

The Puccinosiraceae: Taxonomy of a polyphyletic family of the rust fungi (Uredinales)

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Abstract: This review summarizes the present taxonomic knowledge of the polyphyletic family Puccinosiraceae (Uredinales) and its genera. It shows that the genera are often imprecisely or arbitrarily delimited from each other. The situation is exemplified by the genus *Cionothrix* for which the presence of intercalary cells is reported for the first time.

The members of Puccinosiraceae descended most likely from heteroecious species of the *Puccinia-Uromyces* complex (PUC) but the relationships are still largely unknown. Molecular analyses have not helped so far to remedy this situation because a reasonably complete phylogeny of the PUC to which the members of the Puccinosiraceae could be linked is unavailable.

It is attempted, therefore, to relate members of Puccinosiraceae with possible heteroecious progenitors by analysing host relationships, especially by the application of 'TRANZSCHEL'S rule'. The power and restrictions of this approach are discussed mainly by examples from the genus *Endophyllum*. It is concluded that the analysis of host relationships is an effective method to identify possible heteroecious relatives of endocyclic rust fungi. Molecular studies that include such wisely selected candidate species may produce more reliable phylogenies even if only a restricted number of species are analysed.

Key words: *Cionothrix*, correlated species, *Endophyllum*, endocyclic life cycle, *Puccinia-Uromyces* complex, Pucciniales, TRANZSCHEL'S rule

1. Introduction

The Puccinosiraceae, a heterogeneous group of rust fungi with endocyclic life cycle. – The complete or 'macrocytic' life cycle of a rust fungus comprises teliospores that germinate with basidia, basidiospores, sexually determined spermatia produced in spermogonia (also termed 'pycnidia') and two conidial spore states, the aecio- and the urediniospores. The macrocytic life cycle can be completed on a single host plant species in 'autoecious' rust fungi or may require alternation between two different and phylogenetically unrelated host species in 'heteroecious' rusts (see HENNEN & HENNEN (2000) for a thorough discussion of the terminology of the spore states and life cycles of rust fungi).

Many rust fungi do not pass through a macrocytic life cycle. These so-called short-cycled rust fungi are either 'demicytic', when they lack the uredinial state, or 'microcytic' when only telia are formed that may be accompanied by spermogonia or not. Demicytic rust fungi can be hetero- or autoecious, while microcytic ones are always autoecious. The macrocytic and heteroecious life cycle is considered original in the modern rust fungi while short-cycled rusts are supposed to have evolved from macrocytic progenitors (JACKSON 1931). All members of the Puccinosiraceae are microcytic and hence autoecious.

Telia of microcyclic rust fungi can differ morphologically from the telia of their macrocyclic congeners. While the teliospores look essentially alike, the telia of the microcyclic species are often deep-seated and clustered on swollen host organs (see JACKSON 1931 for examples and discussion). In these characters they resemble the morphology of aecia.

In a lesser number of microcyclic rust species, the telia and teliospores resemble the aecial anamorph genera *Aecidium*, *Caeoma*, *Peridermium* or *Uredo* so closely that they may not be recognized as telia until the spores have germinated with basidia. Such rust fungi are called ‚endo-forms‘ and their life cycle ‚endocyclic‘. Endocyclic rust fungi cannot be linked with related macrocyclic species by telial morphology and it may even be impossible to assign them to one of the known genera. Therefore, endocyclic rust fungi have been grouped in genera of their own that are immanently artificial.

The most prominent example is *Endophyllum* in which the telia look exactly like an *Aecidium* anamorph (Fig. 1). Already TRANZSCHEL (1904) considered *Endophyllum* an artificial group that comprises morphologically similar rust fungi defined by a certain life cycle. DIETEL (1928, p. 92) and JACKSON (1931, p. 53) agreed with this view and hypothesized that *Endophyllum* spp. likely derived from *Puccinia*- or *Uromyces* spp. with macrocyclic life cycle. The close relationship between *Endophyllum* and *Puccinia* and *Uromyces* was originally deduced from the similarity of the aecidia of *Puccinia*- and *Uromyces* spp. and the *Aecidium*-like telia of *Endophyllum*. Later it was shown that all three genera have globose spermogonia with ostiolar periphyses that can be classified as ‚Group V-Type 4‘ according to the terminology of HIRATSUKA & HIRATSUKA (1980). It should be noted in this context that the autonomy of the genera *Puccinia* and *Uromyces* has been questioned since long (cf. FISCHER 1904, HARIOT 1908, ORTON 1912) but only today we are beginning to elucidate their intricate interrelationship (VAN DER MERWE et al. 2007). Therefore, I do not treat *Puccinia* and *Uromyces* as separate genera any longer but refer to both as the ‚*Puccinia-Uromyces* complex‘ (PUc).



Fig. 1: *Endophyllum elytropappi* (living specimen). *Aecidium*-like telia on stems of *Elytropappus rhinocerotis* (Asteraceae). Western Cape, South Africa.

In other endocyclic rust fungi, the similarity of the telia with the aecial anamorph genus *Aecidium* is less pronounced but still noticeable. For such rust fungi the new genera *Didymopsora*, *Dietelia*, *Gambleola*, *Puccinosira* and *Trichopsora* were erected. DIETEL (1928) created a new tribe ‚Puccinosireae‘ within Pucciniaceae for these genera into which he also included *Alveolaria*, *Baeodromus*, *Cionothrix*, *Masseëlla* and *Pucciniostele*. He stated that the tribe was a makeshift (“Notbehelf”) to accommodate microcyclic rust genera with catenulate teliospores for which no better place had been found so far in the system of the rust fungi. In the same paper, DIETEL suggested nevertheless that *Baeodromus*, *Cionothrix*, *Trichopsora*, *Alveolaria*, *Didymopsora* – and probably also *Puccinosira* – could represent a natural group.

JACKSON (1931, p. 79) hypothesized that the genera of Puccinosireae might have evolved by “some further modification in morphology” from the polyphyletic *Endophyllum* or from endocyclic rust fungi in that the telia look like the anamorph genus *Caeoma*. This hypothesis indicates that JACKSON regarded Puccinosireae as an inhomogeneous group admitting at the same time that the members of this group were able to evolve independently from their demi- or macrocyclic ancestors resulting in morphologically different forms.

