



***Austropuccinia*: a new genus name for the myrtle rust *Puccinia psidii* placed within the redefined family Sphaerophragmiaceae (Pucciniales)**

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Abstract

The myrtle rust *Puccinia psidii* originates from South America but is nowadays a very important and invasive pathogen on several genera of Myrtaceae outside of its native area, and especially in Australia, a biodiversity hotspot of Myrtaceae. To date, the taxonomic position of *P. psidii* has been unclear. The present phylogenetic analyses as well as several former studies show that it does not belong to the genus *Puccinia* and appears outside of the family Pucciniales. It is, however, closely related to the genera *Dasyscypha*, *Puccorchidium*, *Sphenorchidium* and *Sphaerophragmium*. Consequently, the new genus *Austropuccinia* has been erected and placed in the newly circumscribed family Sphaerophragmiaceae.

Key words: cryptic genera, *Nyssopsora*, *Puccinia cygnorum*, Phragmidiaceae, Raveneliaceae, *Triphragmium*

Introduction

The rust fungi, Pucciniales, are obligate plant parasites and one of the largest groups in Basidiomycota. Approximately one half of the nearly eight thousand described rust species belong to the genus *Puccinia* Pers., which is mainly characterized by two-celled teliospores (Kirk *et al.* 2008). Several molecular phylogenetic studies have shown that *Puccinia* is not a monophyletic group and some species are erroneously classified under this genus name (e.g., Aime 2006, Beenken & Wood 2015, Minnis *et al.* 2012). Likewise, Beenken & Wood (2015) have shown that the taxonomical classification of the myrtle rust *Puccinia psidii* G. Winter is also not correct, even though it is one of the molecularly best-investigated rust fungi (Tan *et al.* 2014, Sandhu *et al.* 2016).

Winter (1884) described *P. psidii* as a rust fungus occurring on leaves of *Psidium guajava* L. (= *Psidium pomiferum* L.) (Myrtaceae) in Brazil. Today, however, the myrtle rust has spread and become invasive outside of its native area, where it threatens native plants as well as economically important fruit and timber trees. It has been reported on about 56 genera and 244 species of Myrtaceae from South America, Central America, the Caribbean, Southern USA, Hawaii, Japan, China, South Africa and Australia (Coutinho *et al.* 1998, Machado *et al.* 2015 and literature cited therein).

Winter (1884) placed *P. psidii* in the genus *Puccinia* based on its two-celled teliospores. Van der Merwe *et al.* (2008) disagreed with this classification and excluded *P. psidii* from Pucciniaceae but without renaming it. Beenken & Wood (2015) have shown that two-celled puccinioid teliospores evolved independently in several lineages of Pucciniales. In their molecular analyses, the sequences of *P. psidii* did not appear in the *Puccinia*-clade but were found to be close to the genera *Dasyscypha* Berk. & M.A. Curtis, *Puccorchidium* Beenken and *Sphenorchidium* Beenken. Consequently, Beenken & Wood (2015) recommended a new genus for *P. psidii* but refrained from creating it based only on sequences from GenBank. Recently, McTaggart *et al.* (2016) placed *P. psidii* within family Sphaerophragmiaceae Cummins & Hiratsuka (*sensu* Cummins & Hiratsuka 1983) based on a phylogeny using the LSU and SSU regions of ribosomal DNA, and cytochrome c oxidase subunit 3 (CO3) of mitochondrial DNA. Machado *et al.* (2015) designated an epitype of *P. psidii* from a Brazilian collection on *Psidium guajava*, the host of the type collection. On these grounds, it was finally possible to create a new genus for *P. psidii* based on the sequences of the epitype published by Machado *et al.* (2015).

