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A higher-rank classification for rust fungi, with notes on genera

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Abstract: The rust fungi (*Pucciniales*) with 7000+ species comprise one of the largest orders of *Fungi*, and one for which taxonomy at all ranks remains problematic. Here we provide a taxonomic framework, based on 16 years of sampling that includes *ca.* 80 % of accepted genera including type species wherever possible, and three DNA loci used to resolve the deeper nodes of the rust fungus tree of life. *Pucciniales* are comprised of seven suborders – *Araucariomycetinae* subord. nov., *Melampsorinae*, *Mikronegeriinae*, *Raveneliinae* subord. nov., *Rogerpetersoniinae* subord. nov., *Skierkineae* subord. nov., and *Urediniinae* – and 18 families – *Araucariomycetaceae* fam. nov., *Coleosporiaceae*, *Crossosporaceae* fam. nov., *Gymnosporangiaceae*, *Melampsoraceae*, *Milesinaceae* fam. nov., *Ochropsoraceae* fam. & stat. nov., *Phakopsoraceae*, *Phragmidiaceae*, *Pileolariaceae*, *Pucciniaceae*, *Pucciniastriaceae*, *Raveneliaceae*, *Rogerpetersoniaceae* fam. nov., *Skierkaceae* fam. & stat. nov., *Sphaerophragmiaceae*, *Tranzscheliaceae* fam. & stat. nov., and *Zaghouaniaceae*. The new genera *Araucariomyces* (for *Aecidium fragiforme* and *Ae. balansae*), *Neolivea* (for *Olivea tectonae*), *Rogerpetersonia* (for *Caeoma torreyae*), and *Rossmatomyces* (for *Chrysomyxa monesis*, *Ch. pryrolae*, and *Ch. ramischiae*) are proposed. Twenty-one new combinations and one new name are introduced for: *Angiopsora apoda*, *Angiopsora chusqueae*, *Angiopsora paspalicola*, *Araucariomyces balansae*, *Araucariomyces fragiformis*, *Cephalotelium evansii*, *Cephalotelium neocaledoniense*, *Cephalotelium xanthophloeae*, *Ceropsora weirii*, *Gymnotelium speciosum*, *Lipocystis acaciae-pennatulae*, *Neolivea tectonae*, *Neophysopella kraunhia*, *Phakopsora pipturi*, *Rogerpetersonia torreyae*, *Rossmatomyces monesis*, *Rossmatomyces pryrolae*, *Rossmatomyces ramischiae*, *Thekopsora americana*, *Thekopsora potentillae*, *Thekopsora pseudoagrimoniae*, and *Zaghouania notelaeae*. Higher ranks are newly defined with consideration of morphology, host range and life cycle. Finally, we discuss the evolutionary and diversification trends within *Pucciniales*.

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INTRODUCTION

Rust fungi (*Pucciniomycotina*, *Pucciniales*) comprise one of the largest orders in *Fungi*, containing *ca.* 25 % of described *Basidiomycota*. All are obligate pathogens of plants and at *ca.* 7 000+ accepted species (Kirk *et al.* 2008) form the most species-rich group of plant pathogens. Diseases caused by rust fungi have impacted human agriculture and history through time. Rusts likely caused the earliest recognized diseases of agricultural plants (Carefoot & Sprott 1967), and have continued to impact anthropogenic ecosystems through epidemics and localized host extinctions (Carnegie & Pegg 2018). The Green Revolution in the mid to late 20th century that heralded the era of host resistance breeding targeted rust fungi (Philips 2013).

Pucciniales has a suite of characteristics that are rare or unique within *Fungi*, including alternation of generations with separate gametothalli (spermogonia and aecia) and sporothalli (uredinia and telia) that may infect unrelated hosts (heteroecious); and the production of up to five different morphs within the life cycle. These characteristics, together with many

instances of convergent evolution within morphs, repeated evolution of derived life cycle variants, and varying taxonomic emphases on different morph characteristics, have contributed to the development of numerous classification schemes for rust fungi (Fig. S1). Further taxonomic confusion within *Pucciniales* at the species rank has been shaped by separate naming systems under prior nomenclatural codes for sexual and asexual morphs. For instance, prior to the use of molecular data to link morphs, only through painstaking inoculation studies could complete life cycles be elucidated (*e.g.*, Cummins 1978). Consequently, many asexual morphs were unplaceable within a sexual morph-based classification system. Recent changes to the nomenclatural code now allow the placement of taxa within natural genera, regardless of morph (McNeill *et al.* 2012, Turland *et al.* 2018). Although most asexual genera have been reduced to synonymy (Aime *et al.* 2018b), some, such as *Uredo* and *Aecidium* contain species that occur in over 50 sexual genera, and it will be non-trivial to assign these to natural genera.