BURITICÁ & HENNEN (1980) monographed the neotropical Puccinosireae and revised the known genera based on careful morphological investigations. They elaborated and clarified the concept of the Puccinosireae and interpreted them as “a special, polyphyletic tribe in the Pucciniaceae for genera with reduced life cycles, which are derived mostly from long-cycled species of the *Puccinia-Uromyces* complex by way of the endophylloid pathway of life cycle reduction”. According to BURITICÁ & HENNEN (1980) the Puccinosireae comprise nine genera, *Alveolaria*, *Baeodromus*, *Chardonella*, *Cionothrix*, *Didymopsora*, *Dietelia*, *Endophyllum*, *Puccinosira* and *Trichopsora*. *Alveolaria*, *Cionothrix* and *Baeodromus* were left in the tribe just “for convenience”, *Masseëlla* was excluded. CUMMINS & HIRATSUKA (1983) upgraded Puccinosireae to family and added to it an unnamed genus that was later described as *Ceratocoma* by BURITICÁ and HENNEN (BURITICÁ 1991).

In the following, I will give a brief overview of the Puccinosiraceae and the genera placed in the family. I will then discuss which taxonomic status should be given to rust fungi with shortened life cycle in relationship to their supposed progenitors with expanded life cycle. The second part of the discussion will deal with the problem of how microcyclic rust species can be linked to potential progenitors. It will be shown that a careful analysis of host spectra is still the most promising approach to hypothesize such relationships.

Genera of Puccinosiraceae. – The following list of genera of Puccinosiraceae comprises the genera treated by BURITICÁ & HENNEN (1980) plus *Ceratocoma*. I exclude *Alveolaria* whose telia do not look like any aecial anamorph genus and that cannot be positioned within the PUC because it has a

different spermogonial type. The list does not consider either the endocyclic species found in *Endocronartium*, *Monosporidium* and *Endoraecium*. *Endocronartium* is intertwined with *Cronartium* (VOGLER & BRUNS 1998); the position of *Monosporidium* and *Endoraecium* is uncertain but they are definitely not related to the PUc from which they differ in the spermogonial type.

The genera are informally grouped by telial morphology. I start with the ones that look like the anamorph genus *Aecidium*. Then I turn to genera that reveal only some aecidial characters and end with those which look like the anamorph genus *Caeoma* or largely lack similarity with an aecial anamorph genus. The circumscription and validity of the genera are discussed; host families and the overall geographic distribution of the genera are listed in table 1.

2. Overview of the Puccinosiraceae

2.1. Telia distinctly *Aecidium*-like, with peridium; teliospores one-celled, catenulate and separated by intercalary cells

Endophyllum LÉV. 1825 (Fig. 1) comprises ca. 35–40 known species that occur on a broad variety of host families mainly in warm regions of the world (e.g. OLIVE & WHETZEL 1917, STEVENS & MENDIOLA 1931, WOOD & CROUS 2005). It is likely that a lot of *Endophyllum* spp. have been overlooked hitherto because any 'isolated' *Aecidium* sp. could potentially belong to *Endophyllum* but has not been recognized as such due to our ignorance of spore germination. A monograph of the genus is not available.

There is direct and circumstantial evidence that *Endophyllum* is an artificial group of species related to different lineages of the PUc. WOOD & CROUS (2005) showed that three *Endophyllum* spp. on South African Asteraceae fell amidst a clade of *Puccinia* spp. It is further known that a couple of *Puccinia* and *Uromyces* spp. do not only produce ordinary telia with puccinioid teliospores but also an *Endophyllum* telial state, for example *P. japonica* DIETEL, *P. pampeana* SPEG., *P. schultesianthi* PARDO-CARD. et al. and *Uromyces hobsonii* VIZE (Gallo AGUDELO et al. 2011, LINDQUIST 1970, LÓPEZ-FRANCO et al. 1990, PAYAK 1958). Such rust fungi are called 'biteleomorphic'.

The works of ASHWORTH (1934), HOFFMANN (1911), MOREAU & MOREAU (1919) and WOOD & CROUS (2005) provide details on the karyological events that take place in developing telia and basidia of *Endophyllum* spp. and reveal a notable diversity of basidium morphology.

Dietelia HENN. 1897 (incl. *Endophylloides*). The ca. 10 species recognized in *Dietelia* differ from *Endophyllum* mainly in smooth or almost smooth teliospores and more compact, columnar telia. It appears hardly justified to separate both genera upon such insignificant differences and one would likely

synonymize them if this would mean a taxonomic progress. Given that both genera are most probably polyphyletic and that we do not know the exact position of their members in the PUC it seems preferable to keep them separate provisionally.

Endophylloides OLIVE & WHETZEL 1917 does not differ substantially either from *Dietelia* and *Endophyllum* and was synonymized with the former by BURITICÁ & HENNEN (1980). MAIER et al. (2007) showed that *D. mesoamericana* H.C. EVANS & C.A. ELLISON on *Mikania* is related to *Puccinia* spp. *Endophylloides portoricensis* WHETZEL & OLIVE, the type species of *Endophylloides*, grows also on *Mikania* and is also related to *Puccinia* spp. (VAN DER MERWE et al. 2007). The second species of *Endophylloides*, *E. guineensis* VIENN.-BOURG., is quite unlike *E. portoricensis*. It has 'Type-5' spermogonia and firm telial columns lacking a peridium (VIENNOT-BOURGIN 1959). This spermogonial type excludes the species from the Puccinosiraceae. BURITICÁ (1991) combined *E. guineensis* – invalidly – into *Ceratocoma*, but this affiliation is not tenable because *Ceratocoma* has 'Type-4' spermogonia. As *E. guineensis* cannot be placed within Puccinosiraceae and does not fit any other known genus either it would need to be placed in a genus of its own. I do not propose a new genus because I believe that it will be possible to assign *E. guineensis* to one of the existing genera of rust fungi sooner or later.

Jacksoniella J.C. LINDQ. 1972 is monotypic and was established to accommodate *Endophyllum holwayi* H.S. JACKS. whose teliospores are thick-walled, pigmented and have an apical germ pore. BURITICÁ & HENNEN (1980) combined the rust in *Dietelia*. The differences in teliospore morphology may justify maintaining it as a separate genus.

2.2. Telia deep-seated, with well-developed or rudimentary peridium, or peridium absent; teliospores two-celled, *Puccinia*-like, catenulate and separated by intercalary cells

Puccinosira LAGERH. 1891 embraces ca. 13 species characterized by *Puccinia*-like teliospores that are produced in chains alternately with intercalary cells. The sori have a continuous to rudimentary peridium. In some species, the teliospores break easily into halves along their septa. HEIM (1951) investigated *Puccinosira dissotidis* (COOKE) WAKEF. and observed the presence of sori with catenulate teliospores and of sori with pedicellate teliospores. *Puccinosira dissotidis* might hence represent another biteleomorphic *Puccinia* species comparable to *P. japonica*, *P. pampeana* and *P. schultesianthi* in which the endophylloid telia are *Aecidium*-like.

