



# Studies on European rust fungi, *Pucciniales*: molecular phylogeny, taxonomy, and nomenclature of miscellaneous genera and species in *Pucciniastraceae* and *Coleosporiaceae*

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## Abstract

Using molecular phylogenetic analyses (ITS) and morphological data obtained from light and electron microscopy, some European and North American species and genera placed or formerly placed in the genus *Pucciniastrum* in the *Coleosporiaceae* and *Pucciniastraceae* (*Pucciniales*) were taxonomically revised. The ITS analyses confirmed recent familiar concepts based on less variable markers except for the genus *Hyalopsora*. The family *Pucciniastraceae* is characterized by *Abietoideae* (*Abies*, *Tsuga*) aecial hosts. *Pucciniastrum* is described as a genus that consists of host-alternating species forming aecia on needles of *Abies* hosts, with special features of aeciospore morphology, and *Onagraceae* telial hosts. Other genera in the *Pucciniastraceae* are *Calyptospora*, *Melampsorella*, and additional taxa, which are currently provisionally placed in *Pucciniastrum*, but must be revised in future studies. *Pucciniastrum epilobii* (s. lat.), the type species of *Pucciniastraceae*, represents at least two species with different life cycles and urediniospore characteristics and is lecto- and eptytified. The family *Coleosporiaceae*, characterized by *Pinoideae* (*Pinus*) and *Piceoideae* (*Picea*) aecial hosts, contains *Rosaceae* rusts from three well-supported clades represented by three genera, *Thekopsora*, *Quasipucciniastrum*, and *Aculeastrum* gen. nov. *Aculeastrum* is characterized by coarsely arcuate ostiolar peridial cells and infects *Rubus* spp. telial hosts. The following new taxonomic combinations are proposed: *Calyptospora ornamentalis* comb. nov., *Quasipucciniastrum ochraceum* comb. nov., *Q. potentillae* comb. nov., *Aculeastrum americanum* comb. nov., and *A. arcticum* comb. nov. The results are discussed with emphasis on future studies in *Pucciniastrum* and the *P. epilobii* complex and on nomenclatural changes necessary for rust fungi due to the Shenzhen Code.

**Keywords** *Aculeastrum* · *Calyptospora* · *Coleosporiaceae* · *Pucciniastrum* · *Quasipucciniastrum* · *Pucciniastraceae*

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## Introduction

Arthur (1906: p. 337) described the new subfamily *Pucciniastroideae* (as “*Pucciniastratae*”) and assigned it to the family *Uredinaceae* (rust fungi). Sydow and Sydow (1915: p. 333) introduced a new subfamily of rust fungi, *Pucciniastroideae* P. Syd. & Syd. (as “*Pucciniastreeae*”) with *Pucciniastrum* G. H. Oth as type genus and *P. epilobii* G. H. Oth as type species. Together with three additional subfamilies (*Chrysomyxoideae* P. Syd. & Syd., *Cronartioideae* P. Syd. & Syd., and *Melampsoroideae*), Sydow and Sydow placed it in the family *Melampsoraceae* Dietel. Later, Hiratsuka (1936) monographed the *Pucciniastroideae* accepting eight genera, namely *Calyptospora* J.G. Kühn, *Hyalopsora* Magnus, *Melampsorella* J. Schröt., *Melampsoridium* Kleb., *Milesina* Magnus, *Pucciniastrum* G.H. Oth, *Thekopsora* Magnus, and *Uredinopsis* Magnus. Subsequently, most of these subfamilies were treated as families, including *Pucciniastraceae* Gäum. ex Leppik (Leppik

1972: p. 139), based on Gäumann's (1959) invalid family name [= *Pucciniastraceae* (Arthur) Jülich (Jülich 1981), nom. illeg., Art. 53]. The family *Pucciniastraceae* was later mostly accepted and maintained (e.g. Cummins and Hiratsuka 2003), although phylogenetic examinations on the family-level raised doubts as to the justification of this family (Liang et al. 2006, Aime 2006). Aime (2006) regarded the family *Pucciniastraceae* to be redundant and con-familiar with the family *Coleosporiaceae*. Most recently, Zhao et al. (2020) excluded three genera (*Milesina*, *Naohidemyces*, *Uredinopsis*) from *Pucciniastraceae*. Aime and McTaggart (2020) placed those three genera in a separate family, *Milesinaceae* Aime & McTaggart. Several authors, e.g. Hylander et al. (1953) and Braun (1982), authors of the online databases Index of Fungi and MycoBank, synonymized some of the genera (*Calyptospora*, *Thekopsora*) with *Pucciniastrum*. Other authors, e.g. Cummins and Hiratsuka (2003), Klenke and Scholler (2015), and Aime and McTaggart (2020), however, accepted the generic concept of Hiratsuka (1936) and even added one additional genus, *Naohidemyces* S. Sato, Katsuya & Y. Hirats., which was originally part of *Pucciniastrum*. According to Cummins and Hiratsuka (l.c.), species of *Pucciniastraceae* are mainly characterized by their particular life cycle, i.e. mostly host-alternating species with conifer aecial hosts predominantly of the genera *Abies*, *Picea*, and *Tsuga*, and subepidermal or intradermal sessile teliospores forming one cell-layered crusts. Maier et al. (2003) provided the first molecular phylogeny of the rust fungi based on 28S rDNA (domains D1, D2) sequence data. Their phylogeny suggested the family *Pucciniastraceae* and the genera *Thekopsora* and *Pucciniastrum* to be polyphyletic. Two species, *P. pyrolae* and *P. agrimoniae*, do not seem to be related to *Pucciniastrum* s. str. In a recent molecular phylogeny using 18S and 28S markers, Aime et al. (2018) supported the generic concept of Cummins and Hiratsuka (l.c.) and indicated that even more *Pucciniastrum* and *Thekopsora* species need to be placed in other genera. Recently, Aime and McTaggart (2020) provided a phylogeny of rust families using three less variable markers (28S rDNA, 18S rDNA, and CO3). In their study, species formerly placed in the *Pucciniastrum* group in clusters of two different families with *Pinaceae* aecial hosts, namely in *Pucciniastraceae* Gäum. ex Leppik emend. Aime and McTaggart with numerous telial host fern rusts and in *Coleosporiaceae* Dietel emend. Aime and McTaggart with only one genus, *Hyalopsora*, with telial host fern rusts.

In the present study, we sequenced the ITS marker from mainly European species placed or formerly placed in *Pucciniastrum* to re-assess their taxonomic (specific and generic) position within the two families *Coleosporiaceae* and *Pucciniastraceae* s. str. Aime and McTaggart (2020). The basis for our studies is the higher rank phylogeny of Aime and McTaggart (2020) mentioned above. Furthermore, we studied

urediniospore germ pores and spore surface features in *Pucciniastrum epilobii* s. lat. and *Rosaceae* rusts within *Coleosporiaceae* using light and electron microscopy. These features have recently been documented for species and sectional delimitation in *Milesina* (Bubner et al. 2019) but have not been considered in morphological studies of *P. epilobii* s. lat. (Klebahn 1900, 1914; Bisby 1916; Pady 1933) and the rusts on *Rosaceae* (Ziller 1974; Helfer 2005; Qi et al. 2019). Finally, we carried out a detailed study on the taxonomy and nomenclature of these species with respect to the rules of the current "International Code of Nomenclature for algae, fungi, and plants" (Shenzhen Code, 2018), supplemented by the revised version of Chapter F of the Code, incorporating amendments approved by the Fungal Nomenclature Session of the 11th International Mycological Congress held in San Juan, Puerto Rico, in July 2018 (May et al. 2019).

## Materials and methods

### DNA extraction, PCR, and sequencing

Samples for DNA extraction were prepared from herbarium specimens (Table 1) by excising a single sorus including the plant material. They were placed into microtubes with 8–12 ceramic beads, 1.4-mm diameter (Bio-Budget Technologies, Krefeld, Germany), frozen at  $-20\text{ }^{\circ}\text{C}$  overnight, and homogenized on a Bead Ruptor (Biolab Products, Beverly, Germany) at a speed of 7.45 m/s for 25 s. After freezing the samples again for 10 min at  $-20\text{ }^{\circ}\text{C}$ , homogenisation was repeated. DNA was extracted with the DNeasy Plant Mini Kit (Qiagen, Hilden, Germany), following the manufacturer's protocol. Selected samples were homogenised with glass mini mortars and pestles (Roth, Karlsruhe, Germany) in 400  $\mu\text{l}$  of the homogenisation buffer included in the extraction kit.

Molecular barcodes were generated for the ITS region by using the primers ITS1F (Gardes and Bruns 1993) and ITS4rust (Beenken et al. 2012, 2017). PCR was performed with the Accuprime Taq Polymerase System (Life Technologies, Karlsruhe, Germany) using the supplied buffer II and the following final concentrations: 2 mM  $\text{MgCl}_2$ , 0.2 mM of each dNTP, and 500 nM of each primer. The PCR programme was as follows: 3 min denaturation at  $94\text{ }^{\circ}\text{C}$ , 10 cycles with decreasing annealing temperature ( $94\text{ }^{\circ}\text{C}$  for 30 s,  $60\text{--}50\text{ }^{\circ}\text{C}$  for 30 s, and  $68\text{ }^{\circ}\text{C}$  for 60 s), 35 cycles with constant annealing temperature ( $94\text{ }^{\circ}\text{C}$  for 30 s,  $50\text{ }^{\circ}\text{C}$  for 30 s, and  $68\text{ }^{\circ}\text{C}$  for 60 s), and 7 min strand completion at  $68\text{ }^{\circ}\text{C}$ . PCR products were visualised in 1.6% agarose gel.

After purification of the PCR products with QIAquick-PCR Purification Kit (Qiagen, Hilden, Germany), they were sent to GATC Biotech AG (Konstanz, Germany) for sequencing. Sequencing was performed with the same primers used for the PCR. Forward and reverse sequences were edited and

assembled with the software package GENEIOUS 10.0 (Biomatters, Auckland, New Zealand).

### Phylogenetic analysis

Sequences were aligned with the CrustalW algorithm implemented in the programme Bio Edit, version 7.1.3.0 (Hall 1999), using the standard parameters offered by the programme. Two sequences of *Milesina kriegiana* (Bubner et al. 2019) were used as the outgroup. Alignments were used for phylogenetic reconstruction by three different methods:

- i) Maximum likelihood (ML) analysis: The alignment was analysed under the ML criterion on the Web-based RAxML black box (Stamatakis et al. 2008). The substitution model used was GTR without GAMMA correction for amongst-site heterogeneity. Node support values were calculated from 100 bootstrap replicates.
- ii) Bayesian inference (BI) analysis: The DNA-substitution model GTR+I+G was used for performing Bayesian analysis with the programme MrBayes 3.2 (Ronquist et al. 2012). Two independent MCMC runs were performed, each with four chains over 1,000,000 generations. Every 100th tree was sampled. Initial burn-in was 25% and summarisations were calculated after the standard deviation of split frequencies reached below 0.01. The resulting tree file contained posterior probability values for node support.
- iii) Maximum Parsimony (MP) analysis: Phylogenetic reconstruction was performed with the software package MEGA version 10.2.1 (Kumar et al. 2018). Node support values were calculated from 1000 bootstrap replicates.

Tree files resulting from the three methods were visualised using the programme TreeGraph 2 (Stöver and Müller 2010).

### Light and scanning electron microscopy

For microscopical identification and morphological studies of *Pucciniastrum epilobii* s. lat., specimens were mounted in a mixture of lactic acid and glycerol (Kirk et al. 2001) and examined with a Zeiss Axioskop 2 plus microscope (Oberkochen, Germany) at a magnification of  $\times 400$  or  $\times 1000$ . Specimens were identified as described by Klenke and Scholler (2015). Germ pores of urediniospores of *Pucciniastrum epilobii* s. lat. were visualised by the method described in Bubner et al. (2019). For scanning electron microscopy (SEM), uredinia and urediniospores of dried specimens of *P. epilobii* s. lat. were placed on a holder with conductive double-sided tape (Leit-Tabs, Plano GmbH). Scanning electron microscope images were obtained on a

Philips XL 30 FEG environmental scanning electron microscope operated at an acceleration voltage of 12 kV at a chamber pressure of 133 Pa (1 Torr). To achieve better contrast and less charge effects, the samples were coated with a mixture of gold (80%) and palladium (20%) first (MED 020, BAL-TEC). SEM studies were carried out to study surface structures that are not visible by light microscopy. In addition, spine base diameters (30 per species) were measured with SEM and the software ImageJ 1.5.

### Additional specimens examined morphologically

The following is a list of specimens studied morphologically in addition to (also sequenced) specimens listed in Table 1. Spore states of rust fungi are listed in Roman numerals. A Roman numeral in brackets indicates that this spore state was only formed sparsely. Acronyms of countries follow the International Organization for Standardization (ISO) alpha-2 country codes (<https://www.iso.org/home.html>). Fungus names are inferred from voucher specimens; host names are “current names” from the Catalogue of Life (COL | The Catalogue of Life) except for the genus *Chamaenerion* which we separate from *Epilobium*.