Generic-rank classification, even for sexual morph species, is similarly difficult. At least 334 generic names have been described

in *Pucciniales*; most researchers accept *ca.* 130 of these (*e.g.*, Cummins & Hiratsuka 2003). Studies have shown that many diagnostic characters are homoplasious, such as the number of cells per teliospore (Aime 2006, Maier *et al.* 2007, van der Merwe *et al.* 2007, Yun *et al.* 2008, Beenken & Wood 2015). As a result, most taxon-rich genera – the largest being *Puccinia* (*ca.* 4 000 species), *Uromyces* (*ca.* 800 species), and *Ravenelia* (*ca.* 200 species) – are polyphyletic and will need thoughtful re-evaluation for how to reassign these species into monophyletic genera.

At the higher ranks, classification of rust fungi has varied through time as well (Fig. S1). Rust fungi were initially classified into families by characteristics of basidia and teliospores (*e.g.*, Cunningham 1931). This approach divided rusts into three (or four) families, *Melampsoraceae*, (*Coleosporiaceae*), *Pucciniaceae* and *Zaghouaniaceae* (Sydow & Sydow 1915, Cunningham 1931). Arthur (1907–1931), Sydow & Sydow (1915) and Dietel (1928) further classified rusts in subfamilies or tribes based on morphology of telia. Other workers, such as Hiratsuka & Cummins (1963) placed greater emphasis on the gametothallus, especially spermatogonial morphology, resulting in conflicting taxonomic hypotheses. This approach was later combined with teliospore morphology (Cummins & Hiratsuka 1983, 2003) to achieve a 13-family classification that became the most broadly applied in the pre-molecular era.

The first molecular systematic study to test the familial classification of Cummins & Hiratsuka (2003) subdivided the rust fungi into three major radiations, *Mikronegeriineae*, *Melampsorineae*, and *Uredinineae*, that mostly correspond to the earlier three-family approach of Cunningham (1931) (Aime 2006). Within these radiations were (i) several lineages more or less corresponding to families circumscribed by Cummins & Hiratsuka (2003), such as *Coleosporiaceae*, *Melampsoraceae*, *Zaghouaniaceae* (as *Mikronegeriaceae*), *Phragmidiaceae*, *Pileolariaceae*, *Pucciniaceae*, *Pucciniastraceae* and *Raveneliaceae*; (ii) families, such as *Chaoniaceae* and *Phakopsoraceae* that were comprised of polyphyletic assemblages that could not be effectively resolved without data from type species; and (iii) several so-called “orphan” genera that could not confidently be assigned to families (Aime 2006).

Numerous subsequent studies have focused on resolution of single families, *e.g.*, *Sphaerophragmiaceae* (Beenken 2017); polyphyletic genera, *e.g.*, segregation of *Neophysopella* from *Phakopsora* (Ji *et al.* 2019); as well as conservation efforts to stabilize use of generic names (*e.g.*, Aime *et al.* 2018b, 2019a, b). Despite these efforts, a stable and resolved higher-rank classification for the rust fungi has not been achieved. A major bottleneck has been limited sampling of taxa that represent the type species of genera, especially for genera with convergent morphologies, that are polyphyletic, and/or contain species with multiple competing names for different morphs.

The purpose of the present study is to provide a stable higher-rank classification for *Pucciniales* that will serve as a framework for future systematic studies. We have assembled a dataset over the last 16 years that includes exemplars from 113 (*ca.* 80 %) rust genera, including 108 that are represented by sequences from type species (86) or type species proxies (22). Our phylogenetic hypotheses are based on DNA data from three loci (nuclear large subunit and small subunit rDNA, and Cytochrome-c-oxidase subunit 3) with varying evolutionary rates across *Pucciniales* (*e.g.*, Aime 2006, Vialle *et al.* 2009, Feau *et al.* 2011, Aime *et al.* 2018a, McTaggart & Aime 2018). We propose a natural classification for *Pucciniales* based on

combined evidence from morphology, life cycles, hosts, and phylogenetic data. Several new suborders, families, genera, and combinations are proposed, and suborders and families are redefined. Finally, we discuss the evolutionary trends that led to diversification within *Pucciniales* and highlight unresolved areas of the rust family tree for future research.

MATERIALS AND METHODS

Taxon selection

Priority was given to species that represent generic types of rust fungi. If type species were unavailable, wherever possible two congeneric species similar to the type in respect to host genus, morphology, and geography were chosen as proxies (*e.g.*, *Skierka*, *Tranzschelia*, *Uredopeltis* and *Uropyxis*). At least one exemplar was included for every major lineage of *Pucciniales* that had been previously identified (*e.g.*, Aime 2006, 2018a, Beenken 2017). Additional genera were targeted (i) from families that appeared polyphyletic in prior studies (*e.g.*, *Chaoniaceae*, *Phakopsoraceae*); (ii) from previously undersampled families, *e.g.*, *Uropyxidaceae*; and (iii) to broaden sampling of endocyclic species (*e.g.*, *Baeodromus*, *Chardonella*, *Cionothrix*, *Dietelia*, *Puccinosira*). If possible, more than one species was included for genera (i) previously determined as orphaned taxa *sensu* Aime (2006) (*e.g.*, *Gymnosporangium*, *Prospodium*, *Ochropsora*, and *Tranzschelia*) or *incertae sedis sensu* Cummins & Hiratsuka (2003) (*Elateraecium*, *Masseëlla*); and (ii) previously demonstrated as polyphyletic (*e.g.*, *Maravalia*, *Phakopsora*, *Pucciniastrum*, *Ravenelia*). Additional taxa were also included for genera if complete data at the three sequenced loci were available (*e.g.*, *Gymnosporangium*, *Hamaspora*, *Melampsora*, *Neophysopella*, and *Phragmidium*). An initial dataset of 130 rust taxa and three loci (Table 1) was used to determine the familial placement of genera and the relationships between families in an overview tree. The overview tree was rooted with *Ecronartium muscicola*, from the sister order to *Pucciniales* (Aime *et al.* 2006).