Didymopsora DIETEL 1899, with six known species, is separated from *Puccinosira* in telia lacking a peridium and in teliospores that are more irregularly arranged in the distal part of the sori. (BURITICÁ & HENNEN 1980, CUN-

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NINGHAM 1968). The presence of intercalary cells has not been shown in all described species. Like in *Puccinosira*, the teliospores of *Didymopsora* spp. tend to cleave at their septa into halves. The morphological similarity with *Puccinosira* and a similar host spectrum indicate that *Didymopsora* cannot be sharply delimited from *Puccinosira* and should be regarded as a synonym. I keep both genera apart, nevertheless, for the reasons stated under *Dietelia*.

Gambleola MASSEE 1898, with the only known species *G. cornuta* MASSEE, shares essential characters with *Puccinosira* but produces long, rigid and darkly pigmented teliospore threads. The teliospores have two germ pores per cell located close to the septum (MASSEE 1898). Because of these differences I prefer to keep *Gambleola* separate from *Puccinosira* while BURITICÁ & HENNEN (1980) assigned it to the latter.

2.3. Telia deep-seated, without peridium; teliospores one-celled, catenulate, separated by strongly elongating intercalary cells, extruded as long threads; spore wall and wall of intercalary cells at least partly gelatinizing and of fuzzy appearance

Chardoniella KERN 1939 (Fig. 2) comprises four known species, all on members of *Gynoxis* or *Eupatorium* s.l. (Asteraceae) from the tropical Andes. The strongly elongating intercalary cells and the gelatinizing and somewhat fuzzy wall of the teliospores and the intercalary cells are shared with *Trichopsora*. The latter differs from *Chardoniella* in teliospores germinating with an internal basidium and another host family. *Chardoniella* spp. are undoubtedly closely related to each other as indicated by morphology and host selection.



Fig. 2: *Chardoniella andina* (ZT Myc 6047). Filiform telia on leaf of *Eupatorium pseudochilca* (Asteraceae). Ecuador.

Trichopsora LAGERH. 1892 is only known from the type species, *T. tournefortiae* LAGERH. Besides the internal basidium formation, the genus is very similar to *Chardoniella* suggesting a close relationship of both genera. The hosts of *T. tournefortiae*, *Tournefortia* and *Heliotropium*, belong to Boraginaceae.

2.4. Telia ampulliform, without peridium; teliospores one-celled, catenulate, separated by intercalary cells, extruded as short threads

Ceratocoma BURITICÁ & HENNEN 1991 (Fig. 3) is monotypic and was established to accommodate *Cronartium jacksoniae* HENN. ex MCALPINE that grows on woody Fabaceae in south-eastern Australia. It was distinguished from the very similar genus *Cionothrix* because of the presence of intercalary cells between the teliospores and the different host family.



Fig. 3: *Ceratocoma jacksoniae* (Herbarium BERNDT). Columnar telia on young shoot of unidentified Fabaceae shrub. South-eastern Australia.

2.5. Telia ampulliform, peridium lacking, with or without ostiolar paraphyses; teliospores one-celled, catenulate with or without(?) intercalary cells, extruded as long threads

Cionothrix ARTHUR 1907 (Fig. 4) comprises the type species, *C. praelonga* (G. WINTER) ARTHUR, and two other species. All three occur on *Eupatorium* or *Conyza* spp. (Asteraceae) in the neotropics. PETERSON (1973) described the presence of long paraphyses around the telial base. CUMMINS (1978) confirmed this observation but added that paraphyses were absent in *Cionothrix* sp., now known as *C. basicrassa* BURITICÁ & J.F. HENNEN. He remarked, somewhat cautiously, that the teliospore chains were “without obvious intercalary cells”. BURITICÁ & HENNEN (1980) included the presence of telial paraphyses and the absence of intercalary cells in the genus description of *Cionothrix* though they did not describe these characters explicitly in the two non-type species. The authors commented that the telia of *Cionothrix* resembled “only slightly an aecidioid structure” and retained the genus in the Puccinosiraceae just provisionally.



Fig. 4: *Cionothrix praelonga* (Herbarium BERNDT). Filiform telia on leaf of *Eupatorium* sp. (Asteraceae). North-western Argentina.

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Cionothrix differs from *Ceratocoma* essentially in the absence of intercalary cells and the presence of ostiolar paraphyses. A reinvestigation of a type specimen of *C. praelonga* revealed that the teliospores were not sessile but stalked. The stalk cells are evanescent and seem to function as intercalary cells (BERNDT, unpublished results). Ostiolar paraphyses remain the only morphological character, therefore, to separate *Cionothrix* from the younger genus *Ceratocoma*. It is debateable whether this difference suffices to separate both genera and SYDOW & SYDOW (1918) may have had the right instinct when they combined *Cronartium* [= *Ceratocoma*] *jacksoniae* to *Cionothrix jacksoniae* (HENN. ex MCALPINE) SYD. & P. SYD. I keep *Ceratocoma* separate provisionally.

2.6. Telia lentiform, peridium and other bounding structures absent; teliospores one-celled, shortly catenulate, separated by intercalary cells or not

Baeodromus ARTHUR 1905 comprises seven species. The presence of intercalary cells has been demonstrated in only two of them, the type species, *B. holwayi* ARTHUR and in *B. ranunculi* J.R. HERN. & J.F. HENNEN. The species with intercalary cells resemble the aecial anamorph genus *Caecoma*. The remaining species do not fit the current concept of Pucciniosiraceae and may be wrongly placed in *Baeodromus* and in the family. The only *Baeodromus* species on a non-asteraceous host and the only one of the Old World is *B. tranzschelii* AZBUKINA that occurs in Eastern Asia on *Urtica* (Urticaceae).

Tab. 1: The genera of Pucciniosiraceae: species number, host families and distribution. The genera are grouped according to the list of genera provided in the text.