*Pucciniastrum epilobii-dodonaei*:

*Chamaenerion dodonaei* (*Epilobium dodonaei*): AU, Kärnten, Hermagor Kreis, Mauthen, Valentin-Bach, on, Aug. 1940, H. Poeverlein (KR-M-0023486)

*Pucciniastrum epilobii* s. lat.:

*Chamaenerion angustifolium* ( $\equiv$  *Epilobium angustifolium*): CH, Heimberg, undated, G.H. Oth II, III (ZT Myc 43369), Bern, autumn 1869, II, III, Wartmann & Schenck, Schweizerische Kryptogamen 615 (KR-M-13186); DE, Baden-Württemberg, Baiersbronn, Ruhestein, Alte Seekopfhütte, 19 Aug 2018, M. Scholler, II, (III) (KR-M-0049239); Freiburg, Schluchsee, Dresselbad, 23 Aug 2001, H. Jage, II, III (KR-M-0022600); Seebach, 17 Sep. 2012, M. Scholler (KR-M-0035186); Bayern, Cham, Lohberg, 15 Aug 1978, P. Döbbeler, J. Wenninger, (KR-M-0039492); Mecklenburg-Vorpommern, Darss, Drei Eichen 25 Aug 1991, M. Scholler (KR-M-0002728); Sachsen-Anhalt, Salzwedel, 18 Oct 2014, H. Jage (KR-M-0044575); Schleswig-Holstein, Nordfriesland, between Niebüll and Klanxbüll, Gotteskoogsee, 4 Sep. 2016, M. Scholler, II (KR-M-0048573); FL, Helsinki, 18 Sep 2004, P. Döbbeler (KR-M-0038589). *Epilobium ciliatum*: DE, Thüringen, Harz, Brandesbachtal, 27 Aug 2013, H. Thiel (KR-M-0043042); Baden-Württemberg, Freiburg, N Oberried, E Geroldstal, 26 Aug 2007, H. Jage, II (KR-M-0022644); Thüringen, Bleicherode, Bleicheröder Berg, 17 Sep 2011, W. Schulz, II (KR-M-0044576). *E. hirsutum*: DE, Rosenberg, Kimauer Tal, 12 Oct 2005, M. Scholler (KR-M-0018725). *E. montanum*:

**Table 1** Names, specimens, and accession numbers for the ITS barcode. Specimens with lab numbers were sequenced for this study and submitted to GenBank. These specimens were also morphologically studied. Collection data are provided for these specimens

Name in this article	Name on voucher (marked with *)/name in GenBank	Collection data	Host	Voucher	Lab no.	GenBank accession	Reference
<i>Aculeastrum americanum</i>	<i>Pucciniastrum americanum</i> *	12 Sep. 2001, USA, Minnesota, Becker County (R. W. Stack)	<i>Rubus strigosus</i>	BP1871792	B2347	MT022020	
		22 Sep. 2005, USA, Minnesota, Clay County (R. J. M. Hansen)	<i>Rubus strigosus</i>	BP1878095 (epitype)	B2348	MT022021	
		15 Sep. 2001, USA, Minnesota, Becker County (R. W. Stack)	<i>Rubus pubescens</i>	BP1844295	B2349	MT022022	
<i>Calyptospora columnaris</i>	<i>Calyptospora goeppertiana</i> *	20 Jul. 2016, DE, Baden-Württemberg, Ruhestein (M. Scholler)	<i>Abies alba</i>	KR-M-0048514	B1626	MK697284	
		20 Jul. 2016, DE, Baden-Württemberg, Ruhestein (M. Scholler)	<i>Abies alba</i>	KR-M-0048518	B1638	MK697282	
		20 Jul. 2016, DE, Baden-Württemberg, Ruhestein (M. Scholler)	<i>Abies alba</i>	KR-M-0048516	B1650	MK697286	
		13 Sep. 2013, DE, Baden-Württemberg, Ruhestein (M. Scholler)	<i>Vaccinium vitis-idaea</i>	KR-M-0043712	B2289	MK697283	
		31 Jul. 2013, DE, Baden-Württemberg, Sasbachwalden (T. Wolf)	<i>Vaccinium vitis-idaea</i>	KR-M-0038345	B2290	MK697287	
		17 Sep. 2012, DE, Baden-Württemberg, Ruhestein (M. Scholler)	<i>Vaccinium vitis-idaea</i>	KR-M-0035183	B2292	MK697285	
			<i>Abies grandis</i>			L76508	
<i>Calyptospora ornamentalis</i>	<i>Pucciniastrum goeppertianum</i>		<i>Abies grandis</i>			L76509	Vogler and Bruns 1998
			<i>Vincetoxicum nigrum</i>			JN802139	Bon and Guermache 2012
<i>Cronartium flaccidum</i>	<i>Cronartium flaccidum</i>		<i>Melampyrum nenorosum</i>			AY566270	Kaitera et al. 2005
			<i>Pinus halepensis</i>			X83890	Moricca et al. 1996
			<i>Ribes sanguineum</i>			OL471652	
<i>Cronartium ribicola</i>	<i>Cronartium ribicola</i> *	9 Oct. 2014, DE, Sachsen-Anhalt, Kemberg (H. Jage)	<i>Ribes uva-crispa</i>	KR-M-0048156	B1274	OL471653	
		6 Oct. 2011, DE, Sachsen-Anhalt, Kemberg (H. Jage)	<i>Ribes rubrum</i>	KR-M-0048158	B1310	OL471654	
		19 Oct. 2013, DE, Sachsen-Anhalt, Wittenberg (H. Jage)	<i>Ribes nigrum</i>	KR-M-0048159	B1567	OL471655	
<i>Hyalospora aspidiotus</i>	<i>Hyalospora aspidiotus</i>	25 Jul. 2017, DE, Hamburg, Hamburg (M. Scholler)	<i>Gymnocarpion dryopteris</i>	KR-M-0049074	B2030	OL471656	
		21 Jun. 2014, DE, Niedersachsen, Hardegsen, Ertinghausen (H. Thiel)	<i>Abies alba</i>	KR-M-0043166	B1931	OL471657	
<i>Melampsorella caryophyllacearum</i>	<i>Melampsorella caryophyllacearum</i> *	20 Jul. 2016, DE, Baden-Württemberg, Ruhestein (M. Scholler)	<i>Dryopteris dilatata</i>	KR-M-0048515	B2074	OL471657	
						MH908419	

Table 1 (continued)

Name in this article	Name on voucher (marked with *)/name in GenBank	Collection data	Host	Voucher	Lab no.	GenBank accession	Reference
<i>Pucciniastrum</i> aff. <i>circaeae</i>	<i>Pucciniastrum circaeae</i>		<i>Dryopteris dilatata</i>				Bubner et al. 2019
<i>Pucciniastrum circaeae</i>	<i>Pucciniastrum circaeae</i> *	15 Sep. 2012, CH, Fribourg, Montagny (L. Beenken)	<i>Circaea lutetiana</i>	KR-M-0042978	B2413	MH908420	Bubner et al. 2019
		23 Sep. 2012, CH, St. Gallen, Bad Ragaz (L. Beenken)	<i>Circaea lutetiana</i>	KR-M-0042977	B2414	AB221456	Liang et al. 2006
	<i>Pucciniastrum circaeae</i>		<i>Fuchsia magellanica</i>			MN399374	Ferrada et al. 2020
			<i>Fuchsia magellanica</i>			MN399375	Ferrada et al. 2020
			<i>Fuchsia magellanica</i>			MN399376	Ferrada et al. 2020
<i>Pucciniastrum epilobii</i>	<i>Pucciniastrum epilobii</i> *	3 Sep. 2016, DE, Schleswig-Holstein, Lütjenholm (U. Richter)	<i>Chamaenerion angustifolium</i>	KR-M-0048565	B1639	MK697280	
		17 Sep. 2012, DE, Baden-Württemberg, Seebach (M. Scholler)	<i>Chamaenerion angustifolium</i>	KR-M-0035186 (lectotype)	B1872	MK697279	
		4 Sep. 2016, DE, Schleswig-Holstein, Niebüll (M. Scholler)	<i>Chamaenerion angustifolium</i>	KR-M-0048573	B1873	MK697278	
		17 Jun. 2012, DE, Baden-Württemberg, Seebach (M. Scholler)	<i>Abies alba</i>	KR-M-0032739	GBOLI_c9	MK697281	
<i>Pucciniastrum fagi</i>	<i>Pucciniastrum fagi</i>		<i>Fagus crenata</i>			AB221420	Liang et al. 2006
			<i>Fagus japonica</i>			AB221421	Liang et al. 2006
			<i>Fagus crenata</i>			AB221422	Liang et al. 2006
			<i>Fagus crenata</i>		-	AB221423	Liang et al. 2006
			<i>Fagus crenata</i>			AB221424	Liang et al. 2006
			<i>Fagus crenata</i>			AB221425	Liang et al. 2006
<i>Pucciniastrum guttatum</i>	<i>Thekopsora guttata</i> *	30 Sep. 2013, DE, Brandenburg, Klepzig (H. Jage)	<i>Galium saxatile</i>	KR-M-0048351	B1488	OL471660	
		5 Oct. 2014, DE, Sachsen-Anhalt, Großleinungen (A. Hoch)	<i>Galium odoratum</i>	KR-M-0048352	B1489	OL471661	
		23 Jul. 2012, DE, Sachsen-Anhalt, Gräfenhainichen (H. Jage)	<i>Galium odoratum</i>	KR-M-0048353	B1490	OL471662	
		21 Aug. 2001, DE, Baden-Württemberg, Immendingen (H. Jage)	<i>Galium odoratum</i>	KR-M-0022614	B1572	OL471663	
		13 Oct. 2008, DE, Baden-Württemberg, Vogtsburg im Kaiserstuhl (H. Jage)	<i>Galium odoratum</i>	KR-M-0036215	B1575	OL471664	
			<i>Hydrangea peitolaris</i>			AB221438	Liang et al. 2006

Table 1 (continued)

Name in this article	Name on voucher (marked with *)/name in GenBank	Collection data	Host	Voucher	Lab no.	GenBank accession	Reference
<i>Pucciniastrum hydrangeae--petiolaris</i>	<i>Pucciniastrum hydrangeae--petiolaridis</i>		<i>Hydrangea petiolaris</i>			AB221439	Liang et al. 2006
<i>Pucciniastrum minimum</i>	<i>Thekopsora minima</i>		<i>Vaccinium corymbosum</i>			MH029898	Pazdiora et al. 2019
			<i>Vaccinium corymbosum</i>			MN880392	Wichura et al. 2020
			<i>Epilobium watsonii</i>			DQ445907	Hietala et al. 2008
<i>Pucciniastrum pustulatum</i>	<i>Pucciniastrum epilobii</i>		<i>Epilobium ciliatum</i>			MK697275	
	<i>Pucciniastrum epilobii</i> *	29 Aug. 2012, DE, Saarland, Losheim am See (H. Jage, D. Schulz)	<i>Epilobium ciliatum</i>	KR-M-0035529	B1871		
		30 Sep. 2009, DE, Sachsen, Bobritzsch (F. Klenke)	<i>Oenothera acaulis</i>	KR-M-0029499	B2302	MK697277	
		20 Jun. 2008, DE, Sachsen, Bobritzsch (F. Klenke)	<i>Oenothera acaulis</i>	KR-M-0001698	B2303	MK697276	
		10 Sep. 2012, CH, Zürich, Winterthur-Heiligenberg (L. Beenken)	<i>Epilobium montanum</i>	KR-M-0042974	B2386	OL813493	
		3 Oct. 2014, D, Rheinland-Pfalz Siebenbornweiher (L. Beenken)	<i>Epilobium montanum</i>	KR-M-0042976	B2391	OL813494	
		23 Sep. 2012, CH, St. Gallen, Bad Ragaz (L. Beenken)	<i>Epilobium montanum</i>	KR-M-0042975 (neotype)	B2437	OL813495	
<i>Quasipucciniastrum ochraceum</i>	<i>Pucciniastrum agrimoniae</i>		<i>Agrimonia pilosa</i>			MG787116	Ji et al. 2019
			<i>Agrimonia pilosa</i>			MG787117	Ji et al. 2019
			<i>Agrimonia pilosa</i>			MG787118	Ji et al. 2019
			<i>Agrimonia pilosa</i>			MG787119	Ji et al. 2019
			-			KJ486536	Qi et al. 2019
			-			KJ486537	Qi et al. 2019
			<i>Agrimonia eupatoria</i>			MK697303	
	<i>Puccinicastrum agrimoniae</i> *	2 Aug. 2007, DE, Baden-Württemberg, Bad Mergentheim (M. Scholler)	<i>Agrimonia eupatoria</i>	KR-M-0024910 (epitype)	B1674		
		14 Jun. 2013, DE, Thüringen, Seega (U. Richter)	<i>Agrimonia eupatoria</i>	KR-M-0036400	B1868	MK697302	
		10 Sep. 2004, USA, North Carolina, Cataloochee Cove, (M. C. Aime)	<i>Agrimonia parviflora</i>	BPI 878084	B2344	MT022018	
		18 Jun. 2005, USA, North Carolina, Cataloochee Cove (E. B. Lickey)	<i>Agrimonia parviflora</i>	BPI878085	B2345	MT022019	
		28 Sep. 2013, DE, Sachsen, Delitzsch, Laue (H. Jage)	<i>Prunus padus</i>	KR-M-0048354	B1491	OL471664	
		30 Sep. 2011, DE, Sachsen-Anhalt, Lamitz-Hassel-Tal, Rehehausen (H. Jage)	<i>Prunus domestica</i>	KR-M-0048367	B1502	OL471665	
		28 Jun. 2008, DE, Baden-Württemberg, Isny im Allgäu (M. Scholler)	<i>Prunus padus</i>	KR-M-0004078	B1578	OL471666	
<i>Thekopsora areolata</i>	<i>Thekopsora areolata</i> *	30 Aug. 2014, DE, Sachsen-Anhalt, Gohrau (H. Illig)	<i>Prunus padus</i>	KR-M-0044301	B1579	OL471667	
			<i>Prunus padus</i>	KR-M-0036234	B1581	OL471668	

Table 1 (continued)

Name in this article	Name on voucher (marked with */name in GenBank)	Collection data	Host	Voucher	Lab no.	GenBank accession	Reference
		28 Jun. 2008, DE, Baden-Württemberg, Isny im Allgäu, Rohrdorf (H. Jage)					
		11 Oct. 2014, DE, Brandenburg, Potsdam, Groß Glienicke (V. Kummer)	<i>Prunus padus</i>	KR-M-0043210	B1582	OL471669	
		11 Oct. 2014, DE, Brandenburg, Potsdam, Groß Glienicke (V. Kummer)	<i>Prunus virginiana</i>	KR-M-0041930	B1583	OL471670	
		11 Sep. 2016, DE, Bayern, Inning am Ammersee, Bachern am Wörthsee (M. Scholler)	<i>Prunus avium</i>	KR-M-0048592	B1781	OL471671	
		14 Sep. 2016, DE, Bayern, Pähl (M. Scholler)	<i>Prunus avium</i>	KR-M-0048601	B1782	OL471672	x

DE, Baden-Württemberg, Tuttlingen, Mauenheim, 25 Aug 2001, H. Jage, II (KR-M-0022603); Oberwolfach, Mittelthal, 23 Jun 2005, M. Scholler (KR-M-0026899); Sachsen, Bad Lausick, 7 Sep 2007, H. Boyle (KR-M-0027384); Rheinland-Pfalz, Mandern, Siebenbornweiher, 3 Oct 2014, leg. L. Beenken (KR-M-0042976); CH, Kt. Zürich, Winterthur, Heiligberg, 10 Sep 2012, leg. L. Beenken (KR-M-0042974); Kt. St. Gallen, Bad Ragaz, Freudenberg, 23 Sep 2012, L. Beenken (KR-M-0042975). *E. tetragonum*: DE, Baden-Württemberg, Kißlegg, Immenried, 21 Jun 2005, M. Scholler, II (KR-M-0018675).