The circumscription of the family Sphaerophragmiaceae itself is also unclear. Cummins & Hiratsuka (1983)

erected the Sphaerophragmiaceae based mainly on pedicellate teliospores with three or more spherically arranged cells. They included the following genera: *Sphaerophragmium* Magnus, *Cumminsina* Petr., *Hapalophragmium* Syd. & P. Syd. (= *Hapalophragmiopsis* Thurum., = *Triactella* Syd.), *Hennenia* Buriticá, *Nyssopsora* Arthur (= *Ophlophora* Syd.), *Triphragmiopsis* Naumov (= *Nyssopsorella* Syd.) and *Triphragmium* Link. Later, Cummins & Hiratsuka (2003) dissolved the family into Raveneliaceae. McTaggart *et al.* (2016) showed that *Sphaerophragmium acaciae* (Cook) Magnus, the type species of the genus, is separate from Raveneliaceae and forms together with *Dasyspora* spp., *Puccorchidium polyalthiae* (Petch) Beenken (misnamed as *Sphenorchidium polyalthiae*) and *P. psidii*, a highly supported clade. Therefore, McTaggart *et al.* (2016) assigned the species of this clade to the re-erected family Sphaerophragmiaceae. Thus, apart from *Sphaerophragmium*, the Sphaerophragmiaceae did not contain any genus listed in the original description by Cummins & Hiratsuka (1983).

In light of these considerations, the present phylogenetic analyses used more species and genera, including *Nyssopsora* and *Triphragmium*, for the new definition of Sphaerophragmiaceae. *Puccinia cygnorum* R.G. Shivas & J. Walker has been also reported from a Myrtaceae (*Kunzea glabrescens* Toelken) in Australia (Makinson & Butcher 2014, Shiva & Walker 1994, Simpson *et al.* 2006) and was therefore included in the classification of *P. psidii*.

Material and Methods

Two datasets were compiled to determine the taxonomical classification of the species *P. psidii* and of the family Sphaerophragmiaceae by phylogenetic analyses. The combined LSU-SSU dataset of 71 samples and the ITS-LSU dataset of 50 samples were based mainly on the respective datasets in Beenken & Wood (2015). They were complemented with sequences of *P. psidii* from several host plants including the ITS-sequence of the epitype of the species (GenBank accession number KM282154, Machado *et al.* 2015). Sequences of *S. acaciae* and species of *Nyssopsora* and *Triphragmium*, members of Sphaerophragmiaceae *sensu* Cummins & Hiratsuka (1983) were added. Further species of Phragmidiaceae and Pucciniaceae, including *P. cygnorum*, completed the alignments. All sequences were taken from GenBank, and accession numbers are given in Fig. 1 and Fig. 2. Final alignments were performed using MAFFT v7.017 (Kato *et al.* 2002). Ambiguously aligned regions were delimited and excluded from phylogenetic analyses with Gblocks v.0.91b (Castresana 2000).

The datasets were analyzed using the maximum likelihood methods implemented in RAxML version 7.2.8 (Stamatakis 2006). Each analysis was performed assuming a general time-reversible (GTR) model of nucleotide substitution and by estimating a discrete gamma distribution (GTRGAMMA option in RAxML) with partitions according to the sub-matrices, which allowed for multiple models of substitution. One thousand runs with distinct starting trees were completed using the rapid bootstrap (BS) algorithm of RAxML (Stamatakis *et al.* 2008). The resulting phylogenetic ML trees were rooted and visualized using the Dendroscope program (Huson *et al.* 2007). Morphological terms are based on Cummins & Hiratsuka (2003). Herbarium acronyms follow Thiers (2016).

Results

The RAxML analysis from the LSU-SSU dataset is shown in Fig. 1. The resulting tree of the ITS1-5.8S-ITS2-LSU ML analysis is given in Fig. 2. In each of the two analyses, all *P. psidii* sequences appear together outside of the clade of Pucciniaceae and the genus *Puccinia* but inside a very well-supported clade that contains the genera *Dasyspora*, *Puccorchidium*, *Sphenorchidium* and *Sphaerophragmium*. The anamorphic *Uredo baruensis* J.R. Hern. & Aime also belongs to this group that forms the Sphaerophragmiaceae clade (Fig. 2). The two genera with three-celled teliospores, *Nyssopsora* and *Triphragmium*, appear separately outside of the Sphaerophragmiaceae clade (Figs. 1 and 2, indicated by the arrowheads) and outside of the Raveneliaceae clade (Fig. 1). *Triphragmium* appears in the clade containing species of Phragmidiaceae (Fig. 1). The three species of the genus *Nyssopsora* cannot clearly be assigned to a family. *Nyssopsora echinata* (Lév.) Arthur appears close, but not very well supported, to the Pucciniaceae s.l. clade (Fig. 1). The Myrtaceae rust *P. cygnorum* is not related to *P. psidii* but appears in the Pucciniaceae clade of the ITS-LSU analysis (Fig. 2, indicated by the asterisk).