Genus (species number)	Host families (number of associated rust species)	Geographic distribution
<i>Endophyllum</i> (ca. 35–40)	Asteraceae (9), Boraginaceae (1), Caesalpiniaceae (1), Convolvulaceae (1), Crassulaceae (1), Elaeagnaceae (1), Euphorbiaceae (3), Hydrangeaceae (1), Lauraceae (1), Magnoliaceae (1), Malvaceae (3), Montiaceae (1), Onagraceae (1), Phyllanthaceae (1), Rhamnaceae (2), Rubiaceae (3), Schisandraceae (1), Solanaceae (1), Valerianaceae (2), Verbenaceae (2), Vitaceae (1)	Very widely distributed, but mainly warm regions

Puccinosiraceae

Genus (species number)	Host families (number of associated rust species)	Geographic distribution
<i>Dietelia</i> (ca. 10, incl. <i>Endophylloides</i>)	Annonaceae (1), Asteraceae (2), Balsaminaceae (1), Convolvulaceae (1), Euphorbiaceae (2), Malvaceae (1), Primulaceae (1), Sapindaceae (1)	Widely distributed, but mainly warm regions
<i>Jacksoniella</i> (1)	Solanaceae (1)	North-western South America
<i>Puccinosira</i> (ca. 13)	Asteraceae (3), Berberidaceae (1), Gentianaceae (1), Malvaceae (incl. Tiliaceae) (4), Melastomataceae (1), Oleaceae (1), Solanaceae (2)	New World (8), Africa (4), Philippines (1)
<i>Didymopsora</i> (ca. 6)	Asteraceae (2), Malvaceae (incl. Tiliaceae) (1), Melastomataceae (1), Solanaceae (2)	New World (5), Africa (1)
<i>Gambleola</i> (1)	Berberidaceae (1)	South and south-east Asia, at higher altitudes
<i>Chardoniella</i> (4)	Asteraceae (Senecioneae: <i>Gynoxis</i> , Eupatorieae: <i>Eupatorium</i> s.l.) (4)	South America: tropical Andes
<i>Trichopsora</i> (1)	Boraginaceae (Heliotropoideae) (1)	South America: tropical Andes
<i>Ceratocoma</i> (1)	Fabaceae (1)	South-east Australia
<i>Cionothrix</i> (3)	Asteraceae (Eupatorieae: <i>Eupatorium</i> , Astereae: <i>Conyza</i>) (3)	New World: tropical
<i>Baeodromus</i> (ca. 7)	Asteraceae (<i>Senecio</i> [4], <i>Eupatorium</i> [1]) (5), Ranunculaceae (1), Urticaceae (1)	New World (6), Eastern Asia (1)

3. Discussion

Short-cycled rust fungi: just life cycle variants of macrocyclic relatives or 'good' species? – Observations from many groups of rust fungi indicate that micro- and demicyclic rusts evolved from progenitors with a macrocyclic life cycle. Shortening of the life cycle may initially involve omission of the conidial uredinial state and in a second step transfer of karyogamy to the aeciospores, the first dikaryotic spores that are produced in the life cycle after dikaryotization. As a consequence, the aecia and the conidial aeciospores are replaced by telia and teliospores that do not serve any more as conidia but produce basidia (e.g. FISCHER 1898, JACKSON 1931 (and references cited within), MAGNUS 1896, MAGNUS 1898, TRANZSCHEL 1910, WILSON 1948).

Abbreviation of life cycle is generally regarded as a response to certain environmental conditions like short growing seasons, for example in alpine or arctic habitats (e.g. FISCHER 1904, HIRATSUKA 1935, JØRSTAD 1964, SAVILE 1953), or in regions with summer aridity (ANIKSTER & WAHL 1979). But microcyclic rust species are also well represented in lowland tropical regions that do not seem to present a severe environment (ARTHUR 1917, BURITICÁ 2000, GARDNER 1994, ONO 2002). One would hypothesize from these observations that the microcyclic life style came into being repeatedly and independently among rust fungi, apparently as an adaptation to environmental conditions, and one could deduce that the microcyclic rusts are mere life cycle variants of macrocyclic relatives.

JACKSON (1931) and WILSON (1948) mentioned a number of 'unstable' rust species whose life cycle can vary considerably with regard to the presence of spore states and the amount of spores that are produced in a given state. In rust fungi with unstable life cycle, the different variants are morphologically so similar and often linked by intermediate forms, that there is no doubt about their specific identity. *Triphragmium ulmariae* (SCHUM.) LINK, an autoecious, usually macrocyclic rust fungus may serve as an example. In this species, microcyclic forms have been observed in which the large caeomatoid aecia are replaced by telia of similar gross morphology. LAGERHEIM (in VESTERGREN 1902) named this form "var. *alpinum*" referring to the observation that it was most often reported from high elevations or northern latitudes. GÄUMANN (1959) considered this variety unnecessary and there seems to be unwritten agreement among uredinologists that different life cycle morphs of unstable species need not be named.

In other rust fungi, shortened life cycles seem to have become stable and they coexist with the macrocyclic life cycle. The stability and coexistence of life cycles has often been considered a valid criterion to give specific rank to the respective rust fungi (DIETEL 1918, ROY et al. 1998, SAVILE 1968). Their similar morphology and the occurrence on the same or closely related hosts reveal the common origin of these species and they have therefore been de-

signed, correlated species' (JACKSON 1931, ORTON 1912). Examples are the autoecious demicyclic *Puccinia tragopogonis* CORDA and the heteroecious macrocyclic *Tranzschelia pruni-spinosae* (PERS.) DIETEL. The first is correlated with the microcyclic *P. brachycyclica* E. FISCH., the second with the microcyclic *T. fusca* (RELHAN) DIETEL. One may also cite a number of (quasi-)microcyclic *Uromyces* spp. on *Euphorbia* that can be correlated to heteroecious progenitors from the complex of *U. pisi-sativi* (PERS.) LIRO (MAGNUS 1898, PFUNDER et al. 2001, TRANZSCHEL 1910). TRANZSCHEL (1910) hypothesized that *Endophyllum euphorbiae-sylvaticae* (DC.) WINTER is also related to this group of *Uromyces* spp.

Initially, it is difficult to envisage how correlated species should have diverged from each other to form separate species. Because the long-cycled parents and the derived microcyclic species form their gametothallus on the same host species genetic exchange between them remains possible either by somatogamous pairings of haploid nuclei or by dikaryotization via spermatia – if spermogonia are produced (see BULLER (1950) and ONO (2002) for reviews on the possible ways of dikaryotization in rust fungi). Such exchange would counteract the genetic separation of different life cycle forms and subsequent speciation (PARK & WELLINGS 2012, RESTREPO et al. 2014, SCHARDL & CRAVEN 2003).

It is hypothesized that life cycle forms may develop into distinct species nonetheless under certain circumstances: (1) ONO (2002) emphasized that abbreviation of the life cycle may lead to homothallism or apomixis and that both processes will likely reduce genetic exchange with a heterothallic ancestor. (2) Host 'jumps' have been identified as an important mechanism to initiate speciation (e.g. GIRAUD et al. 2010, SAVILE 1968, SZABO 2006). A host jump of the parent species or its correlated microcyclic form(s) would strongly reduce genetic exchange or bring it to a halt. In a heteroecious parent species, the host jump would necessarily need to involve the host of the gametothallus to prevent genetic exchange with the microcyclic descendant. (3) Considering short-cycling as an adaptation to adverse environmental conditions, microcyclic forms will likely perform better under such conditions than their relatives with expanded life cycle. This may eventually lead to geographic or ecological (i.e. altitudinal or latitudinal) isolation of the microcyclic descendants from their parents – though both continue to share the same host species. (4) Unfavourable environmental conditions might finally cause extinction of the long-cycled parents while the microcyclic descendants survive. In this case, the descendants cannot be linked any more to a parent species.