#### Species of *Coleosporiaceae* on *Rosaceae*:

*Pucciniastrum agrimoniae*: On *Agrimonia eupatoria*, DE, Baden-Württemberg, Karlsruhe, Botanical Garden of the University, 27 Sept 2020, M. Scholler (KR-M-0045727); USA, North Carolina, Cataloochee Cove, 18 Jun 2005, E. B. Lickey (BPI 878085).

*Pucciniastrum americanum*: On *Rubus idaeus*: USA, North Carolina, Bakersville, 15 Nov 2007, A. Shank (BPI 878362); Asheville, 21 Sep 2007, D. Ducharme (BPI 878363), Pennsylvania, Moshannon Dam, 9 Sep 1938, L. O. Overholts (BPI 847164).

*Thekopsora areolata*: On *Prunus padus*, DE, Baden-Württemberg, Rohrdorf, 28 Jun 2008, M. Scholler (KR-M-004083); Sachsen, Reibitz, 28 Sept 2013, H. Jage (KR-M-0048130); Hungary, Tarcsafüred, 30 Aug 1916, G. Moesz (KR-M-0005810).

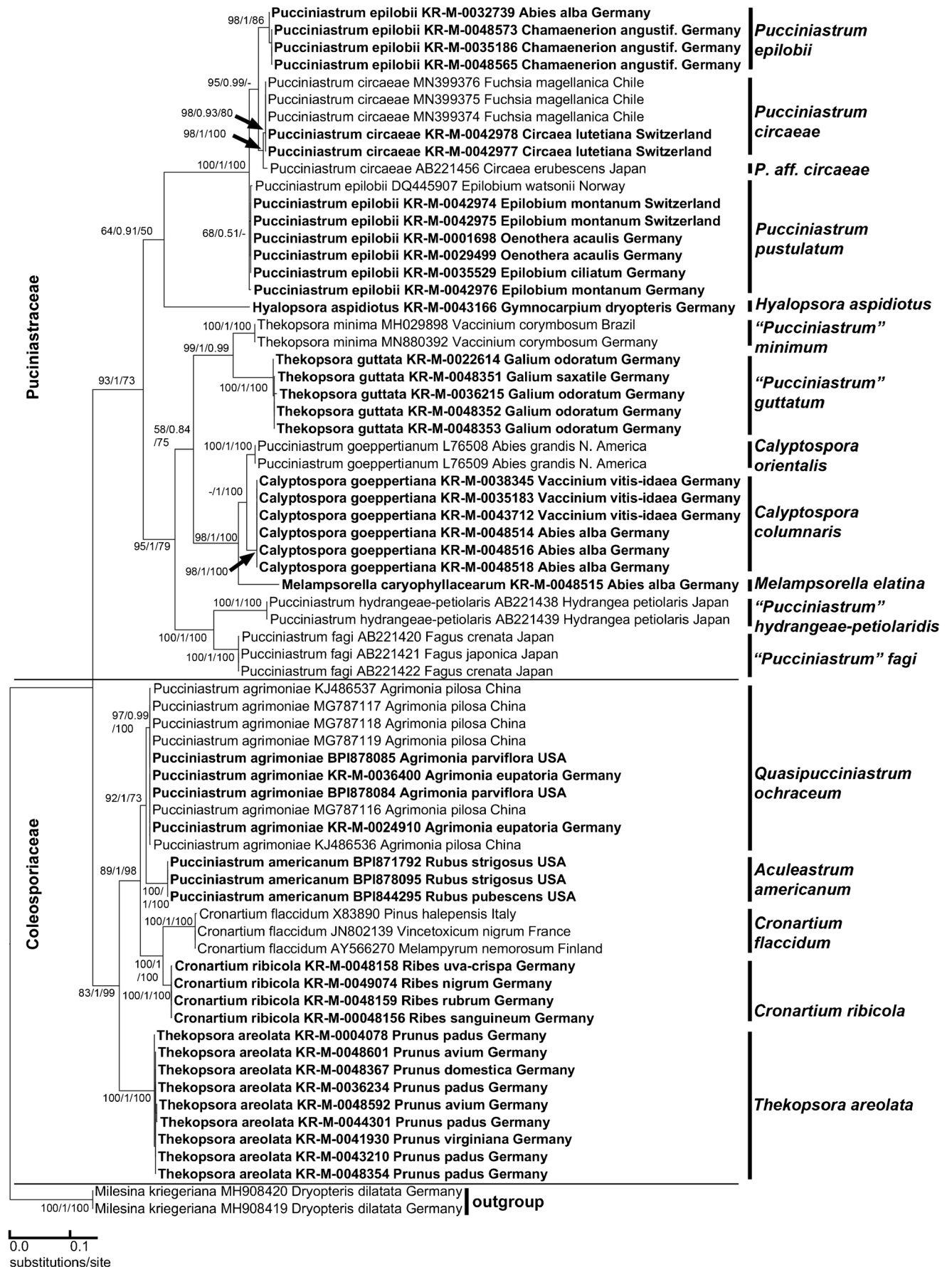
## Results

### Phylogenetic analysis

Two major clades obtained by the analysis of ITS rDNA data of rust species placed or formerly placed in the genus *Pucciniastrum* (Fig. 1) coincide with the families *Pucciniastraceae* and *Coleosporiaceae* as determined with the more conservative markers used by Aime and McTaggart (2020). Specimens named *Pucciniastrum* are mainly found in the *Pucciniastraceae*, but two species originally included in *Pucciniastrum* cluster in the *Coleosporiaceae* s. str. Aime and McTaggart (2020).

### *Pucciniastraceae*

The phylogenetic analysis shows that all species in the *Pucciniastraceae* have aecial host species in the subfamily *Abietoideae* (*Pinaceae*). The position of *Hyalopsora aspidiotus* is not yet clear because the support values for the maximum likelihood and the maximum parsimony analyses are relatively low. The ITS phylogeny places this species in the *Pucciniastraceae* in contrast to the higher rank phylogeny





◀ **Fig. 1** ITS phylogenetic tree of selected *Pucciniastrum* species and related genera. The phylogram is based on a 742-bp alignment. A maximum likelihood (ML) tree is shown with support values for ML, Bayesian Inference (BI), and maximum parsimony (MP), in the order ML/BI/MP. Support values above 50 (ML) or 0.5 (BI, MP) are presented. The host is indicated after the voucher numbers. Sequences in bold type are newly generated for this study. *Pucciniastrum* in quotation marks means that the taxa are not the subject of this study and need revision. They were provisionally placed in *Pucciniastrum*

presented by Aime and McTaggart (2020) which places this species in the *Coleosporiaceae*.

Among the European species of *Pucciniastrum* s. str., two species on *Onagraceae* can be distinguished with high support values, one on *Chamaenerion* and another one on *Epilobium* and *Oenothera* spp. They are not sister species. The reference sequence of *P. circaeae* on *Circaea erubescens* from Japan is clearly distinct from sequences of *P. circaeae* on *Circaea lutetiana* from Switzerland (7 different bases of 606 bp) and *Pucciniastrum* on *Fuchsia*. The Japanese species is considered an undescribed species (*P. aff. circaeae*), whereas the *Fuchsia* rust is conspecific with *P. circaeae*. In this respect, we follow Garibaldi et al. (2012) who previously placed *P. fuchsiae* in *P. circaeae*. The next clade consists of *Thekopsora minima* (host-alternating with *Tsuga*) and *T. guttata* (aecial host unknown), two species that are morphologically poorly known. An important feature in rust fungi, the number and position of pores in urediniospores, e.g., are not known for *T. guttata* (Klenke and Scholler 2015) or for *T. minima* (Arthur 1934). Both species as well as the basal *Pucciniastrum* species from Asia (Fig. 1) should be placed in different genera, but more studies are necessary to describe the genera. We provisionally placed them in *Pucciniastrum*. *Calyptospora* is reported from Europe and North America. In the present phylogeny, the European and the American specimens can be differentiated as two species (Fig. 1). These two species are not closely related to the cluster containing *Pucciniastrum* s. str. Therefore, a placement in a separate genus (*Calyptospora*) is justified from the phylogenetic perspective. The European species was sequenced from both the aecial host, *Abies alba*, and the telial host, *Vaccinium vitis-idea*, thus proving the host alternation of this rare species by molecular methods. The sister genus of *Calyptospora*, *Melampsorella*, is characterized by special symptoms (witches' brooms) and morphology and deserves a separate genus. Both genera have *Abies* aecial hosts.

### **Coleosporiaceae**

The ITS phylogeny shows that *Coleosporiaceae* species are restricted to hosts of the *Pinoideae* (*Pinus*) and *Piceoideae* (*Picea*). All species with *Rosaceae* telial hosts are placed in

*Coleosporiaceae* confirming the results of Aime and McTaggart (2020).

Sequences retrieved from *Pucciniastrum* on *Agrimonia* spp. in Asia (China), Europe (Germany), and North America (USA) cluster together and coincide with each other, suggesting a single species, which is, however, phylogenetically distant from *P. epilobii* and thus *Pucciniastrum* s. str. (for nomenclatural changes see below and right column in Fig. 1). *Pucciniastrum americanum* clusters with *Pucciniastrum* on *Agrimonia* spp. and is phylogenetically closely related. The sequence of the holotype *Quasipucciniastrum agrimoniae* (voucher HMAS248095, GenBank MK208281, Qui et al. 2019) comprises only ITS2 and, therefore, has not been included in the phylogenetic analyses of Fig. 1. Sequence comparisons with the ITS2 showed that it is completely identical with the ITS2 of the newly generated sequences of *Quasipucciniastrum ochraceum*.

## **Taxonomy, morphology, and nomenclature**

### **Puccinastreaceae**

#### ***Pucciniastrum* on *Epilobium* s. lat.**

Our studies show that *Pucciniastrum* species on *Epilobium* s. lat. (*Epilobium* incl. *Chamaenerion*) may be separated into three morpho-taxa which correspond well with the phylogenetic results. These taxa are named *Pucciniastrum epilobii* (on *Ch. angustifolium*), *P. pustulatum* (on *Epilobium* spp. and *Oenothera* spp.), and *P. epilobii-dodonei* (on *Ch. dodonei*). *Pucciniastrum epilobii-dodonei* is characterized by its systemic growth that deforms its host and prevents flowering. This species is known only from *Chamaenerion dodonei*. The species forms uredinia and telia amphigenously. Telia are small, 0.05–0.15 mm. *Pucciniastrum epilobii* is not systemic. The species forms uredinia and telia amphigenously. Telia measure 0.05–0.7 mm. Urediniospores measure 16.5–22.0 × 11.5–15 µm. The surface of spores is usually covered evenly with spines; we found spine-free areas only very rarely (Fig. 2c, d). Urediniospore germ pore number is 4–7. The third species, *P. pustulatum*, is not systemic and was verified on *Epilobium* (s. str.) spp. and on *Oenothera* spp. We did not observe any specimens with telia for this species. Urediniospores match the size, shape, and germ pore number of *P. epilobii*, but about 25% have at least one spine-free zone (Fig. 2e, f). Since all three species may occur on *Ch. dodonei* (Gäumann 1959), these features help to morphologically distinguish the species.

## Key to the *Pucciniastrum* species on *Epilobium* s. lat. in Europe:

- 1 Telia present ..... 2  
 1\* Only uredinia present ..... 3  
 2 Telia 0.05–0.15 mm diam., mycelium systemic, host plant deformed, not flowering, on *Chamaenerion dodonaei* ..... *P. epilobii-dodonaei*  
 2\* Telia 0.05–0.7 mm diam, not systemic, on *Ch. angustifolium* ..... *P. epilobii*  
 3 Mycelium systemic, host plant deformed, not flowering, mainly on *Chamaenerion dodonaei* ..... *P. epilobii-dodonaei*  
 3\* Mycelium not systemic ..... 4  
 4 Urediniospores always uniformly covered with spines, forming III, mostly (only?) on *Ch. angustifolium* ..... *P. epilobii*  
 4\* About 25% of urediniospores with spine-free areas on the spore surface, III usually not formed, on *Epilobium* spp., also on *Oenothera* spp. and possibly on *Clarkia* ..... *P. pustulatum*

*Uredo pustulata*, introduced by Persoon (1801), was the first name involved in the *Pucciniastrum epilobii* complex. Persoon (l.c.) separated this species into two unranked taxa,  $\alpha$ . *epilobii* (on *Epilobium montanum*) and  $\beta$ . *cerastii*. De Candolle (1815) listed *U. pustulata* and its subspecific taxa according to Persoon (l.c.), and he determined them in the accompanying text as varieties. De Candolle used the names “*epilobiorum*” and “*cerastiorum*” (plural) since he cited in each case two hosts for the two taxa, but he did not intend to introduce new varieties, so that “*epilobiorum*” and “*cerastiorum*” should rather be considered orthographic variants of Persoon’s names. Schlechtendal (1824) removed  $\beta$ . (var.) *cerastii* from *U. pustulata* and raised this taxon to species rank as *Caeoma cerastii* (Pers.) Schltdl., which is currently a synonym of *Melampsorella caryophyllacearum* (DC.) J. Schröt. In doing so, Schlechtendal (l.c.) confined *U. pustulata* to var. *epilobii*, which constituted a kind of “indirect lectotypification”. Hence, since that time, the species name *U. pustulata* referred to the rust fungus on *Epilobium* spp., and it was later correctly used in this sense as basionym for several combinations, such as *Erysibe pustulata*, *Melampsora pustulata*, and *Pucciniastrum pustulatum*.