Taxonomy

Austropuccinia Beenken *gen. nov.*

Mycobank number MB 819170

Etymology: from Latin *auster*, *-tri* = south and the genus name *Puccinia*, refer to the South American origin of the *Puccinia*-like genus.

Spermogonia and aecia unknown. Uredia and telia on leaves, buds and fruits of Myrtaceae. Uredinia without sterile elements; urediniospores pedicellate, globose to ovoid, walls hyaline to light-yellow, ornamentation echinulate, sometimes with basal tonsure. Telia without sterile elements, partly developed within uredinia; teliospores puccinioid, with pedicel, two-celled, with a vertical, median septum, ellipsoidal to ovoid, wall smooth, dark yellow to brown, germ-pores one per cell, indistinct, formed by an area of thinned wall. Metabasidia four-celled, producing four basidiospores.

Type species:

Austropuccinia psidii (G. Winter) Beenken *comb. nov.*

Mycobank number MB 819171

Basionym: *Puccinia psidii* G. Winter, Hedwigia 23: 171 (1884).

≡ *Bullaria psidii* (G. Winter) Arthur & Mains, N. Amer. Fl. (New York) 7(7): 488 (1922).

≡ *Dicaeoma psidii* (G. Winter) Kuntze, Revis. gen. pl. (Leipzig) 3 (2): 470 (1898).

Hennen *et al.* (2005) and Simpson *et al.* (2006) listed further synonyms.

Holotype (designated by Machado *et al.* 2015):—BRAZIL. São Francisco do Sul, Prov. St. Catharina, on *Psidium guajava* (= *Psidium pomiferum* L.), Apr 1884, leg. E. Ule nr.14, Rabenhorst-Winter, Fungi europaei nr. 3126 (BR-MYC 80409,93); isolectotypes (designated here):—BRAZIL São Francisco do Sul, Prov. St. Catharina on *Psidium pomiferum*, Apr 1884, leg. E. Ule, Rabenhorst-Winter, Fungi europaei nr. 3126 (M!, ZT-Myc36749!).

Note: The original description printed on the label of the isolectotype in the rust fungi collection of the Zurich herbaria is available on the internet: www.e-pics.ethz.ch. Good illustrations and descriptions of *A. psidii* are found in Coutinho *et al.* (1998), Machado *et al.* (2015), Morin *et al.* (2014), Pegg *et al.* (2014), Perez *et al.* (2011) and Roux *et al.* (2013) for example.

Sphaerophragmiaceae Cummins & Y. Hirats., Illustr. Gen. Rust Fungi, rev. Edn. (St. Paul): 15 (1983) emend. Beenken

Type genus: *Sphaerophragmium* Magnus, Ber. dt.bot. Ges. 9: 121 (1891).

Type species: *Sphaerophragmium acaciae* (Cooke) Magnus, Ber. dt. bot. Ges. 9: 121 (1891).

Family of the Pucciniales, characterized by pedicellate teliospores with two, four or eight cells; cells puccinioid, diorchidioid, square-shaped or spherical arranged; walls smooth, with or without warts and/or long projections; telia rarely with paraphyses. Uredinia of *Uredo* type with or without paraphyses; urediniospores single cells on pedicels, echinate. Spermogonia sub-epidermal, spherical of group V type 4 or flat to lens-shaped of group VI type 5. Aecia of the *Aecidium* type with peridium. Some genera and species have reduced life cycles and do not show all spore states.

Distribution pantropical, known hosts are members of Annonaceae, Fabaceae, Myrtaceae and Sapotaceae.

The following genera belong to Sphaerophragmiaceae: *Austropuccinia*, *Dasyspora*, *Puccorchidium*, *Sphenorchidium* and *Sphaerophragmium*, as well as the anamorphic *Uredo baruensis* (Figs. 1 and 2).

