hosts: *Poa alpigena, P. alpina, P. annua, P. botryoides* Trin., *P. compressa, P. glauca, P. nemoralis, P. ochotensis* Trin. (syn. *P. sphondylodes* Trin.), *P. pratensis, P. pratensis* subsp. *angustifolia* (L.) Hay., *P. remota, P. trivialis.*

In Czechoslovakia var. *poarum* was found on the following hosts:

Poa palustris (6): Smidary (Nový Bydžov), Lipno (Český Krumlov), Třeboň, Albertovec (Hlučín), Troubsko near Brno and Dřevohostice near Bystřice p. Hostýnem.

Poa trivialis (5): Velvary (Kralupy n. Vlt.), Třeboň, Karlova Studánka (Bruntál), Starý Smokovec in Vysoké Tatry Mts and Smolník (Gelnica).

Poa nemoralis (5), all from Slovakia: Pieniny Mts (Spišská Stará Ves), Srdiečko chalet in Nízké Tatry Mts (Brezno), Čingov (Spišská Nová Ves), Henclová and Smolník (Gelnica).

Poa pratensis subsp. *pratensis* (3): Zeleneč near Praha, Mariánské Lázně (Fig. 1A), Troubsko near Brno.

Poa pratensis subsp. *angustifolia* (4): Střevač (Jičín), Bardejovské Kúpele (Bardejov), Trangoška chalet in Nízké Tatry Mts (Brezno) and Čingov (Spišská Nová Ves).

Poa compressa (3): Třeboň, Troubsko near Brno and Bezovec Mt near Piešťany.

Poa remota (1): Ludrová valley in Nízké Tatry Mts (Ružomberok).

Poa sp.: Zeleneč near Praha, Tále (Brezno) and Bardejov.

The highest localities are Srdiečko chalet (c.1200m) and Trangoška chalet (c.1100m) in Nízké Tatry Mts. The lowest localities are: Velvary (c.190m), Smidary (238m), Dřevohostice near Bystřice p. Hostýnem (c.240m), Albertovec and Zeleneč (c. 260m).

As in other countries, *Puccinia poarum* var. *poarum* in Czechoslovakia is obligately heteroecious.* All specimens (33) except one (Bardejovské Kúpele, 22 vii 1985, *Marková*) bear telia, but uredia are scarce and very probably of only short duration because the sori are almost without spores. Teliospores are produced very soon, usually simultaneously with uredia (e.g. on *Poa compressa,* (II)+(III), Bezovec Mt near Piešťany, together with *Tussilago farfara,* 0+I, 29 v 1977, *Urban*). Our more recent collections also show that var. *poarum* is very often accompanied by infected *Tussilago farfara*: on *Poa trivialis,* (II)+III, Třeboň, 26 vi 1984, *Urban & Marková*; —on *Poa* cf. *compressa,* (II)+III, Třeboň, 27 vi 1985, *Turečková*; —on *Poa palustris,* (II)+III, Třeboň, 10 vii 1984, *Urban,*

*Treboux (1914) observed overwintering mycelia in the leaves of *Poa annua* and *P. pratensis* in the surroundings of Riga. However, it is uncertain that these observations were really made on *Puccinia poarum.*

TABLE 2

Diagnostic features for the separation of *Puccinia poarum* var. *poarum* from *P. poae-nemoralis*

	P. poarum var. *poarum*	*P. poae-nemoralis*
uredia	scarce, covered, without thick-walled, capitate paraphyses; occasionally with single, peripheral, short, clavate, thin-walled paraphyses	abundant, numerous, thick-walled, yellow-brownish, bent, capitate paraphyses giving the sori a pulvinate and compact appearance
uredospores		
wall	colourless, 1·5μm thick	pale brownish, c.2μm thick
spine spacing	2–2·5(–3)μm	1·5–2(–2·5)μm
pore caps	absent	minute, visible
wall depression around pores	absent	present
pores in phase-contrast, ×1000	not visible*	visible, can be counted
teliospores		
pedicel type (Urban, 1966b; see Fig. 2)	Crassipes	Semicrassa

*Pores were visible only after staining in Congo red (Urban, 1963).