Otth (1861: p. 71) described the new genus *Pucciniastrum* with *P. epilobii* as type species. “(Pers.) G.H. Otth” was often referred to as author citation for the latter species name, suggesting that Otth (l.c.) had based this name on *Uredo pustulata*  $\alpha$ . *epilobii* (conforming to var. *pustulata*), but this is incorrect. On p. 65, Otth (l.c.) introduced the new combination *Uredo epilobii* (Pers.) G.H. Otth. Under *P. epilobii*, he only stated “first fructification form: *Uredo*. Lévl.” [an indirect reference to Lévillé (1847: pp. 371–372), where only *Uredo pustulata*

had been cited]. *P. epilobii* itself was just introduced as follows: “*P. epilobii*. (*Sclerotium*. Chailllet.)” [and the genus name *Pucciniastrum* as “*Pucciniastrum* Otth (olim *Sclerotium* et *Melampsora*)”]. Otth’s (l.c.) reference to *Sclerotium* and *Melampsora* was undoubtedly related to Lévillé (1847: p. 375), who cited *Sclerotium herbarum* var. *epilobii* Fr. under *Melampsora*. The name concerned had been published by Chailllet in Fries (1828: p. 44) as *Sclerotium herbarum* f. *epilobii*. The question arises as to whether Otth (l.c.) intended to introduce a new combination based on *S. herbarum* f. *epilobii*, as Otth’s (1863: p. 85) later citation of its own name as “*P. epilobii* (Chaill.)” would suggest, or if he had in mind a new species, with *S. herbarum* f. *epilobii* as synonym (the latter name is a forma that does not have priority on species rank). Otth’s treatment of his own name *P. epilobii* in “Wartmann & Schenk, Schweizerische Kryptogamen 615” (Fig. 2a) allows interpretation of Otth’s intentions. In this exsiccata, he cited *S. herbarum* f. *epilobii* as a synonym of *P. epilobii* sp. nov., i.e. he had a new species in mind and did not intend to introduce a new combination (comb. et stat. nov.) based on Chailllet’s forma.

In the original publication, Otth (1861) did not provide details for the specimens examined, but in his supplement (Otth 1863) he listed an undated collection from “Heimberg, on *Epilobium angustifolium*” which is undoubtedly original material (ICN, Art. 9.4) available for lectotypification. This material is preserved and deposited in the herbarium in Zürich as ZT Myc 43369 and the only preserved collection from Otth’s herbarium under the name *P. epilobii* (the material distributed in “Wartmann & Schenk, Schweizerische Kryptogamen 615” was collected in 1869, i.e. it does not represent original material). Whether Otth had examined any material collected by Chailllet, which would also be original material, remains unclear. To stabilize available names within the *P. epilobii* complex, it is necessary to clarify the typification of the names involved and to propose epitypes that can be sequenced to get data for their phylogenetic characterization. The search for type material of Chailllet’s taxon in several herbaria, including G, HAL (herb. Schlechtendal), UPS, and ZT, was not successful, suggesting that type material was probably not preserved.

Importantly, the common *Pucciniastrum* on *Epilobium* spp. without host alternation, usually appearing as uredinia, may also occur on *Chamaenerion* spp. (Gäumann 1941; Hietala et al. 2008).

*Pucciniastrum pustulatum* represents the oldest valid name for *Pucciniastrum* on *Chamaenerion* and *Epilobium* spp. and other species of genera of the *Onagraceae* and would be the correct name if the collections on all hosts were regarded as a single species. Most previous authors used the name *P. epilobii* in this broad sense. On the other hand, some previous authors, such as Kuprevich and Ul’yanishchev (1975), already recognized two species, in the latter case as *P. abietischamaenerii* and *P. pustulata*. However, taking into account

the latest phylogenetic results for the *P. epilobii* complex (Hietala et al. 2008, the present work), connected with the phylogenetic differentiation of *Epilobium* s. lat. into two well-supported clades (*Epilobium* s. str. and *Chamaenerion*, see Baum et al. 1994, Wagner et al. 2007), as well as obvious differences in the development cycles, biological specialization of the taxa involved and morphological differences (see above), this complex must be split into two species, one of them confined to *Chamaenerion* spp. (= *Pucciniastrum epilobii*) and another polyphagous one to species of the genera *Epilobium*, *Oenothera*, and possibly *Clarkia* (Klenke and Scholler 2015) and *Chamaenerion* (Gäumann 1959) (= *P. pustulatum*):

***Pucciniastrum epilobii*** G.H. Otth, Mitt. Naturf. Ges. Bern 476-479: 72, 1861.

Lectotype (designated here, MycoBank, MBT10006098): Switzerland, Heimberg, on *Chamaenerion angustifolium* (= *Epilobium angustifolium*), undated, G.H. Otth (ZT Myc 43369). Epitype (designated here, MycoBank, MBT10006099): Germany, Baden-Württemberg, Ortenaukreis, Seebach, 980 m, 17 Sep 2012, II III, leg. & det. M. Scholler (KR-M-0035186). Ex-lectotype sequence: MK697279.

≡ *Phragmopsora epilobii* (G.H. Otth) Magnus, Hedwigia 14: 123, 1875.

= *Sclerotium herbarum* f. *epilobii* Chaillet, in Fries, Elench. fung. 2: 44, 1828.

≡ *Sclerotium herbarum* var. *epilobii* (Chaillet) Lév., Ann. Sci. Nat., Bot., Sér. 3, 8: 375, 1847.

= *Melampsora epilobii* Fuckel, Fungi Rhen. Exs., Fasc. 3: n. 300, 1863.

= *Pucciniastrum abietis-chamaenerii* Kleb., Jahrb. Wiss. Bot. 34: 387, 1900.

= ? *Pucciniastrum chamaenerii* Rostr., Plantepatologi: 304, 1902.

≡ On *Chamaenerion angustifolium* (and possibly *Ch. dodonaei*) [type host: *Ch. angustifolium*].

Fuckel, in Fungi Rhen. 300, 1863 [and Fuckel (1870: p. 44)] introduced the name *Melampsora epilobii* (Fig. 2b). Fuckel listed two different specimens under no. 300, viz., 300. I. (*Uredo epilobii* DC. on *Epilobium montanum*) and 300. II. (*Melampsora epilobii* Fuckel on *Chamaenerion angustifolium*). The examination of the urediniospores on *Epilobium montanum* (KR), identified by Fuckel as “*Uredo epilobii*”, revealed that they belong to *Uredo pustulata*. Different interpretations of the name *M. epilobii* are possible. Fuckel cited *Uredo epilobii* DC. under *M. epilobii*, which could be interpreted as citation of a synonym for the asexual uredinia/urediniospores on another host (*Epilobium montanum*), i.e. in this scenario, a valid name that should have been adopted according to the current Code would have been included in the protologue. With a different epithet, Fuckel’s

name would in this case be interpretable to be superfluous (nom. illeg. [nom. superfl.], Art. 52.1), but since he used the epithet “*epilobii*” Fuckel’s name could also be considered a new combination based on de Candolle’s *Uredo epilobii*, a species that does, however, not belong to the *Pucciniastrum epilobii* complex. In this case, Fuckel’s *M. epilobii* would be a homotypic synonym of *Uredo epilobii* DC. (This name is still unresolved, but according to the original description, it might rather be a synonym of *Puccinia pulverulenta* Grev.) However, Fuckel (l.c.) indicated that he intended to introduce the name *M. epilobii* only for the telia found on *Chamaenerion angustifolium* (“II. *Melampsora propria*”) [proprius = exclusively belonging to]. Thus instead, *M. epilobii* represents a separate valid species name confined to *Chamaenerion angustifolium* (Art. F.8.1), which has to be reduced to synonymy with *Pucciniastrum epilobii*. This name requires lectotypification: ***Melampsora epilobii*** Fuckel, Fungi Rhen. Exs., Fasc. 3: n. 300, 1863. **Lectotype** (designated here, MycoBank, MBT10006100): Germany, “in sylva Hostrichensi” (Hessen, Oestrich), on *Chamaenerion angustifolium*, autumn, Fuckel, Fungi Rhen. Exs. 300 (HAL, s.n.). Isolectotypes: Fuckel, Fungi Rhen. Exs. 300 (e.g. B, G, WIES).

***Pucciniastrum pustulatum*** (Pers.) Dietel, in Engler & Prantl, Nat. Pflanzenfam., Teil. I (Leipzig) 1(1\*\*): 47, 1897.

≡ *Uredo pustulata* Pers., Syn. meth. fung. (Göttingen) 1: 219, 1801.

≡ *Uredo pustulata* α. (var.) *epilobii* Pers., Syn. meth. (Göttingen) 1: 219, 1801 [de Candolle (1815: 85) as “*epilobiorum*” (orthographic variant)].

≡ *Erysibe pustulata* (Pers.) Wallr., Fl. crypt. Germ. (Norimbergae) 2: 198, 1833.

≡ *Uredo epilobii* (Pers.) G. H. Otth, Mitt. Naturf. Ges. Bern 476-479: 65, 1861, nom. illeg. (Art. 53.1), non DC., 1815.

≡ *Melampsora pustulata* (Pers.) J. Schröt., in Cohn, Krypt.-Fl. Schlesien (Breslau) 3.1(17–24): 364, [1889] 1887.

= ? *Pucciniastrum epilobii* (Chaillet) G. H. Otth f. sp. *palustris* Gäum., Ber. Schweiz. Bot. Ges. 51: 340, 1941.

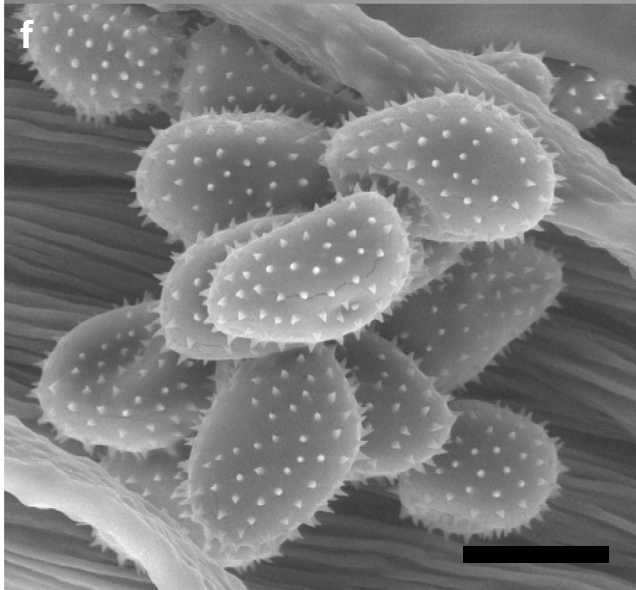
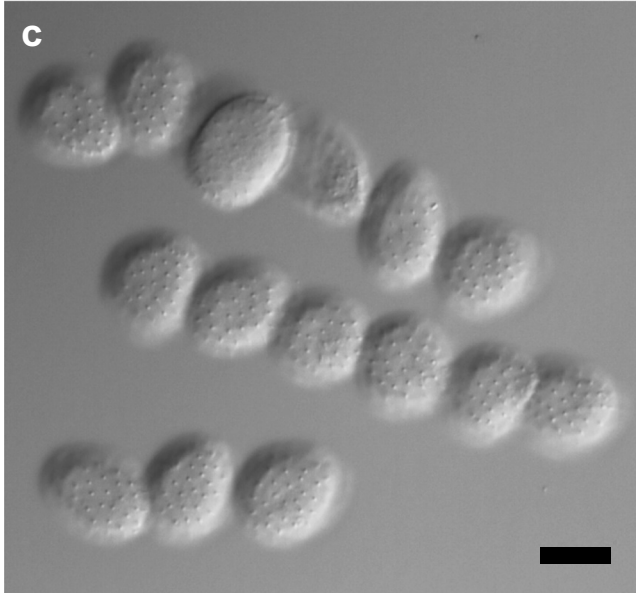
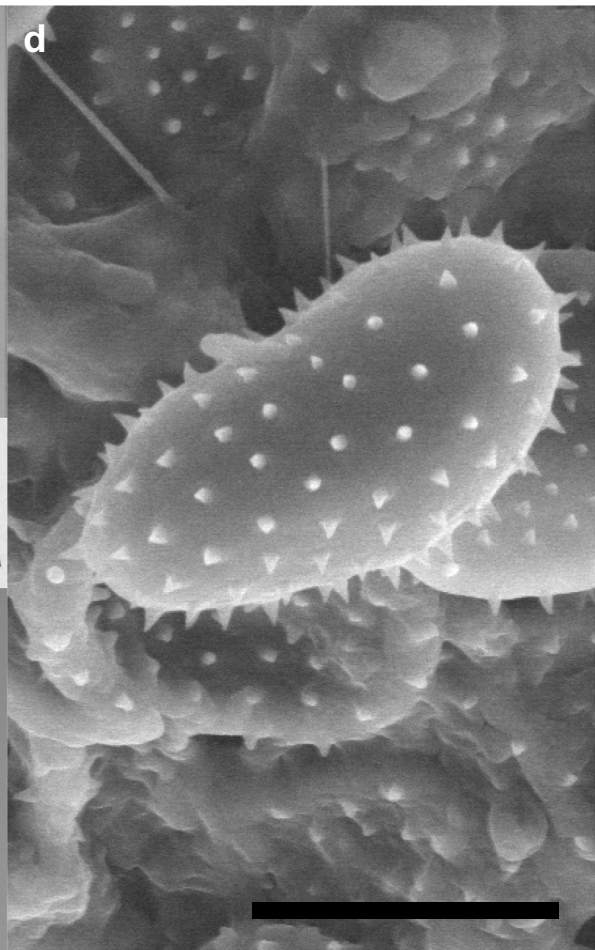
Neotype (designated here, MycoBank, MBT10006101): On *Epilobium montanum*, Switzerland, St. Gallen, Bad Ragaz, Freudenberg, 520 m 47.00789 N, 9.49389 O, 23 Sept 2012, L. Beenken (KR-M-0042975), duplicated in the personal herbarium of L. Beenken, no. 8951). Ex-neotype sequence: OL813495.

On *Epilobium*, ?*Chamaenerion*, ?*Clarkia* and *Oenothera* spp. [type host: *Epilobium montanum*].