Discussion

Genus delimitation

While teliospores are deemed the most important spore state to distinguish genera and families in the classic taxonomy of Pucciniales (Cummins & Hiratsuka 2003), molecular phylogenies show that their morphological characteristics may not always define higher taxa (e.g., Aime 2006, Beenken & Wood 2015). Consequently, several genera have been split off from the huge genus *Puccinia*, in spite of their similar two-celled-teliospore morphology, such as *Allodus* Arthur

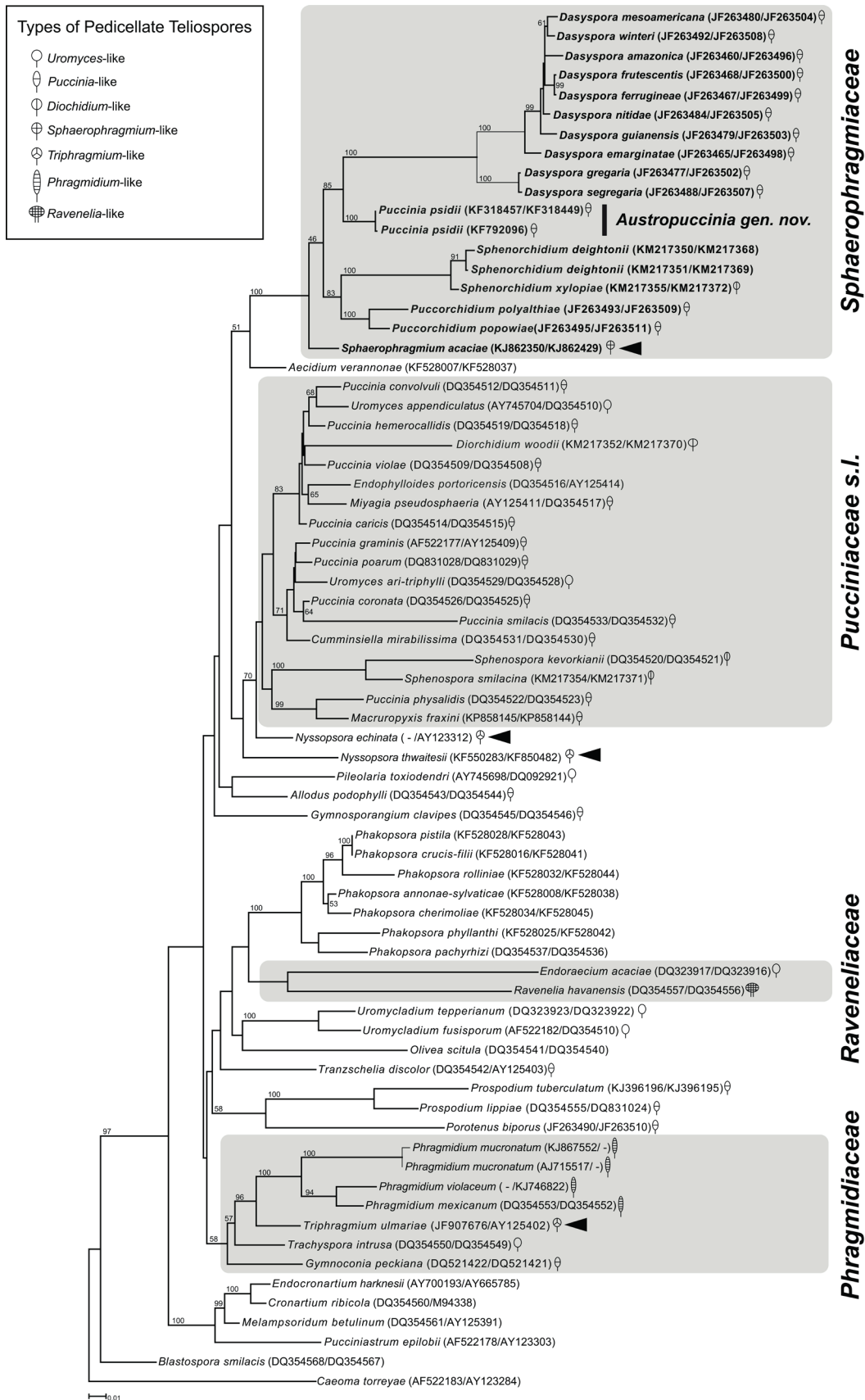


FIGURE 1. Position of the new genus *Austropuccinia* (as *Puccinia*, indicated by the black bar) within Pucciniales and Sphaerophragmiaceae. The various septation types of teliospores are indicated by pictograms (see legend). Species assigned formerly to Sphaerophragmiaceae in Cummins & Hiratsuka (1983) are indicated by the arrowheads. Maximum-likelihood analysis with RAXML version 7.2.6 recovered from combined LSU-SSU sequence data. Numbers at nodes indicate RAXML bootstrap support, GenBank accession numbers of LSU/SSU in parentheses.