With the overview tree as a guide, we divided the data into three subsets, *Melampsorineae* (73 species), *Raveneliineae* (77 species) and *Uredinineae* (164 species), for additional sampling and analyses (Table S1). In expanded sampling, we included taxa only sequenced for one of the three loci in order to broaden both generic representation and species representation for polyphyletic genera. Trees were rooted from the sister lineage as shown by the overview tree, or, in the case of *Raveneliineae*, midpoint rooted.

DNA extraction, PCR and sequencing

DNA was extracted from fresh or herbarium material with the UltraClean Plant DNA Isolation Kit (MoBio Laboratories Inc., Solana Beach, CA, U.S.A.). The nuclear large subunit (28S) region of the ribosomal DNA repeat was amplified with Rust2INV (Aime 2006)/LR6 or LR7 (Vilgalys & Hester 1990) and, for weak products, nested with Rust28SF (Aime *et al.* 2018a)/LR5 or LR6 (Vilgalys & Hester 1990) following the protocols of Aime *et al.* (2018a). The small subunit (18S) region of the ribosomal DNA repeat was amplified with NS1 (White *et al.* 1990)/Rust 18S-R (Aime 2006) and nested with RustNS2-F (Aime *et al.* 2018a)/NS6 (White *et al.* 1990) following the protocols of Aime *et al.* (2018a). Cytochrome-

Table 1. Collection and accession data for sequences used in *Pucciniales* overview tree (Fig. 1).

Taxon	Type status ^a	Voucher number (Collection number) ^b	28S	18S	CO3	Host	Source
<i>Achrotelium ichnocarpi</i>	T	BRIP 55685	KT199393	KT199381	KT199404	<i>Ichnocarpus frutescens</i>	McTaggart et al. (2016)
<i>Aecidium kalanchoe</i>		BPI 843633 (U18, HOLOTYPE)	AY463163	DQ354524	NA	<i>Kalanchoe blossfeldiana</i>	Hernandez et al. (2004)
<i>Allodus podophylli</i>	T	BPI 842277 (U2, NEOTYPE); 28S, 18S; PUR N16753:CO3	DQ354543	DQ354544	MG907270	<i>Podophyllum peltatum</i>	Aime (2006); Aime et al. (2018a)
<i>Angiopsora paspalicola</i>	*	BRIP 55625	MW049243	NA	MW036496	<i>Paspalum</i> sp.	this paper
<i>Aplopsora nyssae</i>	T	BPI 877823 (U1191)	MW049244	NA	NA	<i>Nyssa sylvatica</i>	this paper
<i>Araucariomyces fragiformis</i>	T	BRIP 68996	MW049245	MW049292	MW036497	<i>Agathis robusta</i>	this paper
<i>Austropuccinia psidii</i>	T	BRIP 58164	KF318449	KF318457	KT199419	<i>Rhodammia angustifolia</i>	Pegg et al. (2014); McTaggart et al. (2016)
<i>Baeodromus eupatorii</i>	*	PUR N16312 (U1386)	MW049246	NA	NA	<i>Ageratina</i> sp.	this paper
<i>Bibulocystis pulcherrima</i>	T	BRIP 58450	MW049247	NA	MW036498	<i>Daviesia latifolia</i>	this paper
<i>Blastospora smilacis</i>	T	PUR N270	DQ354568	DQ354567	NA	<i>Smilax sieboldii</i>	Aime (2006)
<i>Bubakia argentinensis</i> (as <i>Phakopsora argentinensis</i>)	*	ZT:RB 8248	KF528009	NA	NA	<i>Croton</i> cf. <i>anisodonitus</i>	Beenken (2014)
<i>Calyptospora goeppertiana</i>	T	BPI 882188 (U866)	MW147023	NA	NA	<i>Abies balsamea</i>	this paper
<i>Catenulopsora flacourtae</i>	T	PUR N13865 (U669)	MW049248	MW049293	NA	<i>Flacourtia indica</i>	this paper
<i>Cephalotelium macowaniana</i> (as <i>Ravenelia macawaniana</i>)	T	PREM 61222	MG946007	NA	NA	<i>Vachellia karroo</i>	Ebinghaus et al. (2018a)
<i>Cephalotelium neocaledoniense</i> (as <i>Ravenelia neocaledoniensis</i>)		BRIP 56908	KJ862348	NA	KJ862460	<i>Vachellia farnesiana</i>	McTaggart et al. (2015)
<i>Ceratocoma jacksoniae</i>	T	BRIP 57717	KT199394	KT199382	KT199405	<i>Daviesia</i> sp.	McTaggart et al. (2016)
<i>Ceropsora weirii</i> (as <i>Chrysomyxa weirii</i>)	*	916CHWPCGS68	FJ666465	NA	NA	n.d.	Vialle et al. (2009)
<i>Chaonia ingae</i>	*	BPI 863575 (GUY74)	MW049249	NA	NA	<i>Inga</i> sp.	this paper
<i>Chardonella gynoxidis</i>	T	R15	MW049250	NA	NA	<i>Gynoxys</i> sp. (cf.)	this paper
<i>Chrysocelis lupini</i>	T	PUR N11562 (U1570)	MW049251	NA	NA	<i>Lupinus</i> sp.	this paper
<i>Chrysomyxa arctostaphyli</i>		CUW CFB 22246	AF522163	AY657009	NA	n.d.	Matheny et al. unpublished
<i>Cionothrix praelonga</i>	T	PUR 90104	MW049252	NA	NA	<i>Eupatorium</i> sp.	this paper
<i>Coleopuccinia sinensis</i>	T	BJFC R02506	MF802285	NA	NA	<i>Cotoneaster microphyllus</i>	Cao et al. (2018)
<i>Coleosporium senecionis</i>	T	PDD 98309	KJ716348	KJ746818	NA	<i>Senecio</i> sp.	Padamsee & McKenzie (2014)
<i>Cronartium flaccidum</i>	T	PUR N16561 (MCA4165)	MW049253	MW049294	NA	<i>Vincetoxicum hirundinaria</i>	this paper
<i>Cronartium harknessii</i> (≡ <i>Endocronartium harknessii</i>)	(T)	CFB22250	AF522175	AY665785	NA	<i>Pinus</i> sp.	Szaro & Bruns unpublished; Matheny et al. unpublished
<i>Crossopora fici</i>		BRIP 58118	MH047207	MH047212	MH047204	<i>Ficus virens</i> var. <i>sublancoelata</i>	this paper