Notes: Jørstad (1958) dealt with the typification of *Aecidium*, *Uredo*, and *Puccinia* names published by Persoon, including some lectotypifications and detailed discussions about suitable and inappropriate collections deposited in Persoon’s herbarium under the names concerned. Only two samples from Persoon’s herbarium, possibly collected until Persoon (1801), are preserved under the name *Uredo*

**a** Wartmann und Schenk, Schweizerische Kryptogamen.  
**615. Pucciniastrum Epilobii Otth**  
 nov. spec.  
 a) Uredo (nicht *U. Epilobii* DC.). Häufchen klein, satt-gelb, meist mehrere zusammen gruppiert. Sporidien gelb, fein punktiert-schärflich, von Anfang an weder gestielt, noch verkettet, sondern konglomeriert, bei der Reife aus einander fallend.  
 b) *Pucciniastrum* (*Sclerotium herbarum*, forma *Epilobii* Chaillet). Zahlreiche, schwarzbraune, oft zusammenfließende Wäzchen, aus ziemlich fest verbundenen Sporangien bestehend. Sporangien glatt, braun, rundlich oder etwas länger als breit, ungestielt, von verschiedener Konformation, nämlich entweder, obgleich seltener, einfach, oder aber bald mit einer Quer-, bald mit einer Vertikal-Scheidewand, bilokular oder auch zuweilen durch Kombination von beiderlei Scheidewänden 3–4zellig.  
 Bei Bern, an der Unterseite der Blätter von *Epilobium angustifolium* L. im Herbst.  
 1869. G. Otth.

**b** 300.  
**Melampsora Epilobii Fekl.**  
 I. Uredo ejus.  
 Syn. *U. Epilobii* DC.  
 Ad *E. montani*, *rosei* et *angustifolii* folia, frequens. Aestate.  
 II. *Melampsora* propria.  
 Acervulis planis, confluentibus, atro-fuscis; sporidiis obovato-clavatis, fuscis.  
 Ad *E. angustifolii* foliorum marcescentium paginam inferiorem, raro. Autumno. in sylvä Hostrichiensi.



◀ **Fig. 2** **a** Label of “Wartmann & Schenk, Schweizerische Kryptogamen 615, 1869” (KR-M-0013186). **b** Label of “Fuckel, Fungi Rhen. 300, 1863” (HAL). **c** *Pucciniastrum epilobii* on *Chamaenerion angustifolium* (KR-M-0048573), urediniospore surface (LM, DIC) (bar = 10 µm) (photograph R. Buchheit). **d** *Pucciniastrum epilobii* on *Ch. angustifolium* (KR-M-0048565), urediniospore surface (SEM) (bar = 10 µm) (photograph R. Buchheit/M. Scholler). **e** *Pucciniastrum pustulatum* on *Epilobium ciliatum* (KR-M-0022644), Urediniospore surface with spine-free surface areas (arrows) (LM, DIC) (bar = 10 µm) (photograph R. Buchheit). **f** *Pucciniastrum pustulatum* on *E. montanum* (KR-M-0022603), urediniospore surface of with spine-free surface areas (SEM) (bar = 10 µm) (photograph R. Buchheit/M. Scholler)

*pustulata*, viz. L 0119128 (= 910264190) and L 0119129 (= 910264191), the latter as “*Uredo epilobiae*” (see also Jørstad 1958: p. 9). All collections are undated. However, Persoon (1801) published *Uredo pustulata* *α. epilobii* on *Epilobium montanum*, whereas the host name for the two collections is given only as “*Epilobium*”. Hence, it is unclear whether these collections are suitable as potential lectotypes and if they were collected prior to 1801. Three additional collections preserved at Leiden herbarium under *Uredo pustulata*, viz., L 0119130 (G.B. Balbis, s.n.), L 0119131 (J.F. Chailett), and L 0119132 (J.F. Chailett), were collected after 1801 and are unsuitable for lectotypification purposes (see also comments in Jørstad 1958). Therefore, the designation of a neotype for this taxon seems to be indicated, which also allows determining the genetic position of this species by ex-neotype sequences.

Another European *Pucciniastrum* species on *Onagraceae* (*Oenothera*), *Pucciniastrum oenotherae* Gaillard, is a chytrid (*Synchytrium fulgens* J. Schröt.) according to Sydow and Sydow (1915).

***Pucciniastrum epilobii-dodonaei*** Dietel & Eichhorn, in Sydow, Ann. Mycol. 40(3/4): 196, 1942.

Lectotype (designated here, MycoBank, MBT10006102): Austria, Kärnten, Hermagor Kreis, Mauthen, Valentin-Bach, on *Chamaenerion dodonaei*, Aug. 1940, H. Poeverlein [Petra, Mycoth. Gen. 1667] (KR-M-0023486). Syntypes: Crypt. Exs. 3415; Petra, Mycoth. Gen. 1667; Syd., Mycoth. Germ. 3447, e.g. B, BPI 144511, 843061; BR5020114094226; F-C0170610F; GZU; K-M186964; NY 71708; S-F30543, 30547; W; WSP19044; Z Myc 6462.

On *Chamaenerion dodonaei*.

## Further *Pucciniastraceae* species and genera

### *Calyptospora*

*Calyptospora* (Kühn 1869), based on *C. goeppertiana* as type species, has proven to be a genus of its own because of its special life cycle (forming no uredinia), its morphological characteristics (telia in particular), and its phylogenetic position distant from *Pucciniastrum* s. str., as determined by its type species, *Pucciniastrum epilobii* (Aime et al. 2018 and

phylogeny in this study). Albertini and von Schweinitz (1805) introduced *Aecidium columnare*, based on spermogonia and aecia on *Abies alba* (*Pinus picea*) in Lusatia (Lausitz, Germany). This name was later reallocated to *Peridermium* (Schmidt and Kunze 1817), *Caeoma* (Link 1825), *Uredo* (Sprengel 1827), *Melampsora* (von Wettstein 1885), and *Thekopsora* (Hiratsuka 1927). Kühn (in Rabenh., Fungi Eur. Exs. 3521, 1886, Fig. 2b) published results of inoculation experiments, distributed several collections, and discussed the taxonomy and nomenclature of *Calyptospora*. He ascertained the synonymy of *Aecidium columnare* and *C. goeppertiana*, and, because of the priority of *A. columnare*, he introduced the new combination *Calyptospora columnaris*. We prefer to maintain the name *Calyptospora columnaris* for this rust fungus, based on the oldest basionym, *Aecidium columnare*, which has priority according to Art. F.8.1, Note 2, although there is not automatism in the nomenclature of pleomorphic fungi, i.e. it would also be possible to propose maintaining the younger teleomorph-typified name *C. goeppertianum* by protection or by adding it to a list of names proposed for protection, according to Art. F.2.1. However, Kühn (1869) accepted the oldest names and introduced the corresponding combination.

Another problem concerns North American collections of *C. goeppertiana* s. lat. Two North American species are known, viz. *Peridermium ornamentale* (Arthur 1901), described based on an aecial host collection on *Abies lasiocarpa* from Washington, and *Pe. holwayi* (Sydow and Sydow 1903), introduced for aecial host spore stages (0 and I) found on *Pseudotsuga menziesii* in Canada, British Columbia. Arthur (1934) reduced both species names to synonymy with *Pucciniastrum goeppertianum*, but Faull (1939) disagreed and emphasized that collections of *C. goeppertiana* s. lat. are morphologically differentiated into two taxa, viz. *C. goeppertiana* s. str. in eastern North America and a taxon in western North America for which the name *Pe. ornamentale* is available. The existence of a different taxon of *Calyptospora*, possibly a species of its own, in western North America was already assumed by Weir (1926). In the western taxon, *Pe. ornamentale*, the aecia and spermogonia (type 3, according to Cummins and Hiratsuka 2003) are formed on current year needles in late summer or early autumn, whereas in *P. goeppertianum* from eastern North America aecia are formed in early summer, but spermogonia are lacking or sometimes developed only in de-generated form (Hiratsuka et al. 1967). *Pe. holwayi* has usually been reduced to synonymy with *Pe. ornamentale*, but the genuine identity of this species, based on an aecial host spore stage on *Pseudotsuga menziesii*, remains unclear and needs further detailed examinations, including phylogenetic analyses. Aecia of *P. holwayi* occur on *Pseudotsuga*, and are formed on previous year needles in early summer, in contrast to *P. ornamentale* growing on *Abies* and forming aecia on current year needles in late summer or early autumn. Vogler and Bruns (1998) generated sequence data retrieved from

*Calyptospora goeppertiana* s. lat. (= *Peridermium ornamentale*) on *Abies grandis* (native to the Pacific Northwest and Northern California), belonging to the western taxon in North America. These sequences have been included in the present phylogenetic analysis. They cluster in sister position to the European sequences of *C. columnaris*. Thus, these preliminary data support Weir's (1926) and Faull's (1939) careful examinations and conclusions that there is a different *Calyptospora* species in western North America for which the name *Pe. ornamentale* is available. However, this can only be the very first step towards a revision of the *C. goeppertiana* complex in North America. The taxonomic and phylogenetic position of *Calyptospora goeppertiana* in eastern North America, although morphologically indistinguishable from European collections of this species, is still unproven, i.e. it remains open whether the eastern North American taxon is actually conspecific with *C. goeppertiana* s. str. or if a third species may exist.

The nomenclature of the two species involved in this complex can be summarized as follows:

***Calyptospora columnaris*** (Alb. & Schwein.) J.G. Kühn, in Winter, Fungi Eur. Extraeur. Exs. (Klotzschii Herb. Viv. Mycol. Continuatio, Editio Nova, Ser. Secunda), Cent. 36: no. 3521, 1886.

Basionym: *Aecidium columnare* Alb. & Schwein., Consp. fung.: 121, 1805.

Holotype: Germany, Lusatia [herb. Schweinitz], s. n., on *Abies alba* [*Pinus picea*] (PH 313374).

≡ *Peridermium columnare* (Alb. & Schwein.) J.C. Schmidt & Kunze, Deutschl. Schwämme, Sechste Lieferung: 4, 1817.

≡ *Caeoma columnare* (Alb. & Schwein.) Link [as 'columnum'], Sp. pl., Edn 4, 6(2): 66, 1825.

≡ *Uredo columnaris* (Alb. & Schwein.) Spreng., Syst. veg. 4(1): 570 1827.

≡ *Melampsora columnaris* (Alb. & Schwein.) Wettst., Verh. K. K. Zool.-Bot. Ges. Wien 35: 551, 1885.

≡ *Thekopsora columnaris* (Alb. & Schwein.) Hirats., J. Soc. Agric. Forest. Sapporo 19(85): 167, 1927.

= *Calyptospora goeppertiana* J.G. Kühn [as 'geoppertiana'], Hedwigia 8: 81, 1869.

≡ *Melampsora goeppertiana* (J.G. Kühn) G. Winter, in Rabenh. Krypt.-Fl., Edn 2 (Leipzig) 1.1: 245, 1881.

≡ *Pucciniastrum goeppertianum* (J.G. Kühn) Kleb., Wirtswechselnde Rostpilze: 391, 1904.

***Calyptospora ornamentalis*** (Arthur) M. Scholler & U. Braun, **comb. nov.**

Mycobank, MB843211.

Basionym: *Peridermium ornamentale* Arthur, Bull. Torrey Bot. Club 28: 665, 1901.

Holotype: USA, Washington, Mount Paddo, on *Abies lasiocarpa*, 4 Sep. 1900, W.N. Suksdorf 588 [ex herb.

Holway] (PUR 4132). Isotypes: BPI 154167; NY 618085, 618086; S-F26253.

## ***Melampsorella***

***Melampsorella elatina*** (Alb. & Schwein.) Arthur, N. Amer. Fl. 7(2): 111, 1907.

≡ *Aecidium elatinum* Alb. & Schwein., Consp. fung.: 121, 1805.

≡ *Peridermium elatinum* (Alb. & Schwein.) J.C. Schmidt & Kunze, Deutschl. Schwämme, Sechste Lieferung: 4, 1817.

≡ *Caeoma elatinum* (Alb. & Schwein.) Link, in Willdenow, Sp. pl., Edn 4, 6(2): 66, 1825.

= *Uredo pustulata* β *cerastii* Pers., Syn. meth. fung. 1: 219, 1801.

≡ *Melampsora cerastii* (Pers.) G. Winter, Rabenh. Krypt.-Fl., Edn 2, 1.1: 242, 1881.

≡ *Melampsorella cerastii* (Pers.) J. Schröt., in Cohn, Krypt.-Fl. Schlesien 3.1(17–24): 366, [1889] 1887.

= *Uredo cerastii* Mart., Prodr. Fl. Mosq.: 231, 1817.

≡ *Caeoma cerastii* (Mart.) Schltdl., Fl. berol. 2: 121, 1824.

[*Caeoma caryophyllacearum* Link, in Willdenow, Sp. pl., Edn 4, 6(2): 26, 1825, nom. illeg. (Art. 52.1)].

= *Melampsorella caryophyllacearum* J. Schröt. [as "caryophylleacearum"], Hedwigia 13: 85, 1874.

≡ *Melampsoridium caryophyllacearum* (J. Schröt.) Blanchette & Biggs [as "(DC.) Blanchette & Biggs"], Defense Mechanisms of Woody Plants Against Fungi: 63, 2013.

Notes: This species has been previously mostly incorrectly cited as "*Melampsorella caryophyllacearum* (DC.) J. Schröt.". This reference seems to be influenced by Schröter (1874), who cited "(D. C. Uredo)". However, the name "*Uredo caryophyllacearum* DC., 1805" does not exist. It was neither published on p. 85 (as cited in the databases), nor in the whole volume of de Candolle (1805), nor de Candolle, in de Lamarck (1806), or de Candolle (1815). *Caeoma caryophyllacearum* Link can also not be considered as a potential basionym for *Melampsorella caryophyllacearum* because Link's *C. caryophyllacearum* is an illegitimate superfluous name (Link cited two older available names, *Caeoma stellariae* Link and *Uredo ovata* F. Strauss, as synonyms in the protologue). Therefore, *Melampsorella caryophyllacearum* must be ascribed to Schröter (1874). *Aecidium elatinum* is the oldest valid species name for this rust, so that *Melampsorella elatina* is the currently correct name.

## ***Pucciniastrum***

***Pucciniastrum circaeae*** (Thüm.) Speg., Dec. Mycol. Ital.: no. 65, 1879.

≡ *Uredo circaeae* Alb. & Schwein., Consp. fung.: 124, 1805, nom. illeg. (Art. 53.1), non Schumach., 1803.