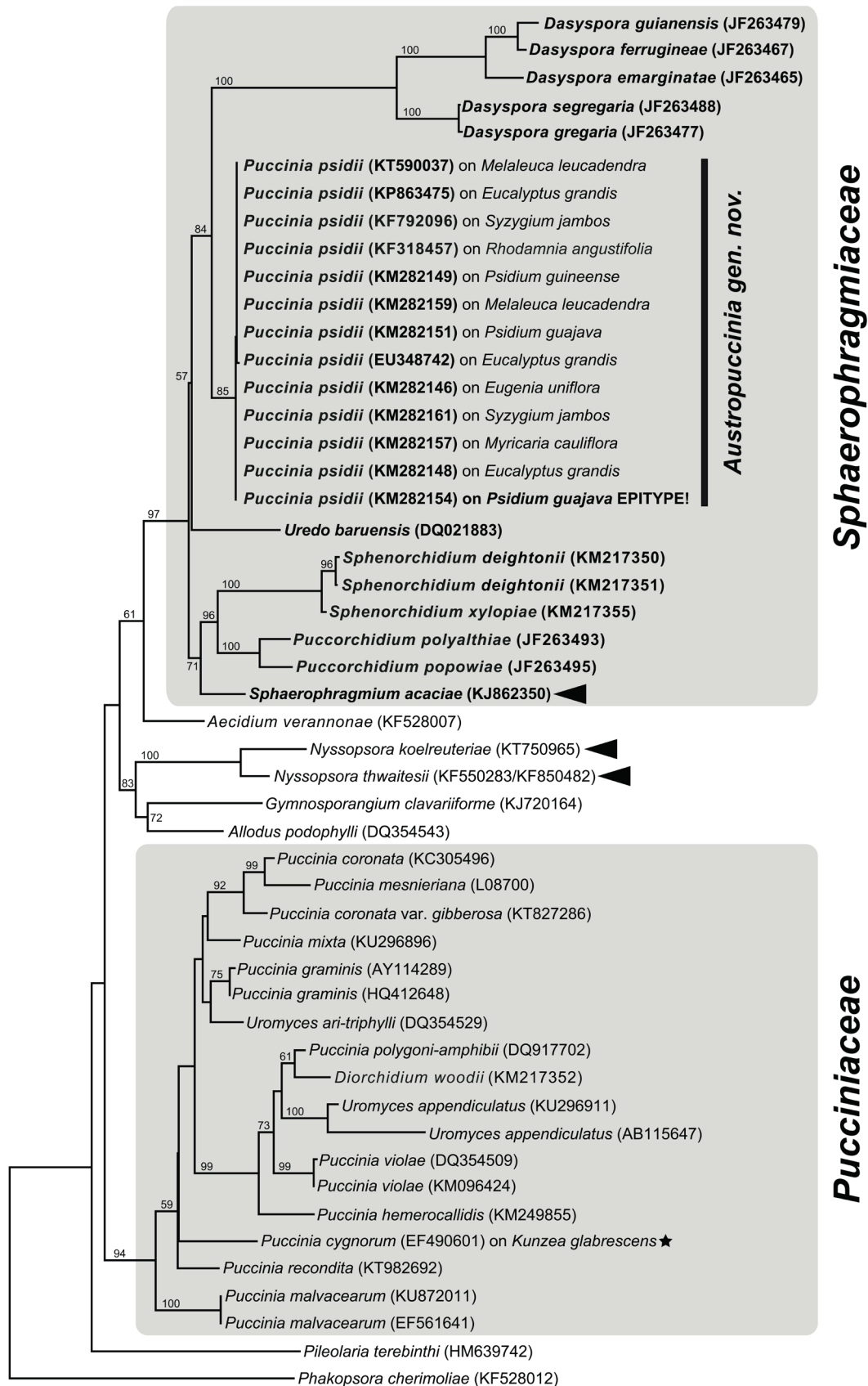


FIGURE 2. Positions of the *Austropuccinia psidii* samples (as *Puccinia psidii*) from several Myrtaceae within Sphaerophragmiaceae. Species assigned formerly to Sphaerophragmiaceae in Cummins & Hiratsuka (1983) are indicated by the arrowheads. The Myrtaceae rust *P. cygnorum* is indicated by the asterisk. Maximum-likelihood analysis with RAXML version 7.2.6 recovered from ITS-LSU sequence data. Numbers at nodes indicate RAXML bootstrap support, GenBank accession numbers of ITS-LSU in parentheses.