Table 1. (Continued).

Taxon	Type status ^a	Voucher number (Collection number) ^b	28S	18S	CO3	Host	Source
<i>Crossopora ziziphi</i>	T	BPI 877877 (U904)	MG744558	NA	NA	<i>Ziziphus mucronata</i>	Souza et al. (2018)
<i>Cumminsiiella mirabilissima</i>	T	BPI 871101 (U480)	DQ354531	DQ354530	NA	<i>Mahonia aquifolium</i>	Aime (2006)
<i>Dasyospora gregaria</i>	T	ZT Myc 3397	JF263477	JF263502	JF263518	<i>Xylopiya cayennensis</i>	Beenken et al. (2012)
<i>Desmella aneimiae</i>	T	BRIP 60995	KM249867	NA	NA	<i>Nephrolepis hirsutula</i>	McTaggart et al. (2014)
<i>Diaphanopellis purpurea</i>	*	BJFC R02448	MK874622	NA	NA	<i>Picea brachytyla</i>	Yang & Wang unpublished
<i>Didymopora solani-argentei</i>	T	PUR N3728	MW049254	NA	NA	<i>Solanum argenteum</i>	this paper
<i>Dietelia codiae</i>	*	PUR N16488	MW049255	NA	NA	<i>Codiaeum variegatum</i>	this paper
<i>Dipyxis mexicana</i>	T	BPI 871906	MW049256	NA	NA	<i>Adenocalymna</i> sp.	this paper
<i>Edythea quitensis</i>	T	QCAM6453	MG596499	NA	NA	<i>Berberis hallii</i>	Barnes & Ordonez unpublished
<i>Elateraecium salaciicola</i>	T	PUR F17677	MW049257	MW049295	NA	<i>Salacia</i> sp.	this paper
<i>Endophylloides portoricensis</i> (as <i>Dietelia portoricensis</i>)	T	BPI 844288 (U322):28S; n.d.:18S	DQ354516	AY125389	NA	<i>Mikania micrantha</i>	Aime (2006); Wingfield et al. (2004)
<i>Endophyllum cassiae</i>	T	BPI 871369 (U525)	MW049258	NA	NA	<i>Cassia obtusifolia</i>	this paper
<i>Endophyllum circumscriptum</i>	T	BPI 872271	MW049259	NA	NA	<i>Cissus</i> sp.	this paper
<i>Endoraecium acaciae</i>	T	BPI 871098 (MCA2957)	DQ323916	DQ323917	NA	<i>Acacia koa</i>	Scholler & Aime (2006)
<i>Econartium muscicola</i>	*	MIN796447:28S; DUKE:DAH(e1):18S	AF014825	DQ241438	NA	NA	Bruns & Szaro unpublished; Henk & Vilgalys (2007)
<i>Gerwasia rubi</i>	T	BRIP 58440	KT199397	NA	KT199408	<i>Rubus</i> sp.	McTaggart et al. (2016)
<i>Gymnoconia interstitialis</i>	T	BPI 747600	JF907677	DQ521422	NA	<i>Rubus allegheniensis</i>	Yun et al. (2011); Matheny et al. unpublished
<i>Gymnosporangium clavariiforme</i> (≡ <i>Podisoma clavariiforme</i>)	(T)	BRIP 59471	MW049261	MW049296	MW036499	<i>Crataegus</i> sp.	this paper
<i>Gymnosporangium sabiniae</i>	T	TNM F0030477	KY964764	KY964764	NA	<i>Pyrus communis</i>	Shen et al. (2018)
<i>Gymnotelium blasdaleanum</i>	*	PUR N10018 (U1469)	MG907218	MG907206	MG907269	<i>Amelanchier alnifolia</i>	Aime et al. (2018a)
<i>Hamaspora acutissima</i>	T	BRIP 56949	KT199398	KT199385	KT199409	<i>Rubus moluccanus</i>	McTaggart et al. (2016)
<i>Hamaspora longissima</i>	T	BPI 871506 (U305)	MW049262	MW049297	NA	<i>Rubus ludwigii</i>	this paper
<i>Haplophragmium derridis</i>	T	PUR N16494	MW049263	NA	NA	unidentified <i>Fabaceae</i>	this paper
<i>Hemileia vastatrix</i>	T	BRIP 61233	KT199399	DQ354565	KT199410	<i>Coffea robusta</i>	McTaggart et al. (2016); Aime (2006)
<i>Hyalopora aspidiotus</i>	T	PUR N4641	MW049264	NA	NA	<i>Gymnocarpium dryopteris</i>	this paper
<i>Kernkampella breyniae</i>	*	BRIP 56909	KJ862346	KJ862428	KJ862459	<i>Breynia cernua</i>	McTaggart et al. (2015)
<i>Kuehneola uredinis</i>	T	BPI 871104 (MCA2830)	DQ354551	DQ092919	NA	<i>Rubus argutus</i>	Aime (2006); Matheny & Hibbett unpublished