≡ *Erysibe pustulata* (Pers.) Wallr.  $\gamma$  *circaeae* Wallr. [as “(Alb. & Schwein.) Wallr.”], Fl. Crypt. Germ. 2: 198, 1833, nom. nov. (Art. 58.1).

≡ *Melampsora circaeae* Thüm. [as “(Alb. & Schwein.) Thüm.”], Mycoth. Univ., Cent. 5: no. 447 (1876), nom. nov. (Art. 58.1).

≡ *Phragmopsora circaeae* (Thüm.) G. Winter [as “(Alb. & Schwein.) G. Winter”], Hedwigia 18: 171, 1879.

= *Uredo circaeae* Schumach. [as “*circaeae*”], Enum. pl. 2: 228, 1803.

= *Caecoma onagrarium* Link, in Willdenow, Sp. pl., Edn 4, 6(2): 29, 1825.

= *Uredo fuchsiae* Arthur & Holway, in Arthur, Amer. J. Bot. 5: 538, 1918, nom. illeg. (Art. 53.1), non *Uredo fuchsiae* (Cooke) Henn., 1903.

≡ *Pucciniastrum fuchsiae* Hirats. f., J. Fac. Agric., Hokkaido Imp. Univ., Sapporo 21(1): 98, 1927, nom. nov. (Art. 58.1).

Note: The combination *Pucciniastrum circaeae* is based on de Thümen’s replacement name *Melampsora circaeae* (≡ *Uredo circaeae* Alb. & Schwein., nom. illeg.) and not on *Uredo circaeae* Schumach., as already correctly cited by Sydow and Sydow (1915: p. 445), so that a combination using the oldest valid name for this taxon, *Uredo circaeae* Schumach., is prevented.

***Pucciniastrum minimum*** (Schwein.) Arthur, Résult. Sci. Congr. Bot. Wien 1905: 337, 1906.

≡ *Uredo minima* Schwein., Schriften Naturf. Ges. Leipzig 1: 70 [44 of Repr.], 1822.

≡ *Thekopsora minima* (Schwein.) P. Syd. & Syd. [as “(Arthur) P. Syd. & Syd.”], Monogr. Uredin. 3(3): 465, 1915.

[*Caecoma azaleae* Schwein., Trans. Amer. Phil. Soc., New Series, 4(2): 291, 1832, nom. illeg. (Art. 52.1).]

= *Peridermium peckii* Thüm., Mitth. Forstl. Versuchswesen Österreichs 2: 370, 1881.

≡ *Aecidium peckii* (Thüm.) Dietel, in Engler & Prantl, Nat. Pflanzenfam., Teil. I, 1(1\*\*): 78, 1897.

Note: *Pucciniastrum minimum* is a combination based on *Uredo minima*. *Caecoma azaleae* is a superfluous name, which was published with reference to *Uredo minima* (as “Syn. Carol. 470”), a name that should have been adopted in *Caecoma*. The species forms a separate clade, needs further investigation, and may be placed in a different genus.

***Pucciniastrum guttatum*** (J. Schröt.) Hyl., Jørst. & Nannf., Opera Bot. 1: 81, 1953.

≡ *Melampsora guttata* J. Schröt., Abh. Schles. Ges. Vaterl. Kult., Abth. Naturw. Med., 48: 26, 1870.

≡ *Thekopsora guttata* (J. Schröt.) P. Syd. & Syd., Monogr. Uredin. 3(3): 467, 1915.

= *Caecoma galii* Link, in Willdenow, Sp. pl., Edn 4, 6(2): 21, 1825, nom. illeg. (Art. 53.1), non (Pers.) Schldtl., 1824.

≡ *Melampsora galii* G. Winter [as “(Link) G. Winter”], Rabenh., Krypt.-Fl., Edn 2, 1.1: 244, 1881, nom. nov. (Art. 55.1).

≡ *Thekopsora galii* (G. Winter) De Toni [as “(Link) de Toni”], in Berlese, De Toni & Fischer, Syll. fung. 7(2): 765, 1888.

≡ *Pucciniastrum galii* (G. Winter) E. Fisch. [as “(Link) E. Fisch.”], Ured. der Schweiz: 471, 1904.

= *Uredo galii* Duby, Bot. Gall., Edn 2, 2: 896, 1830.

≡ *Trichobasis galii* (Duby) Lév., in Orbigny, Dict. Univ. Hist. Nat. 12: 785, 1849, nom. inval. (Art. 35.2).

≡ *Trichobasis galii* (Duby) Niessl, Verh. Nat. Ver. Brünn 3: 116, 1864, nom. illeg. (Art. 53.1), non Castagne 1842.

Note: *Melampsora guttata* is the nomenclaturally correct basionym for this species. *Caecoma galii* Link is an illegitimate younger homonym of *C. galii* (Pers.) Schldtl., which was only validated in 1881 as *Melampsora galii* G. Winter. *Uredo galii* Duby is not a replacement name for *Caecoma galii* Link since Duby (1830) only cited the latter name as a questionable synonym (with question mark), whereas Winter (l.c.) did not cite Duby’s name at all. The species forms a separate clade in our ITS phylogeny. It needs further investigation and may be placed into a different genus.

This also applies to *P. fagi* G. Yamada and *P. hydrangeae-petiolaris* Hirats. fil. which form a basal clade in our ITS phylogeny (Fig. 1).

## Coleosporiaceae

### Taxonomy, morphology, and nomenclature of genera and species with Rosaceae hosts

In the higher rank phylogeny of Aime and McTaggart (2020), rusts on *Rosaceae* in the *Coleosporiaceae* formerly placed in *Pucciniastrum* form a single clade with species on *Agrimonia*, *Potentilla*, *Prunus*, and *Rubus* with two well-supported subclades formed by species on *Rubus* and *Prunus*. The authors placed all species in the genus *Thekopsora* based on phylogenetic data exclusively. Our ITS phylogeny (Fig. 1) confirms that species on *Rosaceae* belong to *Coleosporiaceae*. There are three highly supported clades, one clade with *Agrimonia* as host which forms a sister clade with *Rubus* rusts and one clade with *Prunus* as host. Since there are remarkable differences between species representing the three clades, we propose placing them in three different genera, *Quasipucciniastrum* for species on *Agrimonia* and *Potentilla*, *Thekopsora* for species on *Prunus* (represented by two species, the type species *T. areolata* (Fr.) Magnus and *T. pseudo-cerasi* Hiratsuka fil.), and for species on *Rubus* we propose a new genus. Differences between them concern host range, life cycle, symptomology, and morphology and are listed in Table 2. This requires nomenclatural changes:

**Table 2** Features of the the three rosaceous rust genera *Aculeastrum*, *Quasipucciniastrum*, and *Thekopsora* (*Coleosporiaceae*) formerly placed in *Pucciniastrum*. Features of uredinia and urediniospores are inferred from this study; all other data are from Fischer (1904), Hefler (2005), Hiratsuka et al. (1992), Qi et al. (2019) (species of genera *Quasipucciniastrum*, *Thekopsora*), and from Arthur (1934) and Ziller (1974) (genus *Aculeastrum*)

	<i>Aculeastrum</i>	<i>Quasipucciniastrum</i>	<i>Thekopsora</i>
Species known	( <i>A. arcticum, americanum</i> )	( <i>Q. ochraceum, potentillae</i> )	( <i>T. areolata, T. pseudo-cerasi</i> )
Geographical distribution	Northern Hemisphere (A. <i>americanum</i> only N America)	Northern Hemisphere, Brasil	Eurasia
Life cycle and spore states	0 I/II III IV (host-alternating)	II III IV	0 I/II III IV (host-alternating)
Aecial host (plant organ)	<i>Picea</i> (needles)	-	<i>Picea</i> (cone scales)
Aeciospores	Wall 2–3 µm, verrucose, with smooth spot	-	Thick-walled (up to 6 µm), verrucose, with thin smooth stripe
Telial host: genus (subfamily)	<i>Rubus</i> (Rosoidae)	<i>Agrimonia, Potentilla</i> (Rosoidae)	<i>Prunus</i> ( <i>Spiraeoideae</i> )
# and position of urediniospore germ pores	4–6 (7), strictly bipolar	(5) 6–10, scattered	(4) 5–7(8), bipolar or scattered
Urediniospore spines	Shorter in central surface (Fig. 10)	± same length (Fig. 11)	± same length
Urediniospore powder	Yellow	Yellow	Whitish
Ostiole cells of uredinial peridium	Smooth below, coarsely arcuate above (Figs. 8, 9)	Smooth (Fig. 11)	Smooth
Teliospore formation	Intercellular, subepidermal	Intercellular, subepidermal	Intracellular in epidermis cells
Teliospore germ pores	No visible pores in mostly two- or four-celled spores	No visible pores in mostly two- or four-celled spores	One conspicuous pore/cell; pores in four-celled spores arranged very close in inner edge



### *Quasipucciniastrum* on *Agrimonia*

*Uredo potentillarum* var. *agrimoniae-eupatoriae* (de Candolle 1815), based on European type material on *Agrimonia eupatoria*, is the oldest taxon introduced for a rust species previously usually referred to as *Pucciniastrum agrimoniae* or *Thekopsora agrimoniae*. De Candolle's (l.c.) variety was later raised to species rank as *Uredo agrimoniae-eupatoriae* (Winter 1881), which is, thus, the relevant date (year) for priority purposes of this name on species rank (Art. 11.2). However, *Caeoma agrimoniae* (von Schweinitz 1832), described from North America on *Agrimonia* sp., represents the oldest species name within the *Pucciniastrum* complex on *Agrimonia* spp. This name is relevant for the present species owing to the current phylogenetic results, which have shown that a single species widespread on *Agrimonia* spp. in Asia, Europe, and North America is involved. *Coleosporium ochraceum* (Bonorden 1860) is the next and oldest available name in this complex. Schröter, in Cohn (1887), erroneously introduced the combination "*Uredo agrimoniae* (DC.) J. Schröt." that must be corrected to *Uredo agrimoniae-eupatoriae* (DC.) J. Schröt. because *Uredo potentillarum* var. *agrimoniae-eupatoriae* was cited as a basionym.

Dietel (1890) provided the first description of telia/teliospores of this species. He named this species "*Thekopsora agrimoniae* (DC.)", suggesting that he based this name on *Uredo potentillarum* var. *agrimoniae-eupatoriae* as basionym and intended a new combination, based on de Candolle's (1815) variety. However, he did not use the name "*Thekopsora agrimoniae-eupatoriae*" but *T. agrimoniae* [the name "*Thekopsora agrimoniae*" was previously, under the rules of the Codes before 2012, prior to the Melbourne Code, ascribed to Dietel as teleomorph-typified name, and in the event that the original author intended to introduce a new teleomorph-typified name, which can be assumed in this case, *T. agrimoniae* can actually be ascribed to Dietel and represents a legitimate name, according to the current Code (Art. F.8.1)]. The nomenclature of Dietel's (1890) name influences the nomenclature of *Pucciniastrum agrimoniae* (Dietel) Tranzschel (Tranzschel 1893) as well. Later, Tranzschel (1939) probably realized that *Caeoma agrimoniae* represents the oldest name in this taxonomic-nomenclatural complex and introduced the new combination *Pucciniastrum agrimoniae* (Schwein.) Tranzschel.

Recent phylogenetic analyses showed that *Pucciniastrum* on *Agrimonia* spp. in Asia must be excluded from *Pucciniastrum* s. str. Qi et al. (2019) introduced the new genus name *Quasipucciniastrum* with its type species *Q. agrimoniae* X.H. Qi, P. Zhao & L. Cai. However, there are two basic problems in the latter publication lying in the missing phylogenetic comparison of the new genus with *Pucciniastrum* s. str., determined by its type species, *P. epilobii*, from which the new genus has been segregated, and a missing comparison with sequence data of *Pucciniastrum* on *Agrimonia eupatoria*

from Europe for which older species names are available. In a comprehensive phylogenetic study on rust fungi, Aime and McTaggart (2010) showed that *Q. agrimoniae* and the fungus previously referred to as *Pucciniastrum agrimoniae* cluster together with sequences retrieved from *Thekopsora areolata*, the type species of *Thekopsora*, i.e. the species on *Agrimonia* spp., was considered to be congeneric with *Thekopsora*. However, the present phylogenetic examinations revealed that a single species in the Northern hemisphere (Asia, Europe, and North America) is involved (see "Introduction"). These results raise the question as to the correct naming of the species involved. The oldest epithet ("*agrimoniae*" – from *Caeoma agrimoniae*) is not available in *Thekopsora* since "*agrimoniae*" is preoccupied in this genus by *Thekopsora agrimoniae*. *Coleosporium ochraceum* represents the next name within the synonymy that is available and would have priority in *Thekopsora*. However, because our own phylogenetic examinations support the conclusion that the former *Pucciniastrum/Thekopsora agrimoniae* on *Agrimonia* spp. deserves a genus of its own, we accept *Quasipucciniastrum* as introduced by Qi et al. (2019). However, the oldest epithet "*agrimoniae*" (from *Caeoma agrimoniae*) is also not available in *Quasipucciniastrum* and preoccupied by the recently introduced *Q. agrimoniae*, so that the next available name, *Coleosporium ochraceum*, takes priority:

***Quasipucciniastrum ochraceum* (Bonord.) M. Scholler & U. Braun, comb. nov.**

Mycobank, MB843212.

Basionym: *Coleosporium ochraceum* Bonord., Abh. Naturf. Ges. Halle 5: 186, 1860.

Lectotype (designated here, MycoBank, MBT10006103): Bonorden, Abh. Naturf. Ges. Halle 5: Table I, Fig. 15, 1860 (on *Agrimonia eupatoria*). Epitype (designated here, MycoBank, MBT10006104): on *Agrimonia eupatoria*, Germany, Baden-Württemberg, Bad Mergentheim, W Edelfingen, NSG Weinhalde, orchard, 230 m, II, 2 Aug. 2007, leg./det. M. Scholler (KR-M-0024910; uredinia see Fig. 3d). Ex-epitype sequence: MK697303.

≡ *Caeoma ochraceum* (Bonord.) Niessl, Verh. Nat. Ver. Brünn 3: 106, 1864.

= *Caeoma agrimoniae* Schwein., Trans. Am. Phil. Soc., New Series 4(2): 291, 1832.