(+*Uromyces poae* Rabenh. III); —on *Poa* cf. *trivialis,* II+III, Starý Smokovec, 14 vii 1955, *Urban*; —on *Poa* sp. and *P. pratensis* subsp. *angustifolia,* (II)+III, Bardejovské Kúpele, 22 vii 1985, *Marková*; —on *Poa* sp., (II)+III, and *P. poae-nemoralis* Otth, II, Snakov near Bardejov, 27 vii 1985, *Marková*; —on *Poa* sp., II+III, Brezno, above Partyzán hotel in Bystrá dolina valley, 1 ix 1985, *Formanová & Turečková*; —on *Poa nemoralis,* (III), and *P. poae-nemoralis,* II, Brezno, below Srdiečko chalet, 8 ix 1977, *Marková*; —on *Poa remota,* (II)+III, Ružomberok, Ludrová dolina valley, 18 ix 1980, *Urban*; —on *Poa* cf. *pratensis* subsp. *angustifolia,* III, and *P. poae-nemoralis* II+(III), Střevač, 27 ix 1986, *Urban*; —on *Poa* cf. *pratensis* subsp. *angustifolia,* (II)+III, Spišská Nová Ves, Čingov, Lesnica stream, 29 ix 1986, *Urban*; —on *Poa nemoralis,* (II)+III, Spišská Nová Ves, Čingov, 29 ix 1986, *Marková*; —on *Poa* cf. *pratensis,* 3 collections II+III; III; III, Zeleneč near Praha, 19 x 1986, *Urban.*

In Czechoslovakia, *Puccinia poarum* var. *poarum* has often been found together with uredia of *P. poae-nemoralis* Otth. Uredia of the last species were plentiful not only on the same plants but even on the same leaves. These rusts can be distinguished by the characteristics given in Table 2.

Puccinia poarum var. **petasiti-pulchellae** (Lüdi) Urban & Marková, **comb. et stat. nov.** Figs 1B, 3.

Syn.: *Puccinia petasiti-pulchellae* Lüdi in Centrabl. Bakteriol. 2. Abth. 48:85 (1917).

Puccinia petasiti-melicae Gäum. in Phytopath. Zeitschr. 13:627 (1941).

Puccinia taminensis Gäum. Ibid. 13:629 (1941).

Puccinia kummeri Gäum. Ibid. 13:632 (1941).