Relationships between members of Puccinosiraceae and the PUC. – I regard the rust fungi embraced by the Puccinosiraceae as species because their life cycles seem to be fixed. Some members of *Endophyllum* may be an exception, namely those that are known to belong to biteleomorphic *Puccinia*

spp. This view is recognized good practice in uredinology and supported by the available molecular data on correlated but well differentiated rust species (CHATASIRI & ONO 2006, MAIER et al. 2003, VAN DER MERWE 2007, ZAMBINO & SZABO 1993). ROY et al. (1998) presented contradictory results for the macrocyclic heteroecious *Puccinia monoica* ARTHUR, the supposedly correlated demicyclic *P. consimilis* ELLIS & EVERH. (ARTHUR 1934) and the microcyclic *P. thlaspeos* FICINUS & C. SCHUB. The authors found that collections of *P. monoica*, *P. consimilis* and *P. thlaspeos* intermingled in the same clade and concluded that the different life cycles were not a useful character to separate these species. It should be noted, however, that *P. thlaspeos* is well separable from the other investigated species by morphologically different teliospores. It is puzzling, therefore, that this species could not be distinguished by the molecular analysis.

If it was true that the Pucciniosiraceae and the encompassed genera are completely polyphyletic each species belonging to the family should be more closely related to an ancestral species with expanded life cycle than to any other endocyclic species. If, in contrast, endocyclic rust species were able to evolve independently one should find groups of such fungi that are more closely related to each other than to any supposed macrocyclic progenitor. One would assume that it is straightforward nowadays to find out the origin of the endocyclic rust fungi by DNA sequencing and phylogenetic reconstruction. Unexpectedly, there are very few molecular studies focussing on the evolution and taxonomic status of presumed correlated species (CHATASIRI & ONO 2006, PFUNDER et al. 2001, ROY et al. 1998, VOGLER & BRUNS 1998) and none deals specifically with Pucciniosiraceae. Single pairs of correlated species and single members of Pucciniosiraceae can be found interspersed in broader phylogenetic analyses whose study organisms have not been selected with the aim to tackle the problems outlined here (e.g. AIME 2006, MAIER et al. 2003, VAN DER MERWE et al. 2007, ZAMBINO & SZABO 1993). Yet, the low number of investigated species of the Pucciniosiraceae is only one hindrance to elucidate the links of the family with the PUC. One would need to have a highly resolved and reasonably complete phylogeny of the entire complex to be able to link the endocyclic rust fungi with possible progenitors or to place them in the right clades at least. Such a phylogeny is presently not available. The PUC may count up to 4–5,000 species while available studies on this complex deal with some 60 (VAN DER MERWE et al. 2007) or 70 species (MAIER et al. 2007). At the moment, ca. 250 named *Puccinia* and ca. 75 named *Uromyces* spp. are deposited in GenBank (NCBI, without date), representing less than 10 % of the assumed species of the PUC. With such an incomplete data basis it is virtually impossible to place the endocyclic rusts correctly because most of their parent species will just not have been sequenced so far (comp. SCHOLLER et al. 2011).

Host relationships and 'TRANZSCHEL's rule' as an aid to hypothesize correlations between endocyclic rust fungi and possible macrocyclic progenitors. – Lacking fundamental data we rely on circumstantial evidence when we try to link members of Puccinosiraceae to potential progenitors. Evidence may come from host relationships of the involved rust fungi and from the application of TRANZSCHEL's rule. It has been known since long that phylogenetically related rust fungi are often restricted to well-defined host kinships (e.g. CUMMINS 1940, DURRIEU 1987, EL-GAZZAR 1979, GJÆRUM & CUMMINS 1982, KERN 1973, LEPIK 1972, SAVILE 1979). The occurrence of rust fungi on a certain host species, host genus or even family may hint therefore at their relatedness and sometimes their taxonomic affiliation. One would therefore start looking for potential progenitors of a given microcyclic rust fungus among those rust fungi that grow on the same host species, or host genus, tribe or – finally – the same family. As the endocyclic rust fungi likely descended from heteroecious species both the telial and the aecial hosts of the heteroecious species would need to be considered potentially. It has been observed, however, that in correlated rust fungi, the microcyclic species always grow on the aecial host of the related heteroecious species (e.g. ANIKSTER & WAHL 1979, SHATTOCK & PREECE 2000, TRANZSCHEL 1904, TRAVELBEE 1914). This phenomenon has been recognized as a general rule and is nowadays known as 'TRANZSCHEL's rule' or 'TRANZSCHEL's law'.

JOHNSON and NEWTON (1938) described that selfing of physiological races of *Puccinia graminis* led to the formation of hemicyclic (i.e. producing uredinia and telia) or demicyclic forms of the rust on *Berberis*, the aecial host. CRITOPoulos (1947) reported that a demicyclic or macrocyclic form of *P. graminis* existed in Greece on *B. cretica*. These observations imply that not only microcyclic but also also hemi-, demi- or macrocyclic autoecious rust fungi may be correlated to heteroecious progenitors according to TRANZSCHEL's rule.

The application of TRANZSCHEL's rule to the Puccinosiraceae and the PUC. – Instructive examples for the application of TRANZSCHEL's rule can be found among *Endophyllum* spp. from the temperate zones.

TRANZSCHEL's rule indicates that certain microcyclic *Uromyces* spp. on *Euphorbia* (Euphorbiaceae) derived from heteroecious *Uromyces* spp. that alternate between Fabaceae (telial hosts) and *Euphorbia* (aecial hosts) (TRANZSCHEL 1910). The same origin can be supposed for *E. euphorbiae-sylvaticae*, whose telia and growth habit resemble the aecial state of the heteroecious *Uromyces* spp. on *Euphorbia* closely (DIETEL 1928, MAGNUS 1898, TRANZSCHEL 1910). JØRSTAD (1952) consequently transferred *E. euphorbiae-sylvaticae* to *Uromyces* as *U. euphorbiae-sylvaticae* (DC.) JØRST. A molecular study of MAIER et al. (2007) confirmed the position of *E. euphorbiae-sylvaticae* among *Uromyces* spp. that are microcyclic on *Euphorbia* or alternate between Fabaceae and *Euphorbia*. It is likely that the euphorbiicolous *E. characiatis* LIOU and

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E. euphorbiae-nicaeensis LIOU (LIOU TCHEN-NGO 1929) also belong to this group. They evoke malformation and castration of shoots of two mediterranean *Euphorbia* spp. in a similar way as *E. euphorbiae-sylvaticae*.