≡ *Pucciniastrum agrimoniae* (Schwein.) Tranzschel, Obzor rzhavchinnikh gribov SSSR: 226, 1939, nom. illeg. (Art. 53.1), non *Pucciniastrum agrimoniae* (Dietel) Tranzschel, 1895.

= *Uredo potentillarum* var. *agrimoniae-eupatoriae* DC. [as '*ζ Agrimoniae eupatoriae*'], Fl. franç., Edn 3 (Paris) 5/6: 81, 1815.

≡ *Uredo agrimoniae-eupatoriae* (DC.) G. Winter [as '*agrimoniae eupatoriae*'], Rabenh. Krypt.-Fl., Edn 2 (Leipzig) 1.1: 252, 1881.

≡ *Uredo agrimoniae-eupatoriae* (DC.) J. Schröt. [as “*agrimoniae* (De Candolle)”], in Cohn, Krypt.-Fl. Schlesien (Breslau) **3.1**(17–24): 374, 1887, isonym.

≡ *Pucciniastrum agrimoniae-eupatoriae* (DC.) Lagerh., Tromö Mus. Aarsh. **17**: 92, 1895.

= *Thekopsora agrimoniae* Dietel [as “*agrimoniae* (DC.)”], Hedwigia **29**: 153, 1890, nom. legit. (Art. F.8.1).

≡ *Pucciniastrum agrimoniae* (Dietel) Tranzschel, Scripta Bot. Horti Univ. Imper. Petrop. **4**(2): 301, 1895

= *Quasipucciniastrum agrimoniae* X.H. Qi, P. Zhao & L. Cai, Mycology **10**(3): 145, 2019.

≡ *Thekopsora pseudoagrimoniae* (X.H. Qi, P. Zhao & L. Cai) Aime & McTaggart, Fungal Syst. Evol. **7**: 34, 2020, non *Thekopsora agrimoniae* Dietel 1890.

Notes: Herbarium material authentic for Bonordon’s (l.c.) name is not preserved, but he provided an original illustration, which is original material in the sense of the Code (Art. 9.4) that has to be taken into consideration for a lectotypification (Art. 9.3). The application of Bonordon’s name is established by epitypification.

***Quasipucciniastrum potentillae* (Kom.) M. Scholler & U. Braun, comb. nov.**

Mycobank, MB843213.

Basionym: *Pucciniastrum potentillae* Kom., Fungi Ross. Exs.: no. 327, 1900.

≡ *Thekopsora potentillae* (Kom.) Aime & McTaggart, Fungal Syst. Evol. **7**: 34, 2020.

Note: *Pucciniastrum potentillae*, a species distributed in the northern hemisphere, resembles *Q. ochraceum* but has smaller urediniospores and teliospores (Arthur 1934). No ITS sequence is available but Aime and McTaggart (2020) proved in their higher rank phylogeny that it is closely related to *Q. ochraceum* (*Thekopsora pseudoagrimoniae*). Because of this and because of its morphological similarity to *Q. ochraceum*, we suggest placing this species in *Quasipucciniastrum* as well.

### ***Pucciniastrum on Rubus***

*Pucciniastrum americanum* and *P. arcticum* on *Rubus* spp. (host-alternating with *Picea glauca*) have not only several features in common with *Quasipucciniastrum* and with *Thekopsora* but also features which differentiate them from the latter genera. All features concerning host range, geographical distribution, symptomology, life cycle, and morphology are listed in Table 2. Besides the host plants, *Rubus* rusts (*P. americanum* and *P. arcticum*) have several morphological features that are missing in *Thekopsora* and *Quasipucciniastrum* and all other species so far placed in *Pucciniastrum*: Uredinia have four to six ostiolar knob-like and conspicuously spiny cells (Fig. 3a, b; for comparison see uredinia of *Q. agrimoniae* in Fig. 3c), the germ pore number and position are different (Table 2) and finally echinulation (shorter spines on central surface)

differs from the other two genera (Fig. 3c). Also, spermogonia and aecia are formed on *Picea* needles, not on cones as in *Thekopsora*. Based on differences in morphology, symptomology, life cycle features, and host range, supported by two rDNA phylogenies, we propose placing *Pucciniastrum americanum* and *P. arcticum* in a different genus:

***Aculeastrum* M. Scholler, U. Braun & Bubner gen. nov.**

Mycobank, MB843210.

Etymology: composed of aculeus = spine + Latin substantival suffix -astrum (= incomplete resemblance), taken from *Quasipucciniastrum*.

Type species: *Aculeastrum americanum* (≡ *Pucciniastrum arcticum* var. *americanum*).

*Aculeastrum* differs from related *Coleosporiaceae* genera on *Rosaceae* telial hosts, *Quasipucciniastrum* and *Thekopsora*, in having a different telial host range (*Agrimonia*, *Potentilla*), by coarsely spiny ostiolar cells, by fewer (mostly 4–6) strictly bipolar urediniospore germ pores, by shorter urediniospore spines in the center of the spore, and by forming spermogonia and aecia on needles of the aecial host (*Picea*).

***Aculeastrum americanum* (Farl.) M. Scholler & U. Braun, comb. nov.**

Mycobank, MB843214.

Basionym: *Pucciniastrum arcticum* var. *americanum* Farl., Rhodora **10**: 16, 1908.

≡ *Pucciniastrum americanum* (Farl.) Arthur, Bul. Torrey Bot. Club **47**: 468, 1926.

≡ *Thekopsora americana* (Farl.) Aime & McTaggart, Fungal Syst. Evol. **7**: 34, 2020.

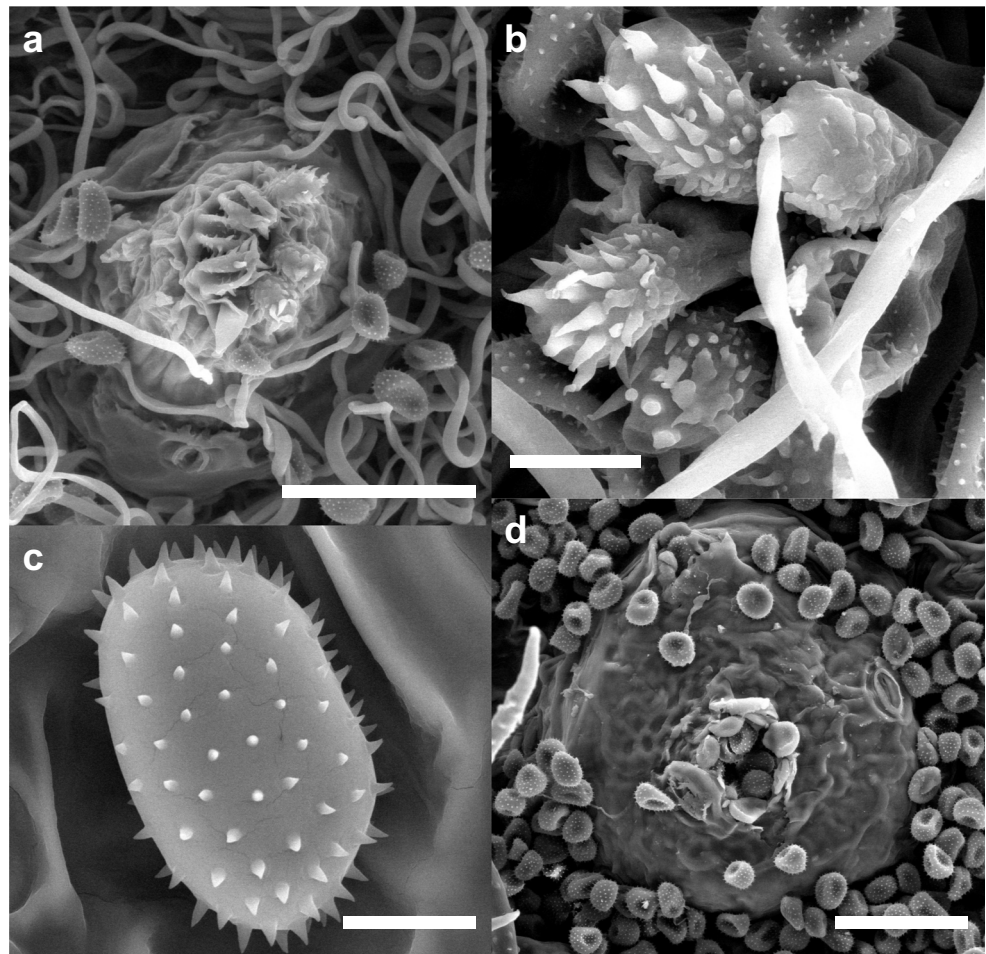
Lectotype (designated here, Mycobank, MBT10006105): *Rubus strigosus*, USA, Massachusetts, Arlington Heights, 5 Oct 1893, leg. B. M. Davis, det. W. G. Farlow (FH) (contains spore states II, III). Epitype (designated here, Mycobank, MBT10006106): *Rubus strigosus*, USA, Minnesota, Clay County, 22 Sep 2005, R. J. M. Hansen (BPI878095, GenBank acc. no. MT022021, see Fig. 3a, b, c).

Additional original collections (syntypes): *Rubus* × *neglectus* USA, Massachusetts, Bussey, 1 Oct 1875, W. G. Farlow (PUR 3566); *R. strigosus*, USA, New Hampshire, Ellis River, 13 August 1889, L. M. Underwood (PUR 3606); *R. strigosus*, USA, Wisconsin, Madison, 1 Oct 1882, W. Trelease (BPI 143983, PUR 3550, 3551); *R. sp.*, USA, Massachusetts, Newton, Sep 1877, W. G. Farlow (FH, PUR 3611); *R. sp.*, USA, Massachusetts, Arlington Heights, 15 Oct 1893, B. M. Davis (PUR 3576).

***Aculeastrum arcticum* (Tranzschel) M. Scholler & U. Braun, comb. nov.**

Mycobank, MB843215.

**Fig. 3** **a** *Aculeastrum americanum* (BPI 878095, epitype), uredinia with ostiolar cells and urediniospores (SEM) (bar = 50 μm) (photograph M. Scholler). **b** *Aculeastrum americanum* (BPI 878095, epitype), uredinia, spiny ostiolar cells (SEM) (bar = 10 μm) (photograph M. Scholler). **c** *Aculeastrum americanum* (BPI 878095, epitype), urediniospore (bar = 5 μm) (photograph M. Scholler). **d** *Thekopsora ochracea* (KR-M-0024910, epitype) (SEM), uredinia and urediniospores (bar = 50 μm) (photograph M. Scholler)



Basionym: *Pucciniastrum arcticum* Tranzschel, Scripta Bot. Horti Univ. Imper. Petrop. 4: 300, 1895.

Note: This species strongly resembles *A. americanum*. The main feature of *Aculeastrum* species, the coarsely arcuate ostiolar cells are well-developed in this species. *Aculeastrum arcticum* differs from *A. americanum* in its host range (other *Picea* and *Rubus* species), by uredinia which only scarcely protrude above the epidermis, and by its peridial cell morphology (Moss 1926; Arthur 1934; Hiratsuka 1936; Ziller 1974).

**Key to the rust genera in *Coleosporiaceae* with *Rosaceae* telial hosts:**

- 1 On acial host (*Picea*) ..... 2
- 1\* On telial host (*Rosaceae*) ..... 3
- 2 On cone scales; aeciospore wall up to 6 μm thick ..... *Thekopsora*
- 2\* On needles; aeciospore wall up to 3 μm thick ..... *Aculeastrum*
- 3 Urediniospore powder whitish; ostiolar cells smooth; urediniospores with one conspicuous germ pore; teliospores intercellular; on *Prunus* ..... *Thekopsora*

- 3\* Urediniospore powder yellow; teliospores without visible pores, intracellular; on other hosts ..... 4
- 4 Ostiolar cells of uredinia smooth; urediniospore germ pores scattered, mostly 6–10; on *Agrimonia* and *Potentilla* ..... *Quasipucciniastrum*
- 4 Ostiolar cells of uredinia coarsely acute, urediniospore germ pores bipolar, mostly 4–6, on *Rubus* ..... *Aculeastrum*

**Discussion**

**Use of ITS rDNA data and delimitation of genera**

This study is based on ITS rDNA data because the aim was to explore species delimitation in the genus *Pucciniastrum* s. lat. A previous study in rust fungi showed that for species delimitation, ITS rDNA data are more suitable because it is more variable than, for instance, the marker 28S rDNA.

However, phylogenetic analyses in *Pucciniastrum* have already shown that this genus in its previously wide circumscription is a heterogeneous, non-monophyletic complex, i.e.

in a phylogenetic context some species should be placed in different genera (Maier et al. 2003; Aime et al. 2018; Qi et al. 2019). The most recent and most comprehensive study that includes members of the genus *Pucciniastrum* s. lat. is the study of Aime and McTaggart (2020). Because it is a study on higher rank classification, authors used the markers 28S, 18S, and CO3. Aime and McTaggart (2020) showed that *Pucciniastrum* in its wide circumscription comprises species that are so distantly related that they are even placed in different families, *Coleosporaceae* and *Pucciniastraceae*. Despite the large genetic distance, our study of *Pucciniastrum* s. lat. and related genera based on ITS showed almost the same basic structure in the monophyletic groups as the study of Aime and McTaggart (2020). There is only one genus, *Hyalopsora*, which in our ITS phylogeny is placed in *Pucciniastraceae*, whereas Aime and McTaggart (2020) placed it in the *Coleosporiaceae*. Considering co-evolutionary arguments and thus also host plants of *Hyalopsora* (*Abies*, fern), our ITS phylogeny is more convincing because this host-parasite combination occurs in the *Pucciniastraceae* but does not occur in species of *Coleosporiaceae*. Our study is a complement to the study of Aime and McTaggart (2020) by adding specimens of *Pucciniastrum* species on different *Onagraceae* hosts and specimens of species that are now placed in the genera *Thekopsora*, *Quasipucciniastrum*, and *Calyptospora*. ITS is a suitable marker to resolve terminal nodes. Thus, *Pucciniastrum epilobii* could be resolved to comprise the species *P. epilobii* restricted to a limited host spectrum (*Chamaenerion angustifolium*) and *P. pustulatum* with a wider host spectrum in the *Onagraceae*. By including more specimens of *Thekopsora areolata* and for the species known as *Pucciniastrum agrimoniae* and *P. americanum*, the separation of the two genera *Quasipucciniastrum* and *Thekopsora* was confirmed. This is the only major difference on a generic level to Aime and McTaggart (2020), where *Pucciniastrum agrimoniae*, *P. americanum*, and *Thekopsora areolata* are assigned to the genus *Thekopsora*.