Table 1. (Continued).

Taxon	Type status ^a	Voucher number (Collection number) ^b	28S	18S	CO3	Host	Source
<i>Kwellingia bambusae</i>	T	PUR F18200	MW147026	NA	NA	<i>Bambusa</i> sp.	this paper
<i>Lipocystis acaciae-pennatulae</i> (as <i>Ravenelia acaciae-pennatulae</i>)		BPI 864189 (U115)	MG907213	MG907204	MG907264	<i>Vachellia pennatulata</i>	Aime <i>et al.</i> (2018a)
<i>Lipocystis caesalpiniae</i>	T	BPI 863966	MW049265	NA	NA	<i>Mimosa ceratonia</i>	this paper
<i>Macruropyxis fraxini</i>	T	ZT Myc 56551	KP858145	KP858144	NA	<i>Fraxinus platypoda</i>	Beenken & Wood (2015)
<i>Maravalia limoniformis</i>	*	BRIP 59649	MW049266	NA	MW036500	<i>Austrosteenisia blackii</i>	this paper
<i>Masseëlla capparisi</i>	T	BRIP 56844	JX136798	NA	KT199413	<i>Flueggea virosa</i>	McTaggart <i>et al.</i> (2016)
<i>Melampsora euphorbiae</i>	T	BPI 863501 (U138)	DQ437504	DQ789986	MW036501	<i>Euphorbia macroclada</i>	Aime (2006); this paper
<i>Melampsora laricis-populina</i>		strain 98AG31	NW6768836	NW6768836	NW6768836	<i>Populus</i> sp.	Duplessis <i>et al.</i> unpublished
<i>Melampsorella caryophyllacearum</i>	T	PUR ex-MPPD-40507	MG907233	NA	NA	<i>Cerastium fontanum</i>	Aime <i>et al.</i> (2018a); this paper
<i>Melampsorium betulinum</i>	T	BPI 871107 (MCA2884):28S; n.d.: 18S	DQ354561	AY125391	NA	<i>Alnus</i> sp.	Aime (2006); Wingfield <i>et al.</i> (2004)
<i>Mikronegeria fagi</i>	T	PUR N16373	MW049267	MW049298	NA	<i>Nothofagus obliqua</i>	this paper
<i>Mikronegeria fuchsiae</i>	T	PDD 101517	KJ716350	KJ746826	NA	<i>Phyllocladus trichomanoides</i>	Padamsee & McKenzie (2014)
<i>Milesia polypodii</i> (as <i>Milesina polypodii</i>)	T	KRM0043190	MK302190	NA	NA	<i>Polypodium vulgare</i>	Bubner <i>et al.</i> (2019)
<i>Milesina kriegiana</i>	T	KRM0048480	MK302207	NA	NA	<i>Dryopteris dilatata</i>	Bubner <i>et al.</i> (2019)
<i>Miyagia pseudosphaeria</i>	*	BPI 842230 (U63):28S; n.d.: 18S	DQ354517	AY125411	NA	<i>Sonchus oleraceus</i>	Aime (2006); Wingfield <i>et al.</i> (2004)
<i>Naohidemycetes vaccinii</i>	T	BPI 871754 (MCA2780)	DQ354563	DQ354562	NA	<i>Vaccinium ovatum</i>	Aime (2006)
<i>Neolivea tectonae</i>	T	PUR N15331 (MCA6480)	MW049282	MW049307	MW036507	<i>Tectona grandis</i>	this paper
<i>Neophysopella ampelopsidis</i> (as <i>Phakopsora ampelopsidis</i>)	T	IBA 8597	AB354738	NA	NA	<i>Ampelopsis brevipedunculata</i>	Chatasiri & Ono (2008)
<i>Neophysopella kraunhiae</i>		PUR N15073	MW049242	NA	NA	<i>Wisteria floribunda</i>	this paper
<i>Neophysopella meliosmae-myrianthae</i>		BRIP 58404	MW049270	NA	NA	<i>Vitrus</i> sp.	this paper
<i>Newinia heterophragmatis</i>	T	PUR N16505	MW049271	NA	NA	<i>Kigelia cf. africana</i>	this paper
<i>Nothoravenelia japonica</i>	T	HMJAU8598	MK296509	NA	NA	n.d.	Ji unpublished
<i>Nyssopora echinata</i>	T	KR-0012164 (U1022):28S; ESS244:18S	MW049272	U77061	NA	<i>Meum athamanticum</i>	this paper; Swann & Taylor (1995)
<i>Ochropsora ariae</i>	T	KR-0015027 (U1036)	MW049273	NA	NA	<i>Anemone nemorosa</i>	this paper
<i>Olivea capituliformis</i>	T	BPI 863670	MW049274	NA	NA	<i>Alchornea latifolia</i>	this paper
<i>Peridiopsis mori</i>		PUR N11676 (MCA4685)	MW147025	NA	MW166323	<i>Morus alba</i>	this paper
<i>Phakopsora crucis-filii</i>	T	ZT Myc 48990	KF528016	KF528041	KF528049	<i>Annona paludosa</i>	Beenken (2014)