Two *Endophyllum* spp. are known on Valerianaceae: *E. centranthi-rubri* POIR. on *Centranthus* spp. and *E. valerianae-tuberosae* MAIRE on *Valeriana*. They might be related to not less than three heteroecious *Puccinia* spp. whose aecial state occurs on Valerianaceae. These are *P. cynodontis* LACROIX ex DESM. with the sporothallus on *Cynodon dactylon* (L.) PERS. (Poaceae), *P. gladioli* CASTAGNE with the sporothallus on *Gladiolus* spp. (Iridaceae) and aecia on *Valerianella* and *P. isiacae* (THÜM.) G. WINTER with the sporothallus on *Phragmites* (Poaceae) and aecia on *Valerianella* as well (D'OLIVEIRA 1949, GÄUMANN 1959, TRANZSCHEL 1907). The aecia of the last species do not coincide with the *Endophyllum* spp. in question because the aeciospores are white (TRANZSCHEL 1907). According to the descriptions in GÄUMANN (1959), *P. cynodontis* might be related to *E. valerianae-tuberosae*. Yet, *Valeriana* has not been reported as an aecial host of *P. cynodontis* to my knowledge. It is unclear whether the 'isolated' *Aecidium* spp. *A. fediae-olitoriae* BALS.-CRIV. & DE NOT., *A. valerianellae* BIV. and *A. velenovskyi* BUBÁK, all on members of Valerianaceae, belong to the named *Puccinia* spp. and represent their aecial state (GÄUMANN 1959). They could also be correlated *Endophyllum* spp.

Endophyllum sempervivi (ALB. & SCHWEIN.) DE BARY is a systemic parasite of *Sempervivum* spp. (Crassulaceae). *Puccinia longissima* J. SCHRÖT., *P. australis* KÖRN. and *P. triseti* ERIKSS. are potential correlates of *E. sempervivi* because they alternate between Crassulaceae (aecial host) and Poaceae (telial host). It should be noted that *Puccinia triseti* is likely correlated with the 'ordinary' microcyclic *P. sedi* KÖRN. *Endophyllum sempervivi* is sister of *P. poarum* NIELSEN according to the molecular study of MAIER et al. (2007). This is probably not correct as *P. poarum* produces aecia on Asteraceae. Some microcyclic *Puccinia* spp. allegedly correlated with *P. poarum* also occur on Asteraceae (GÄUMANN 1959).

ARTHUR (1934) linked the North American *E. tuberculatum* (ELLIS & KELLERM.) ARTHUR & FROMME on Malvaceae with *Puccinia interveniens* BETHEL whose aecia are morphologically very similar and grow on Malvaceae as well. BURITICÁ (1991) transferred *E. tuberculatum* to *Pucciniosira*.

Endophyllum lacus-regis SAVILE & PARMELEE was described on a Portulacaceae from Quebec, Canada. SAVILE & PARMELEE (1956) assumed that *E. lacus-regis* arose from a long-cycled species with systemic aecia or telia but that no such rust was known on Portulacaceae. *Puccinia leptochloae* ARTHUR & FROMME may provide a clue for the origin of *E. lacus-regis*. Its sporothallus grows on Poaceae, while the gametothallus is on *Talinum* of Portulacaceae (CUMMINS 1971). *Puccinia leptochloae* occurs in warm regions from the southern United States to Argentina and is unlikely a progenitor of *E. lacus-*

regis, but it suggests that the relatives of the latter could be sought among heteroecious grass rusts.

SAVILE (1962) related *E. alaskanum* SAVILE on *Epilobium* (Onagraceae) to the heteroecious *P. veratri* DUBY whose gametothallus is found on *Epilobium* spp. while the sporothallus grows on *Veratrum* (Melanthiaceae). The morphological similarity between the teliospores of *P. veratri* and *P. epilobii* DC., an 'ordinary' microcyclic rust of *Epilobium* spp., indicates that both are also correlated (GÄUMANN 1959).

We enter the wide field of endocyclic species that cannot be readily correlated with members of the PUc by the use of TRANZSCHEL's rule. It is evident that TRANZSCHEL's rule can only be applied to hypothesize links between endocyclic rust fungi and potentially ancestral heteroecious rust fungi when the latter are existent. Uredinologists working in the tropics and subtropics have noticed that heteroecious rust fungi are rare in these regions (ARTHUR 1917, BURITICÁ 2000, GARDNER 1994). The relationships of the tropical and subtropical species of the Puccinosiraceae – and they are the majority – is difficult to elucidate therefore. One of the few exceptions is the neotropical *E. guttatum* (KUNZE) SYD. & P. SYD. on Vitaceae. Four members of the PUc are known on Vitaceae: The microcyclic *Puccinia cissi* from Kenya is the only known *Puccinia* sp. reported on Vitaceae (*P. dubia* MAYOR, also reported from Vitaceae, is most likely synonymous with *P. spegazzinii* DE TONI on *Mikania*, Asteraceae). The remainder are *Uromyces* spp. Two of them are microcyclic on *Cissus* in Africa. The third species, the pan-tropical *U. commelinae* COOKE forms its sporothallus on Commelinaceae, the gametothallus on Vitaceae. It might potentially be linked with *E. guttatum*.

Two examples of *Endophyllum* spp. from the Old World tropics that cannot be linked are *E. cassiae* (BRES.) F. STEVENS & MENDIOLA on *Cassia* or *Senna* (Caesalpiniaceae) and *E. emasculatum* ARTHUR & CUMMINS (\equiv *Dietelia emasculata* (ARTHUR & CUMMINS) BURITICÁ & HENNEN) on *Breynia* or *Securinega* (Phyllanthaceae). Only one species of the PUc, the macrocyclic autoecious *Uromyces neurocarpi* DIETEL, has been reported on Caesalpiniaceae (KERN et al. 1933). It normally occurs on members of Fabaceae and its presence on *Martiodendron* of the Caesalpiniaceae is astonishing. A relationship between *U. neurocarpi* and *E. cassiae* is very improbable. Spermogonia are unknown in *E. cassiae* and I suppose that it is not related to the PUc at all. *Endophyllum emasculatum* may not belong to the PUc either. Its spermogonia are unknown and ARTHUR & CUMMINS (1937) affiliated it with *Endophyllum* only tentatively. *Puccinia aequalis* HENN. may be the only member of the PUc that occurs on Phyllanthaceae, but this is uncertain as the host could not be determined safely. It is noteworthy that the endocyclic *Monosporidium andrachnes* BARCLAY occurs on Phyllanthaceae as well. *Monosporidium* spp. have Type-5 or 7

spermogonia and are probably related to Phakopsoraceae. A relationship of *E. emasculatum* and *Monosporidium* cannot be ruled out.