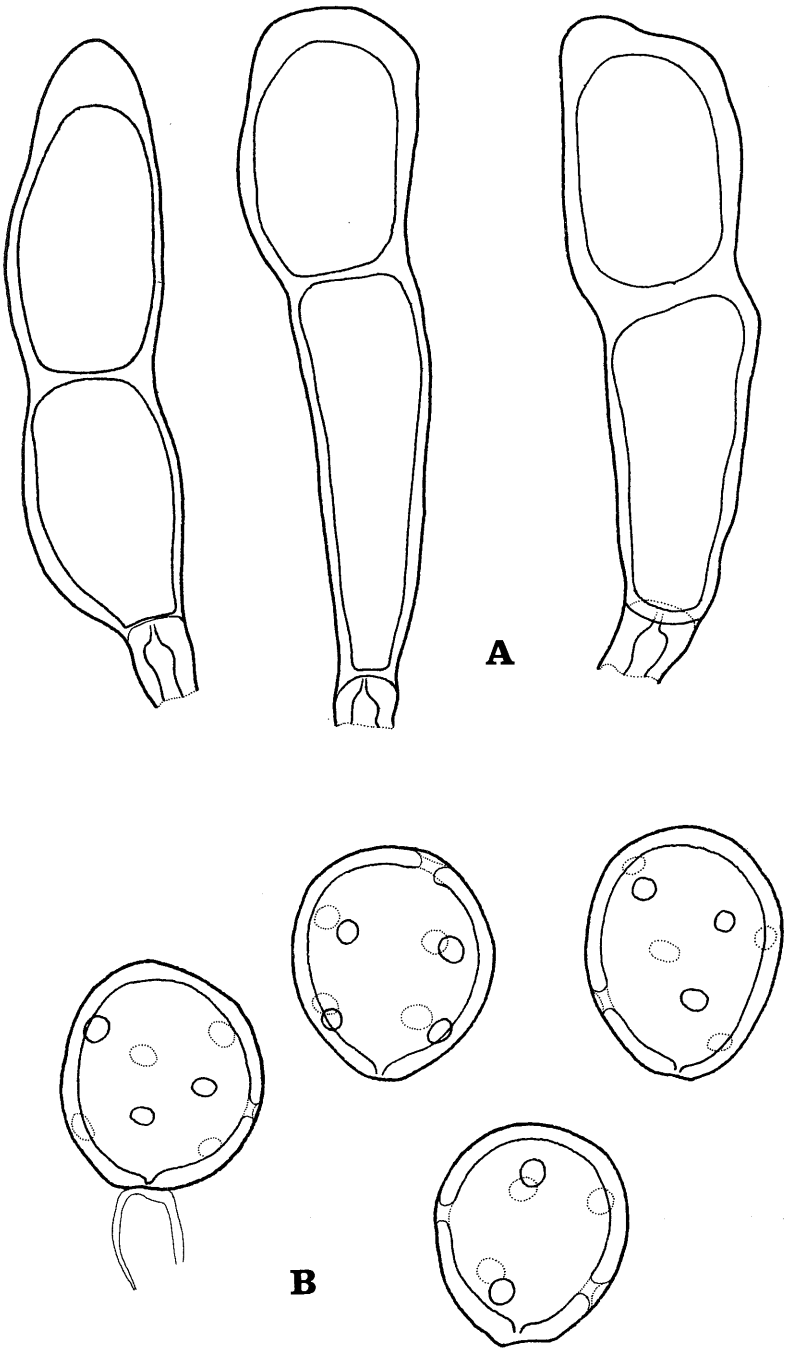


FIG. 3. *Puccinia poarum* var. *petasiti-pulchellae*: A, III from *Festuca carpatica*, Temnosmrečinová dolina valley, 19 viii 1947, *Hadač*; B, II from *Poa nemoralis*, Vernár, 6 viii 1961, *Urban*.

Puccinia petasiti-poarum Gäum. & Eichh. Ibid. 13:637 (1941).
Puccinia baldensis Gäum. in Ber. Schw. Bot. Ges. 61:48 (1951).

A varietate *poarum* differt teliosporis omnibus perennantibus; aecidia a Mayo mense ad medium Augustum inveniuntur.

Type: *Festuca pulchella* Schrad., Schweiz: Kt. Bern, Brünnlihorn bei Mürren, 12 x 1915, *W. Lüdi* (ZT).

Distribution: in the hilly, submontane to supramontane (500–1500m) and subalpine (to 1800m) belt in Switzerland, Austria, German Federal Republic, German Democratic Republic, Denmark, Czechoslovakia, Poland, European part of the USSR, Rumanian and Bulgarian Carpathes and the mountains in SE Yugoslavia.

Aecial hosts: *Petasites albus, P. frigidus, P. hybridus, P. kablikianus, P. laevigatus* (Willd.) Reichenb., *P. niveus* Baumg., *P. spurius* (Retz.) Reichenb., and possibly *Tussilago farfara.*

Uredial and telial hosts: *Agrostis alba, Festuca carpatica, F. pulchella, Melica nutans, Milium effusum* subsp. *alpicola* Chrtek, *Phleum michelii* All., *Poa alpina, P. nemoralis, P. pratensis* subsp. *angustifolia* (L.) Hay.

In Czechoslovakia var. *petasiti-pulchellae* has been reported on the following host-plants (for aecial hosts see Table 1):

Festuca carpatica: Vysoké Tatry Mts, Temnosmrečinová dolina valley, c.1760m, 19 viii 1947, *Hadač*, (11)+III, uredospores 25–29 × 21–24μm, 6–8 pores, teliospores 53–73 × 16–22·5μm (upper cell) Fig. 3A; Belianské Tatry Mts, Siedmich prameňov valley, path to the Protež chalet, 13 vii 1959, together with *Aecidium tussilaginis*, II+III, uredospores 25–30 × 17·5–22μm, teliospores 35–52·5 × 17·5–25μm (upper cell); Hĺboký potok stream, 31 vii 1959, III, 50–67·5 × 17·5–22·5(–26)μm (upper cell), mesospores also present; Protež chalet, 7 viii 1960, *Hadač*, (II)+III, uredospores 22·5–27·5 × 20–22·5μm, 8–10 pores, teliospores 42·5–67·5 × 16–21μm (upper cell).

Milium effusum subsp. *alpicola*: Brezno, Nízké Tatry Mts, Trangoška chalet, 6 ix 1960, *Urban,* III, 37·5–65 × 17·5–25 × 14–24μm, $\bar{x}$ = 51·9 × 20·8 × 19·4μm (n = 39), single germinated uredospores, wall c.1·5μm, spine spacing (2–)2·5(–3)μm, c.8 pores, Fig. 1B; *ibidem*, c.1125m, 2 ix 1985, *Urban & Marková,* (II)+III, uredospores 26–30 × 22–25μm, teliospores 47–55(–58) × 15–18μm (lower cell); *ibidem*, bus-stop, 14 viii 1986, *Urban,* (II)+III, uredospores (21–)25–30 × (20–)22–24(–25)μm (n = 50), wall 1–1·5μm, spine spacing 2–2·5–3μm, (6–)8–9(–10) pores.

Poa nemoralis: Nízké Tatry Mts, railway station Vernár, c.930m, 6 viii 1961, (II)+III, uredospores 19–26 × 19–22·5μm, spine spacing 1·5–2·5μm, (7–)8(–9) pores scattered or bizonate, teliospores 38–45 × 13–21 × 13–17μm, occasionally 3-celled, together with effete *Aecidium petasitis* on *Petasites* sp. Fig. 3B.