(Minnis *et al.* 2012) and *Puccorchidium* (Beenken & Wood 2015). On the other hand, genera that have been separated from *Puccinia* based on differences in their morphology appear within *Puccinia*—such as *Uromyces* (Link) Unger, *Diorchidium* Kalchbr., *Cumminsiella* Arthur and *Miyagia* Miyabe ex Syd. & P. Syd. (Fig. 1, e.g., Aime 2006, Beenken & Wood 2015, van der Merve *et al.* 2008). *Austropuccinia psidii* is a further example of a species that is indistinguishable from the genus *Puccinia* by any specific morphological feature, and yet is clearly distinct genetically. On these grounds it does not even belong to the family Pucciniaceae.

Puccinia psidii fits neither morphologically nor molecularly to any currently valid genera (cf., Cummins & Hiratsuka 2003, Fig. 1). Although there exist two homotypic synonyms of *P. psidii*, namely *Bullaria psidii* and *Dicaeoma psidii*, these names cannot be resurrected. The genera *Bullaria* DC and *Dicaeoma* Gray were originally described on Apiaceae and Polygonaceae, respectively, in Europe, and rightly synonymized with *Puccinia* (Arthur 1934, Dietel 1928, Cummins & Hiratsuka 1983). In any case, no other previously proposed genus names can be found for it. Thus, a new genus with the new name *Austropuccinia* is required for *P. psidii*.

At the moment, *Austropuccinia* is a monotypic genus. Since several authors (e.g., Graça *et al.* 2013, Sandhu *et al.* 2016) assume that the myrtle rust is a species complex, future research will show how many species exist in the new genus.

Genera that cannot be distinguished from each other by morphology but can be well-separated by molecular data (e.g., *Austropuccinia*, *Allodus*, *Puccorchidium* and *Puccinia*) may be called “cryptic genera”. They can be defined as two or more distinct genera that have been erroneously classified and hidden under one genus name, analogous to the definition of “cryptic species” in Bickford *et al.* (2007).

Morphology

Austropuccinia psidii belongs to a group of tropical rust fungi, from which it differs clearly in its morphology. The related genera *Dasyscypha* and *Puccorchidium* are similar in terms of their two-celled teliospores but differ from the smooth teliospores of *A. psidii* in their prominent ornamentation (Beenken *et al.* 2012, Beenken & Wood 2015). The teliospores of *Sphenorchidium* differ in shape and in the arrangement of their cells (Beenken & Wood 2015). The teliospores in the genus *Sphaerophragmium* are composed of 2, 4 or 8 cells spherically arranged bearing tuberculate, spiny or furcate appendages (Beenken & Berndt 2010, Lohsomboon *et al.* 1994). *Uredo baruensis* is also related to this group but it is only known from uredinia on leaves of *Chrysophyllum sparsiflorum* Klotzsch ex Miqu. (Sapotaceae) (Hernandes *et al.* 2005).