Table 1. (Continued).

Taxon	Type status ^a	Voucher number (Collection number) ^b	28S	18S	CO3	Host	Source
<i>Phakopsora fici</i>		BRIP 59463	MH047210	MW049299	MW036502	<i>Ficus carica</i>	this paper
<i>Phakopsora pachyrhizi</i>	T	BRIP 56941	KP729475	MW049300	MW036503	<i>Neonotonia wightii</i>	Maier et al. (2016); this paper
<i>Phragmidium mucronatum</i>	T	BRIP 60097	MW049275	NA	NA	<i>Rosa rubiginosa</i>	this paper
<i>Phragmidium tormentillae</i> (≡ <i>Frommeëlla tormentillae</i>)	(T)	BPI 843392 (U3)	DQ354553	DQ354552	MG907265	<i>Potentilla canadensis</i>	Aime (2006); Aime et al. (2018a)
<i>Pileolaria brevipes</i>		PUR N16525 (MCA3477); 28S; CO3; BPI 877989 (MCA3223); 18S	MG907216	MW049301	MG907267	<i>Toxicodendron</i> sp.	Aime et al. (2018a); this paper
<i>Pileolaria shiriana</i>		BRIP 58344	KJ651957	NA	NA	<i>Rhus japonica</i>	Doungsa-ard et al. (2018)
<i>Pileolaria terebinthi</i>	T	PUR N11686 (U1282)	KY796222	NA	NA	<i>Pistacia terebinthus</i>	Ishaq et al. (2019)
<i>Porotenus biporus</i>	*	ZT Myc 3414	JF263494	JF263510	NA	<i>Memora flavida</i>	Beenken et al. (2012)
<i>Prospodium appendiculatum</i>	T	BPI 879956 (U753)	MW049276	NA	NA	<i>Tecoma stans</i>	this paper
<i>Prospodium lippiae</i>		BPI 843901 (U152)	DQ354555	DQ831024	NA	<i>Aloysia polystachya</i>	Aime (2006)
<i>Prospodium tuberculatum</i>		BRIP 57630	KJ396195	KJ396196	MW036504	<i>Lantana camara</i>	Pegg et al. (2014); this paper
<i>Puccinia graminis</i>	T	BRIP 60137	KM249852	MW049302	MW036505	<i>Glyceria maxima</i>	McTaggart et al. (2016); this paper
<i>Pucciniastrum epilobii</i>	T	PUR N11088 (MCA5308)	MW049277	NA	NA	<i>Epilobium angustifolium</i>	this paper
<i>Pucciniastrum minimum</i>		BRIP 57654	KC7633401	KT199391	KT199422	<i>Vaccinium corymbosum</i>	McTaggart et al. (2016)
<i>Puccinosira pallidula</i>	*	BPI 863541 (U282)	DQ354534	MW049303	NA	<i>Triumfetta semitriloba</i>	Aime (2006); this paper
<i>Puccinosira solani</i>		n.d.	EU851137	NA	NA	<i>Solanum aphyodendron</i>	Zuluaga et al. unpublished
<i>Puccorchidium polyalthiae</i>	T	ZT HeRB 251	JF263493	JF263509	JF263525	<i>Polyalthia longifolia</i>	Beenken & Wood (2015)
<i>Ravenelia</i> sp.	*	PUR F19717	MW147024	MW166323	MW166322	<i>Tephrosia</i> sp.	this paper
<i>Rogerpetersonia torreyae</i> (as <i>Caeoma torreyae</i>)	T	BPI 877825 (U1168); 28S; CO3; BPI 877824 (U808); 18S	MG907207	MG907197	MG907254	<i>Torreya californica</i>	Aime et al. (2018a)
<i>Rossmannomyces pyrolae</i> (as <i>Chrysomyxa pyrolae</i>)	T	390CHPPCGVF1	FJ666456	NA	NA	n.d.	Vialle et al. (2009)
<i>Skierka diploglottidis</i>	*	BRIP 59646	MW049278	MW049304	MW036506	<i>Dictyonera obtusa</i>	this paper
<i>Skierka robusta</i>	*	BPI 879954 (U747)	MW049279	MW049305	NA	<i>Rhoicissus rhomboidea</i>	this paper
<i>Sorataea arayatensis</i>		U416	MW049280	NA	NA	<i>Derris elliptica</i>	this paper
<i>Sphaerophragmium acaciae</i>	T	BRIP 56910	KJ862350	KJ862429	KJ862462	<i>Albizia</i> sp.	McTaggart et al. (2015)
<i>Sphenorchidium xylopiiae</i>	T	n.d.	KM217355	KM217372	NA	<i>Xylopiia aethiopica</i>	Beenken & Wood (2015)
<i>Sphenospora kevorkianii</i>		BPI 863558 (U10)	DQ354521	DQ354520	NA	<i>Stanhopea candida</i>	Aime (2006)