The general difficulty of marker sequencing from rust vouchers is a further argument for concentrating on ITS rDNA in this study. We tried different markers (28S, nad6) but were not able to generate a complete set for all samples (unpublished data). In some cases, nad6 or 28S worked for a sample, but not ITS. Therefore, it was not possible to build a concatenated tree and it would have been necessary to build three separate phylogenies all comprising different sets of specimens. Because ITS worked for the majority of the samples, the much smaller trees with nad6 and 28S would have provided only limited additional information. Combining all the above listed arguments, we consider it suitable and sufficient to base

all conclusions in the scope of this paper on an ITS phylogeny.

### The genus *Pucciniastrum*

One basic issue has thus far been unresolved, viz., the phylogenetic circumscription of *Pucciniastrum* s. str., based on its type species (*P. epilobii*), which is essential for the further phylogenetic splitting of this complex. This problem has been addressed in the present work for European species.

Phylogenetic analysis of collections of *P. epilobii* (s. lat.) on various hosts revealed that this taxon is composed of two species. One is *P. epilobii* (s. str.) with *Abies* spp. as aecial hosts and *Chamaenerion* spp. as telial hosts. The other is *P. pustulatum*, a non-host-alternating, plurivorous species on *Epilobium*, *Oenothera* spp., and possibly on *Chamaenerion* and *Clarkia* usually without formation of telia. Whether *Chamaenerion* is indeed a host of *P. pustulatum* remains doubtful since the host *Ch. angustifolium* of the pertinent reference from Norway (DQ445906) (Hiatala et al. 2008) not exist (H. Solheim, pers. com.). Therefore, it is still not certain whether the host range of the two species overlaps. Differences in the phylogenetic placement were supported by differences in urediniospore morphology.

Our delimitation of *Pucciniastrum* from related genera remains provisional and only applies to European species and follows mainly morphological and life cycle criteria. Besides species of the *Pucciniastrum epilobii* complex, we maintain *P. minima* and *P. guttata*, formerly placed in *Thekopsora*, in *Pucciniastrum* because of similar morphological features. The taxa in the group consisting of *Calyptospora* and *Melampsorella* differ strongly from latter taxa in aeciospore and teliospore features and life cycle. Therefore, we decided to keep them separate from *Pucciniastrum*. However, this remains a provisional “European solution” as well. As mentioned above, additional species, particularly from Asia, must be studied for a future generic concept within *Pucciniastraceae*. Therefore, we did not place *P. hydrangeae-petiolaris* and *P. fagi* in new genera, although our phylogeny (Fig. 1) and other phylogenies (e.g. Aime and McTaggart 2020) favour such a conclusion.

### Rosaceae rusts in *Coleosporiaceae*

The hitherto sequenced species of *Thekopsora* belong to two families, namely *Coleosporiaceae* and *Pucciniastraceae*, as formerly shown by Aime and McTaggart (2020). *Thekopsora areolata*, the type species, is host-alternating between *Picea* [cones] (*Pinaceae*) and *Prunus* s. lat. (*Rosaceae*), and is a member of the *Coleosporiaceae*. Our *Coleosporiaceae* ITS phylogeny differs from the 28S-18S-CO3 *Coleosporiaceae* phylogeny presented by Aime and McTaggart (2020) in one aspect. In our phylogeny, species

on *Rosaceae* host-alternating with *Picea* or supposed to host-alternate with *Picea* form three different clades (*Quasipucciniastrum*, *Thekopsora*, *Aculeastrum*), whereas Aime and McTaggart (2020) placed them in a single genus (*Thekopsora*). However, the unifying node in the phylogeny of Aime and McTaggart (2020) has no assigned support value. In the same figure, *Thekopsora aerolata* is separated from *Thekopsora americana* (*Aculeastrum americanum* in our paper) by a long branch length. Thus, even in this figure, you find evidence that supports our view to place the three clades in different genera. The proposed new genus *Aculeastrum* belongs to a group of three genera that all have telial hosts within the *Rosaceae* family. They differ in morphology, life cycle, symptomology, and host range (Table 2) and form a separate group in our ITS phylogeny (Fig. 1). The name-giving feature, the arcuate ostiolar peridial cells, is also a characteristic of two other species placed in *Pucciniastrum*, namely *P. pyrolae* (H. Mart.) J. Schröt. (remarks to the nomenclature, see below) with short spines, and *P. enkianthi* Y.M. Liang & Kakish. (= *P. hakkodaense* Y.M. Liang & Kakish.) with coarse spines like in *Aculeastrum*. The hosts of both species belong to *Ericaceae*. So far, however, only an insufficient 28S rDNA (domains D1, D2) sequence of *P. pyrolae* (Maier et al. 2003) is available and no sequence data are available for *P. enkianthi*. Before placing them in a genus or family (*Pucciniastraceae*, *Milesiaceae*), further sequence data (ITS, LSU, CO3) are required.

### Nomenclatural problems and spelling of names in rust fungi

The applications of genus names are ruled by the corresponding type species. Therefore, it is necessary to clarify the nomenclature, phylogenetic position, and the type species of *Pucciniastrum*, *P. epilobii*. An examination of the protologues of all names involved in this complex showed that the previous ascription of the name of the type species solely to G. H. Otth is correct, and that *Sclerotium herbarum* f. *epilobii* was meant to be only a synonym. To stabilize the application of the latter name and thereby of the genus name *Pucciniastrum*, a lectotype and new material as epitype have been designated and an ex-epitype sequence has been generated for its phylogenetic characterisation. Based on the phylogenetic position of its type species, the genus name *Pucciniastrum* s. str. now represents a small group of species related to *P. epilobii*.

Because of the changes in the code of nomenclature (ICN) since 2012 (Melbourne Code), in particular the discontinuation of the dual nomenclature of pleomorphic fungi, it was necessary to reconsider the nomenclature of the name *Calyptospora goeppertiana* and its correction to *C. columnaris*. In this publication, a morphologically and genetically distinguished North American “sister species” of *C. columnaris* occurring as aecia on *Abies* spp. in western

North America is referred to as *C. ornamentalis*. Although for the American species only sequences for the aecial host, *Abies grandis*, are available, sequences for the European species *C. columnaris* originate both from the aecial host, *Abies alba*, and the uredinial host, *Vaccinium vitis-idea*. The alternation between those two host species is known from inoculation experiments (Gäumann 1959), but, in addition, it is here confirmed for the first time based on ITS sequences.

*Quasipucciniastrum* (*Coleosporiaceae*) was recently introduced, segregated from *Pucciniastrum* and typified by a new species, *Q. agrimoniae*, based on Chinese rust material on *Agrimonia pilosa* (Qi et al. 2019). The results of our phylogenetic analyses confirmed the phylogenetic position of *Quasipucciniastrum* distant from *Thekopsora*, i.e. what we are dealing with is a distinct genus. However, the introduction of a new species, *Q. agrimoniae*, on *Agrimonia pilosa* has turned out to be precipitous. A species on *Agrimonia* spp., which is widespread and common in the Northern hemisphere, must be assigned to the new genus *Quasipucciniastrum*. But in this case, it was also necessary to perform a detailed nomenclatural analysis to find the correct denomination of the species concerned, which led to the introduction of the new combination *Q. ochraceum*.

The present revision and splitting of *Pucciniastrum* (s. lat.) is only a first step. Many other *Pucciniastrum* and *Thekopsora* species are not congeneric with these genera, form separate clades in phylogenetic analyses (Maier et al. 2003; Aime et al. 2018; Yang et al. 2015), Ji et al. 2019, Qi et al. 2019), such as *Pucciniastrum boehmeriae* (Dietel) Syd. & P. Syd., *P. kusanoi* Dietel, *P. miyabeana* Hirats., and some additional East Asian species that form a separate clade requiring a distinct genus. Morphological re-examinations of the species concerned and more specimens are necessary to further split *Pucciniastrum*. Many other questions must be clarified in detail, for instance, the true species identity of North American specimens of *Pucciniastrum epilobii*.

A general nomenclatural problem within the rust fungi results from the current Code (ICN) and the nomenclatural equality of all fungal names in the synonymy of pleomorphic fungi, independent of the particular morphs that typify these names, whether asexual or sexual. In the present work, such problems became evident in the case of *Calyptospora goeppertiana* and *Pucciniastrum epilobii*. So far, only a fraction of names of rust species has been checked in terms of nomenclatural implications of the changed Code (ICN), although these problems have to be taken into consideration. The nomenclature of all *Pucciniastrum* names must be proven and clarified. *Pucciniastrum pyrolae*, cited below, is a case in point for a name cited with different authorships, viz. “(J.F. Gmel.) J. Schröt.” in *Index fungorum* and “Dietel ex Arthur” in MycoBank. However, *Pucciniastrum pyrolae* (H. Mart.) J. Schröt. is the correct name, based on the current Code

[Schröter 1881 cited *Uredo pyrolae* H. Mart. as basionym for his combination]:

***Pucciniastrum pyrolae*** (H. Mart.) J. Schröt. [as “*pirolae*”], Jahresber. Schles. Ges. Vaterl. Kultur **58**: 167, 1881.

≡ *Uredo pyrolae* H. Mart. [as “*pirolae*”], Prodr. Fl. Mosq., edn 2: 229, 1817.

≡ *Caecoma pyrolae* (H. Mart.) Schltld. [as “*pirolae*”], Fl. berol. **2**: 122, 1824.

≡ *Thekopsora pyrolae* (H. Mart.) P. Karst. [as “*pirolae*”], Bidrag Kännedom Finlands Natur Folk **31**: 59, 1879.

≡ *Physonema pyrolae* (H. Mart.) Niessl, Verh. Naturf. Vereines Brünn **3**: 104, 1864.

= *Aecidium pyrolae* J.F. Gmel. [as “*pynolae*”], Syst. Nat., Edn 13, **2**(2): 1473, 1792.

≡ *Melampsora pyrolae* (J.F. Gmel.) J. Schröt. [as “*pirolae*”], in Cohn, Krypt.-Fl. Schlesien **3.1**(17–24): 366, 1887.

= *Aecidium pyrolae* Schultz, Prodr. Fl. Starg.: 452, 1806, nom. illeg. (Art. 53.1).

= *Uredo polymorpha* var. *pyrolae* F. Strauss, Ann. Wetter. Ges. Gesammte Naturk. **2**: 87, 1811.

≡ *Hypodermium pyrolae* (F. Strauss) Link, Mag. Gesell. Naturf. Freunde, Berlin **8**: 28, 1816.

= *Trichobasis pyrolae* Berk., Outl. Brit. Fung.: 332, 1860, nom. inval. [nom. nud.] (Art. 38.1.a)

Finally, we would like to briefly discuss the different spellings of epithets derived from names of host plants of pathogenic fungi. Usually they are used in genitive, also in case of dual hyphenated epithets referring to the host genus and the host species. In other cases, especially in rust fungi, dual hyphenated epithets refer to host alternations (from aecial hosts to telial hosts) in the development cycle of the species concerned, e.g. *Uromyces euphorbiae-corniculati* Jordi, referring to *Euphorbia* and *Lotus corniculatus* as alternate hosts. In several of his basic publications dealing with host changes of rust fungi, H. Klebahn introduced unusual bipartite epithets reflecting telial hosts, in some cases with the first element in dative, connected with a second element in genitive, for instance, *Melampsora larici-pentandrae* Kleb. (referring to *Larix* and *Salix pentandra*) and *M. larici-daphnoidis* Kleb. (referring to *Larix* and *Salix daphnoides*). In the different volumes of his “Sylloge fungorum”, Saccardo changed the spelling in all comparable cases to genitive for both elements of the bipartite names (e.g. *larici* to *laricis*), and these corrected versions are maintained in the databases Index Fungorum and MycoBank and should be followed. Other epithets were even more unusual, such as *Melampsora allii-populina* Kleb., referring to *Allium* and *Populus* as telial host, but in this case the name is composed of a genus name in genitive (first element) and an adjective as second element (*Populus* + -ina as adjectival suffix [belonging to]). One name involved in the *Pucciniastrum epilobii* complex is concerned, viz., *Pucciniastrum abietis-chamaenerii* (original spelling “*abieti-*

*chamaenerii*”). There are also different spellings of the genitive of *Chamaenerion* in literature (the nomenclature of this genus name has been discussed in detail by Sennikov 2011), but this neuter name of Greek origin ending in -on is declined as a comparable name, such as *Halarachnion* and *Lithothamnion* (word stem + i, *Chamaeneri-i*, see Stern 1992). In contrast to genus names, which are individual, unchangeable names, epithets must be linguistically correct, and orthographical and grammatical mistakes have to be corrected. The applied names should be proper and uniform. Authors should follow the databases (IF and MB) in using the valid versions of the particular names, i.e. uncritical applications of original spellings should be avoided.

**Supplementary Information** The online version contains supplementary material available at <https://doi.org/10.1007/s11557-022-01810-3>.

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**Code availability** Not applicable

**Author Contribution** All the authors contributed to the study. M. Scholler initiated the study, was in charge of it, and deserves to be the corresponding author. M. Scholler and R. Buchheit did the fieldwork (collecting), mounted and digitalized specimens for the herbarium, and carried out the microscopical (morphological) work (LM, SEM). M. Scholler selected specimens for sequencing and provided spore samples for DNA extraction. B. Bubner and Th. Schulte carried out the lab work, including DNA extraction and amplification (PCR), edited sequences, and performed a phylogenetic tree. U. Braun did the major work on nomenclature and checked protologues and other important literature. Also, he wrote the section in the discussion on nomenclature and spelling of epithets. B. Bubner, U. Braun, and M. Scholler wrote the manuscript and all the authors read, commented on, and approved the final manuscript.

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**Data availability** Datasets generated during and/or analyzed during the current study are available on GenBank, from the corresponding author M. Scholler (morphological data) and Ben Bubner (lab protocols) upon request.

## Declarations

**Ethics approval** Not applicable

**Conflict of interest** Not applicable.

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