The uppermost locality was with *Festuca carpatica* in Vysoké Tatry Mts, c.1760m, the lowest one with *Poa nemoralis* at Vernár, c.930m in Nízké Tatry Mts. It should be noted that *Aecidium petasitis* was collected on about 10 occasions at altitudes between 400 and 900m (see p. 362).

Puccinia poarum var. *petasiti-pulchellae* in Czechoslovakia, as in Switzerland, seems to be obligately heteroecious. Collections on *Milium, Poa* and *Festuca carpatica* on the path to Protež chalet were discussed

earlier (see p. 361, 363). According to Dr E. Hadač (pers. comm.) in Temnosmrečinová dolina valley host alternation of *Festuca carpatica* with *Petasites kablikianus* is very probable. The two other specimens on *F. carpatica* from Belianské Tatry Mts may be annotated as follows:

a. in the ravine of Hĺboký potok stream (1095–1220m) where four plant communities were described belonging to the alliance *Petasition officinalis* Sillinger (Hadač, 1969); these include *Petasites kablikianus* and *P. hybridus* and also *P. albus* and *Tussilago farfara* (the last two less regularly). Additional grass species were: *Poa nemoralis, P. trivialis* and *Milium effusum*. The presence of *Festuca carpatica* could be due to occasional migration down from higher elevations.

b. the rust at Protež chalet could alternate either with *Tussilago farfara* or *Petasites kablikianus*. At the chalet three avalanche lines meet which, in their upper parts, possess plant communities belonging to the *Seslerion tatrae* Pawl. and *Delphinion elati* Hadač (1962). All phytocoenoses regularly include *Festuca carpatica, Tussilago farfara* and *Petasites kablikianus* (the last in ass. *Petasito-Senecietum nemorensis* Hadač, 1969). In this case, too, the hosts have occasionally migrated down to lower altitudes.

Puccinia poarum var. *petasiti-pulchellae,* like var. *poarum,* can thrive together with *Puccinia poae-nemoralis*. This was established, e.g., by the revision of the two type specimens from Zürich (ZT):

a. '*Puccinia baldensis* Gm./*Poa pratensis* (Schmelzbergstrasse)/infiziert von *Senecio brachychaetus*/21 vi 1949 Monte Baldo, Refugio Graziani'—*Puccinia poarum* var. *petasiti-pulchellae* (II)+III together with *P. poae-nemoralis* II.

b. '*Puccinia baldensis* Gm./*Poa pratensis*/Infektionsmaterial aus Versuchen/Rückversuch von *Senecio brachychaete* I 1950/Ursprungsmaterial *Senecio brachychaete* 1949/Monte Baldo'—only *Puccinia poae-nemoralis* II.

This is why the original description of *Puccinia baldensis* erroneously incorporates the characteristic: '*Uredolager* . . . von keuligen oder kopfigen, bis 75μm langen, oben 12–21μm breiten, am Scheitel deutlich verdickten Paraphysen durchsetzt'.

Additional Taxonomic Notes

According to Gäumann (1959) *Puccinia poarum* Nielsen (i.e. *P. poarum* var. *poarum*) does not possess coloured, cylindrical paraphyses in the telia. In all Czechoslovak specimens, however, we found teliosori separated into locules by cylindrical, chestnut-coloured paraphyses. The same characteristic was observed in rusts on *Festuca* and *Milium* and in all revised material from Zürich (var. *petasiti-pulchellae*) too.

Before the publication of Greene & Cummins (1967) we had already made a revision of the type specimens of the following species: *Puccinia poaetrivialis* Bub., *P. petasiti-pulchellae* Lüdi, *P. petasiti-melicae* Gäum. & Eichh. and *P. baldensis* Gäum. (BKL, ZT). We were agreed that the type

specimen of *P. petasiti-poarum* included *P. graminis* III. Three specimens sent from Zürich as type material of *P. kummeri* included only uredia and uredospores like *P. poarum*: 24–26 × (18–)20–21 μm; —uredospores from inoculation experiments: 20–22·5 × 17.5–20 μm; —22.5–24(–25) × (17·5–)20–22·5 μm, wall subhyaline, 1–1·25 μm thick, spine spacing 2–2·5 μm, pores without caps, not visible without staining, (6–)7–8(–9) ± bizonate, single thin-walled clavate paraphyses 40–45 × 11–14 μm. The specimen labelled '*Puccinia kummeri* Gm./*Agrostis alba*/Calfeis, hinter Gigerwald, 28 viii 40. Gm.' included a black, very obsolete stromatic ascomycete or deuteromycete.

Gäumann (1959, p. 540) placed *Uredo poae-cenisiae* Lüdi (in *Mitt. naturf. Ges. Bern,* 1927: xxxiii, 1928) close to *Puccinia petasiti-poarum*. Because of the predominance of long, capitate paraphyses in the sori this species is actually related to *P. poae-nemoralis*.

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