Endophyllum pumilio (KUNZE) SYD., essentially restricted to *Wedelia* and *Clibadium* (Asteraceae), may be cited as an example from the Neotropics. There are no representatives of the PUC on *Clibadium*, but *Wedelia* is parasitized by at least 14 autoecious *Puccinia* spp. and about eight autoecious *Uromyces* spp. One of these *Puccinia* spp. is *P. cnici-oleracei* PERS. that is supposed to be a microform correlated to a heteroecious *Puccinia* of the ‚Formenkreis‘ *P. dioicae* MAGNUS (GÄUMANN 1959). The members of this ‚Formenkreis‘ produce the sporothallus on *Carex* spp. (Cyperaceae) and the gametothallus on various Asteraceae. It is speculative but possible, therefore, that *E. pumilio* was originally related to a heteroecious rust on *Carex*. This may also hold true for two other members of neotropical Pucciniosiraceae. VAN DER MERWE et al. (2007) presented a phylogram in that *D. portoricensis* (WHETZEL & OLIVE) BURITICÁ & J.F. HENNEN (\equiv *Endophylloides portoricensis*), on *Mikania* (Asteraceae), associated with *P. cnici-oleracei* PERS. and *P. rupestris* JUEL. *Puccinia rupestris* is heteroecious, with the sporothallus on *Carex* and the gametothallus on Asteraceae. It belongs to the ‚Formenkreis‘ of *P. dioicae* like *P. cnici-oleracei* (ZWETKO 1993). I need to mention, however, that *P. cnici-oleacei* is circumscribed very differently. GÄUMANN (1959) used the name in a narrow sense for rusts on *Cirsium* spp. while other authors, like CUMMINS (1978) and HYLANDER et al. (1953), adopted it very broadly for rusts on a wider range of Asteraceae genera. SAVILE (1970) argued against the broad circumscription of *P. cnici-oleracei* referring to morphological differences and the host range. SEIER et al. (2009) found that *D. portoricensis* clustered with *P. xanthii* SCHWEIN. and *P. melampodii* DIETEL & HOLW. DIETEL (1918) identified *P. xanthii* as a microcyclic correlate of the heteroecious *P. canaliculata* (SCHWEIN.) LAGERH. that alternates between *Cyperus* (sporothallus) and Asteraceae (gametothallus). MAIER et al. (2007) found that *Dietelia mesoamericana* H.C. EVANS & C.A. ELLISON, like *D. portoricensis* on *Mikania*, is related to *P. senecionis-acuteformis* HASLER, MAYOR & CRUCHET. This rust fungus alternates between *Carex* (sporothallus) and Asteraceae (gametothallus) as well. It is highly unlikely that the Old World species *P. rupestris* and *P. senecionis-acuteformis* are the progenitors of *D. mesoamericana* and *D. portoricensis* from the New World. But it seems plausible to hypothesize a relationship between neotropical *Endophyllum* and *Dietelia* spp. growing on Asteraceae with heteroecious rusts alternating between Cyperaceae and Asteraceae.

About 12 *Endophyllum* spp. occur in Africa. WOOD & CROUS (2005) showed that three astericolous species from South Africa, *E. osteospermi* (DOIDGE) A.R. WOOD, *E. dimorphothecae* A.R. WOOD & CROUS on Calenduleae and *E. elytropappi* (HENN.) A.R. WOOD & CROUS on Gnaphalieae, were specifically distinct and formed a common clade that was most closely related to a number of species of the *P. monoica* complex (JACKSON 1931, ROY et al. 1998).

Puccinia monoica alternates between Poaceae (sporothallus) and Brassicaceae (gametothallus). It correlates with the demicyclic *P. consimilis* ELLIS & EVERH., autoecious on Brassicaceae, and the microcyclic *P. holboellii* also on Brassicaceae (JACKSON & ARTHUR 1922, TRAVELBEE 1914). It is most improbable that members of the *P. monoica* complex are the closest relatives of astericolous *Endophyllum* spp. in South Africa. The result is not supported by TRANZSCHEL's rule, and members of the *P. monoica* complex are unknown in sub-Saharan Africa. To my knowledge, *P. acutiuscula* JØRST. on *Cardamine* from Kenya is the only report of a member of the PUC on Brassicaceae in Africa. It is questionable either whether the *Endophyllum* spp. studied by WOOD & CROUS (2005) would have clustered together if they had been aligned with a more representative selection of species of the PUC covering a broader taxonomic range of host plants.

The New World tropics in general and particularly the Andean region harbour a great diversity of rust fungi on Solanaceae, especially *Puccinia* spp. but also members of Puccinosiraceae (comp. PARDO CARDONA 2001). With a few exceptions the species are autoecious and pass through a micro- or demicyclic life cycle. *Puccinia pampeana* and *P. schultesianthi* are biteleomorphic. They produce two telial states, 'ordinary' telia with puccinioid teliospores and an *Endophyllum*-telial state. Five additional endophylloid rust fungi are known: The *Endophyllum*-like *Jacksonia holwayi* (H.S. JACKS.) J.C. LINDQ. shares *Salpichroa* as a host genus with *P. pampeana*. *Puccinosira holwayi* H.S. JACKS., *P. solani* LAGERH., *Didymopsora solani* DIETEL and *D. solani-argentei* (HENN.) DIETEL grow on *Solanum* spp. These endocyclic species may be related to each other and perhaps also to microcyclic *Puccinia* spp. on *Solanum* that occur in the same region. One could speculate that the neotropical *Puccinia* spp. on Solanaceae are a young and closely related group in that different ways of life cycle shortening are still being 'tried out'. There is one heteroecious *Puccinia* species in the region, *P. substriata* ELLIS & BARTHOL., whose gametothallus is formed on Solanaceae, the sporothallus on Poaceae. This suggests that the ancestors of the short-cycled neotropical *Puccinia* spp. might be found on similar grass rusts.