Life cycle and host range

Rust fungi show a complex life cycle with up to five spore states and up to two alternate hosts, although the life cycle can be modified and reduced (Cummins & Hiratsuka 2003). Whereas the life cycles of rust fungi from temperate zones are well investigated, the life cycles of most tropical species have not been definitively clarified and cycles with alternate hosts have been largely undetected up to now. This is also the case with the life cycle of *A. psidii*. Coutinho *et al.* (1998) assumed it to have a macrocyclic, autoecious life cycle. In contrast, the more recent study of Morin *et al.* (2014) could not confirm this kind of cycle, although it cannot be ruled out that it is heteroecious with an unknown alternate host bearing spermogonia and aecia. Thus, *A. psidii* proliferates mainly asexually by uredinospores onto many species of different genera in Myrtaceae, especially in those areas where it is not native (Machado *et al.* 2015). It is conspicuous that all closely related genera form their spermogonia and aecia on Annonaceae. The *Dasyscypha* species are microcyclic and autoecious with spermogonia and telia on leaves of *Xylopi* spp. (Annonaceae) (Beenken *et al.* 2012). The two species of the genus *Puccorchidium* are autoecious as well, and form aecia and telia on *Polyalthia* and *Monanthotaxis*, respectively, which are also Annonaceae (Beenken & Wood 2015). The spermogonia and aecia of *Sphenorchidium deightonii* (Syd.) Beenken have been observed on *Xylopi aethiopica* A. Rich. (Beenken & Wood 2015). The species of the genus *Sphaerophragmium* form either uredinia and telia or only telia on Fabaceae and Annonaceae, while spermogonia and aecia are unknown (Beenken & Berndt 2010, Lohsomboon *et al.* 1994). *Aecidium verannonae* Beenken is a further closely related species with spermogonia and aecia occurring on *Annona* spp. (Beenken 2014). Thus, it seems reasonable to look for the potential aecial host of *A. psidii* within the Annonaceae as well.

The family Sphaerophragmiaceae

The genera *Austropuccinia*, *Dasyscypha*, *Puccorchidium*, *Sphenorchidium*, *Sphaerophragmium* and *Uredo baruensis* form a well-separated monophyletic group in both phylogenetic trees (Figs. 1 and 2), in such a way that justifies a separate family for them. The family Sphaerophragmiaceae (Cummins & Hiratsuka 1983) was re-erected because its

type genus *Sphaerophragmium* belongs to this group. However, a new definition of the family Sphaerophragmiaceae based mainly on molecular data is necessary. On the one hand, the genera *Triphragmium* and *Nyssopsora*, which were originally assigned to this family, are now excluded. On the other hand, the new members show high morphological diversity. There are no morphological characteristics that are unique to Sphaerophragmiaceae and differentiate it from other families. This applied to neither the type of spermogonia nor the number and arrangement of teliospore cells. The combination of spermogonia of group V type 4 and two-celled teliospores is not only typical of the genus *Sphenorchidium* but also of *Puccinia* (Beenken & Wood 2015). Spermogonia of group VI in combination with two-celled teliospores have been found in the genus *Dasyspora* (Beenken *et al.* 2012) as well as in the family Raveneliaceae (Cummins & Hiratsuka 2003).

The anamorphic *Aecidium verannonae* appears in a sister position to the clade Sphaerophragmiaceae but not with very strong support from both analyses (Figs. 1 and 2). Thus, further investigation is needed to show whether this species, which is only known from spermogonia and aecia on *Annona spraguei* Saff. and *A. holosericea* Saff. in Central America (Beenken 2014), belongs to Sphaerophragmiaceae.

The genera *Triphragmium* and *Nyssopsora* were originally assigned to Sphaerophragmiaceae because of their teliospores with three cells arranged in a triangle (Cummins & Hiratsuka 1983). However, their sequenced species appear neither within Sphaerophragmiaceae nor Raveneliaceae, where they were later placed by Cummins & Hiratsuka (2003) (Fig. 1). *Triphragmium ulmariae* (DC.) Link, type species of the genus *Triphragmium*, appeared within the Phragmidiaceae clade (Fig. 1) and was already transferred to this family by Maier *et al.* (2003). The species of the genus *Nyssopsora*, *N. echinata* (type species), *N. thwaitesii* (Berk. & Broome) Syd. and *N. koelreuteriae* (Syd. & P. Syd.) Tranzschel, could not be assigned either to Sphaerophragmiaceae or to another rust family in the present phylogenies (Figs. 1 and 2).

As shown for two-celled teliospores (Beenken & Wood 2015), teliospores with three cells arranged in a triangle have evolved at least twice (Fig. 1). Consequently, the families Sphaerophragmiaceae and Phragmidiaceae contain species with various numbers and arrangements of teliospore cells.

Conclusion

The creation of the new genus *Austropuccinia* and the emendation of the family Sphaerophragmiaceae are further examples that the classic, morphologically defined taxonomy is often in conflict with molecular phylogenies. The fact that morphology of rust fungi has been probably stronger affected by adaptations to their environment than by their phylogeny show how poorly the evolution of Pucciniales is currently understood.

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