Table 1. (Continued).

Taxon	Type status ^a	Voucher number (Collection number) ^b	28S	18S	CO3	Host	Source
<i>Stereostromatum corticioides</i>	T	BPI 842314 (U27)	MW049281	MW049306	NA	<i>Bambusa</i> sp.	this paper
<i>Stomatiosora psychotriicola</i>	*	PREM 60886	NG059953	NA	NA	<i>Psychotria capensis</i>	Wood <i>et al.</i> (2014)
<i>Tegillum scitulum</i> (as <i>Olivea scitula</i>)	*	BPI 871108 (U668)	DQ354541	DQ354540	NA	<i>Vitex doniana</i>	Aime (2006)
<i>Thekopsora areolata</i>	T	n.d.	KJ546894	NA	NA	<i>Picea engelmannii</i>	Kaitera <i>et al.</i> unpublished
<i>Trachyspora intrusa</i>	T	BPI 84328 (MCA2384)	DQ354550	DQ354549	MW036508	<i>Alchemilla vulgaris</i>	Aime (2006); this paper
<i>Tranzschelia discolor</i>	*	BRIP 57662	KR995082	KR994969	KR995082	<i>Prunus persica</i>	Doungsa-ard <i>et al.</i> (2018)
<i>Tranzschelia mexicana</i>	*	KR-M-0040855	KP308391	NA	NA	<i>Prunus salicifolia</i>	Blomquist <i>et al.</i> (2015)
<i>Triphragmium ulmariae</i>	T	BPI 881364 (MCA2378); 28S; n.d.:18S	JF907676	AY125401	NA	<i>Filipendula ulmaria</i>	Yun <i>et al.</i> (2011); Wingfield <i>et al.</i> (2004)
<i>Uredinopsis filicina</i>	T	WM112	AF426237	NA	NA	<i>Phegopteris connectilis</i>	Maier <i>et al.</i> (2003)
<i>Uredo cryptostegiae</i> (as <i>Maravalia cryptostegiae</i>)	T	BRIP 56898	KT199401	KT199387	KT199412	<i>Cryptostegia grandiflora</i>	McTaggart <i>et al.</i> (2016)
<i>Uredo elephantopodis</i>		BRIP 58415	MW049283	NA	MW036509	<i>Elephantopus scaber</i>	this paper
<i>Uredo hiulca</i>		BRIP 53244	MW049284	NA	MW036510	<i>Dioscorea transversa</i>	this paper
<i>Uredo trichosanthis</i>		PUR N3445	MW049285	MW049309	NA	<i>Trichosanthes bracteata</i>	this paper
<i>Uredopeltis atrides</i>	*	PUR N13866 (U454)	MW049286	NA	NA	<i>Grewia flavescens</i>	this paper
<i>Uredopeltis chevalieri</i>	*	BRIP 56924	MW049287	NA	NA	<i>Grewia retusifolia</i>	this paper
<i>Uromyces appendiculatus</i>	T	BRIP 60020	KM249870	DQ354510	KX999933	<i>Phaseolus vulgaris</i>	Aime (2006); McTaggart <i>et al.</i> (2014)
<i>Uromykladium simplex</i>	T	BRIP 59214	KJ632990	KJ633029	KJ639078	<i>Acacia pycnantha</i>	Doungsa-ard <i>et al.</i> (2014)
<i>Uropyxis daleae</i>	*	BPI 910337	KY798364	NA	NA	<i>Dalea pringlei</i>	Demers & Castlebury unpublished
<i>Uropyxis diphyssae</i>	*	BPI 864148	MW049288	NA	NA	<i>Diphysa americana</i>	this paper
<i>Xenodoichus carbonarius</i>	T	PUR N15566 (U1534)	MW049289	NA	NA	<i>Sanguisorba officinalis</i>	this paper
<i>Xenosteles litseae</i>	*	BRIP 53335	MW049290	MW049310	NA	<i>Neolitsea dealbata</i>	this paper
<i>Ypsilospora tucumanensis</i>	*	BPI 863688	MW049291	NA	NA	<i>Inga</i> sp.	this paper
<i>Zaghouania notelaeae</i> (as <i>Cystopsora notelaeae</i>)	*	BRIP 58325	KT199396	KT199384	KT199407	<i>Notelaea microcarpa</i>	McTaggart <i>et al.</i> (2016)