Puccinosira clemensiae ARTHUR & CUMMINS and *Gambleola cornuta* MASSEE are restricted to *Mahonia* and *Berberis* (Berberidaceae) in south and south-east Asia where they occur in high altitudes. TRANZSCHEL's rule would suggest that potential progenitors can be found among heteroecious *Puccinia* spp. that produce their gametothallus on Berberidaceae as well. This is the case in a number of grass rusts like *Puccinia arrhenatheri* (KLEB.) ERIKSS., *P. brachypodii* G.H. OTTH, *P. graminis* PERS., *P. poae-nemoralis* G.H. OTTH and *P. gymmaea*, but also in *P. oxalidis* DIETEL & ELLIS whose sporothallus does not grow on Poaceae but on *Oxalis* spp. (Oxalidaceae). There are no clues, however, to indicate that *P. clemensiae* and *G. cornuta* are correlated with any of these species. It is even questionable whether *G. cornuta* could be linked to any

of them at all because it has two germ pores per teliospore cell. It resembles *Gymnosporangium* and *Cumminsiella* in this character, but this coincidence does not necessarily indicate closer relationship. *Cumminsiella* spp. occur on *Mahonia* or *Berberis* like *Gambleola* but they are restricted to the New World. *Gymnosporangium* forms the gametothallus on members of Rosaceae or, very exceptionally, on Myricaceae or Hydrangeaceae. It is worthy of mention that *Berberis* is host of ca. five microcyclic *Puccinia* spp. in the Andes and Mexican mountains. They may have derived also from heteroecious graminicolous *Puccinia* spp. like the ones given above. In addition, the microcyclic *Edythea soratensis* RITSCHEL occurs on Andean *Berberis* (BERNDT et al. 2007). The position of *Edythea* in the system of rust fungi is unknown but it cannot be ruled out that it is related to a heteroecious *Puccinia* as well.

Chardonella spp. on *Gynoxis* and *Eupatorium* are morphologically very similar and probably closely related. A relationship may also exist with the microcyclic *Chrysopsora gynoxidis* LAGERH. that occurs on *Gynoxis* as well. It has puccinioid teliospores and produces internal basidia. Heteroecious rusts are unknown on *Gynoxis* and the position of *Chardonella* in the PUC remains obscure.

Cionothrix spp. on *Eupatorium* and *Conyza* cannot be linked either to any possible progenitor. *Eupatorium* spp. are hosts of numerous autoecious *Puccinia* spp. (e.g. CUMMINS 1978) but heteroecious species are apparently lacking. There is no clue whether *Cionothrix* spp. are related to the autoecious *Puccinia* spp.

Limitations of TRANZSCHEL's rule. – The last examples show that the power of TRANZSCHEL's rule to hypothesize possible heteroecious progenitors of microcyclic, especially endocyclic rust fungi, is limited. The principle does not work where there are no heteroecious rust fungi that can be correlated to the microcyclic species in question by the link of the aecial host. It is also difficult to hypothesize a correlation when there are numerous potential candidates for a heteroecious progenitor species or when the potential candidates occur only far away from the distribution area of a microcyclic species. The endophylloid microcyclic rust fungi are particularly difficult to link because their telia mimic the aecia of their progenitors so that a possible correlation with a heteroecious species cannot be corroborated by morphological similarity of the telia. As it has been mentioned before, it becomes impossible to place a microcyclic rust fungus exactly if its heteroecious progenitor is not existent any more.

Despite of these limitations, the hosts of the rust fungi can still provide valuable clues for inferring phylogenetic relationships. CRITOPOULOS (1947) discovered demi- or macrocyclic forms of *P. graminis* on *Berberis*, the aecial host, in nature. This observation shows that a close kinship may not only exist between microcyclic and heteroecious rust fungi that occur on the same host

plant but also between microcyclic and long-cycled autoecious species that share a host. Host comparisons are therefore a suitable way to hypothesize candidate species to which endocyclic and other microcyclic rust fungi are likely related. Molecular phylogenetic analyses that aim at elucidating such relationships cannot resort presently to a reasonably complete phylogeny of the PUC or the rust fungi in general. To mitigate this deficit such studies should include the candidate species that have been identified by host comparisons. It is expected that molecular analyses that are based on a restricted species sampling will place microcyclic rust fungi more confidently when the species included in the study have been selected upon well-founded hypotheses rather than randomly.

4. Conclusions

(1) Many rust fungi are restricted to a single host plant on which they pass through a shortened, often microcyclic life cycle. There is evidence that such short-cycled rusts descended from heteroecious progenitors and it has been observed that they always inhabit the host on which the heteroecious progenitor produces the gametothallus. This pattern has been generalized as TRANZSCHEL'S rule. The endocyclic microcyclic rust fungi have a modified microcyclic life cycle in that the telia resemble or mimic the anamorph genus *Aecidium* or – more rarely – *Caeoma*. Rust fungi with this life cycle and a supposed origin among the Pucciniaceae have been pooled in the artificial family Puccinosiraceae for convenience. The genera comprised by the Puccinosiraceae are delimited by subtle or uncertain characters and are not monophyletic either.

(2) Molecular sequence analysis should permit to link the members of Puccinosiraceae with their progenitors or at least to place them in the correct clade of the *Puccinia-Uromyces* complex if the direct progenitors are not existent any more.

(3) Although the molecular approach seems promising and straightforward it is not feasible at the moment because we lack a reasonably complete phylogeny of the *Puccinia-Uromyces* complex. With only circa 10–15 % of the species of the *Puccinia-Uromyces* complex sequenced and available for comparison, endocyclic rust fungi will likely cluster incorrectly and erratically in any analysis.

(4) More reliable results can be expected by hypothesis-based species sampling. This means that analyses that are based on a restricted species sampling should include those species whose relatedness with the involved microcyclic rust fungi has already been hypothesized by the application of TRANZSCHEL'S rule, by other host relationships and by morphological similarity.

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(5) Members of Puccinosiraceae occur mainly in tropical and other warm regions where heteroecious rust fungi are rare. TRANZSCHEL's rule is not applicable, therefore, in most cases to hypothesize their progenitors. The occurrence on the same host plants may nonetheless provide useful clues to hypothesize relationships between microcyclic and long-cycled autoecious rust fungi.

(6) The *Puccinia-Uromyces* complex counts 4–5,000 species and will likely undergo taxonomic restructuring in future. I suggest that members of Puccinosiraceae should not be combined into *Puccinia* or *Uromyces* thoughtlessly and prematurely though this might be done in a number of species in agreement with the rules of the Melbourne Code of Nomenclature.

(7) Efforts should be made to collect tropical rust fungi in order to obtain good material from which useful DNA can be extracted. Correct determinations have to be ascertained by comparing the collections with type specimens or other authentic material or by consulting a specialist to aid determination.

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