^aType Status: T = type species for the genus; * = proxy for generic type (see methods for explanation).

^bNumbers in parentheses are collection numbers, preceded by herbarium accession numbers. When sequences from more than one collection are used, data are separated by a /.

n.d. = no data.

NA = not applicable.

bold = new sequences generated for this paper.

c-oxidase subunit 3 (CO3) of the mitochondrial DNA was amplified with CO3_F1/CO3_R1 (Vialle *et al.* 2009) following the protocols of Vialle *et al.* (2009). PCR products were cleaned and sequenced with the amplification primers by Macrogen (Seoul, Korea) or Beckman Coulter Sequencing (Danvers, Massachusetts, USA). Sequences were edited in Sequencher v. 4.5–5.4 (Gene Codes Corp., Ann Arbor, Michigan, USA) and verified by BLASTn against the NCBI database (Altschul *et al.* 1990). Sequence accession numbers are provided in Tables 1 and S1.

Phylogenetic analyses

The 28S, 18S and CO3 sequences were aligned in four datasets, (i) *Pucciniales* overview, (ii) *Melampsorineae*, (iii) *Raveneliineae*, and (iv) *Urediniaceae* with the GUIDANCE2 webserver (Sela *et al.*, 2015; available at <http://guidance.tau.ac.il/ver2/credits.php>) (alignments are available from TreeBASE, study TB2:S27114). The aligned loci were concatenated and run as partitioned datasets with maximum likelihood (ML). We searched for the most likely tree in IQTree v. 1.7 beta (Nguyen *et al.* 2015) with a GTR gamma FreeRate heterogeneity model of evolution and a different rate for each partition (command -spp -m GTR+R), 10 000 ultrafast bootstraps (Hoang *et al.* 2018), an approximate likelihood ratio test with 10 000 replicates (Guindon *et al.* 2010) and genealogical concordance factors calculated from each locus (Minh *et al.* 2018).

We used the concatenated three-locus alignment of the familial-overview dataset to estimate the divergence dates of genera with BEAST v. 2.5 (Bouckaert *et al.* 2019). We calibrated the most recent common ancestor of the *Pucciniales* at 175 M yr and the *Melampsorineae* at 91 M yr based on Aime *et al.* (2018a). The dating analyses were constrained to the topology of the ML tree, and run for 150 M generations, with a BEAST model test for each partition and a relaxed log normal clock. Convergence of all priors was visualised in Tracer v. 1.7 (Rambaut *et al.* 2018) and 135 001 trees were summarised with TreeAnnotator, part of the BEAST v. 2.5 package.

We attempted to provide better resolution of genera and families within *Raveneliineae* by multiple means including removal of incongruent (rogue) taxa, constructing alignments with stricter and weaker gap opening penalties, pruning taxa with missing sequence data, removal of 18S and CO3 loci, and rooting with different outgroups from the *Melampsorineae* and *Urediniaceae*. The 28S data of *Raveneliineae* were analysed with SplitsTree4 (Huson & Bryant 2005) to visualize the evolution as a network in order to determine if groups were supported when not constrained by dichotomous evolution as imposed by ML analyses.

RESULTS

Phylogenetic analyses

The ML tree based on three concatenated loci (Fig. 1) was mostly congruent with prior studies of more limited taxon and locus sampling (Aime 2006, Beenken & Wood 2015, McTaggart *et al.*

2016, Aime *et al.* 2017, 2018a, Beenken 2017, Souza *et al.* 2018). Sampled trees constrained to the ML topology in the dating analyses converged after 150 M generations, supported by all effective sample size values over 200. We recovered support for placement of previously unsupported or unplaceable taxa such as *Tranzschelia*. Newly sequenced taxa resolved include the rust fungi on *Agathis*, genera such as *Elateraecium*, *Masseëlla*, and *Skierka*, and most of the endocyclic *Puccinosiraceae*. Despite numerous attempts with different alignments and taxon selection, some families/genera could not be confidently resolved, namely: *Pucciniastrum* and *Pucciniastraceae*; *Raveneliaceae*; and *Allodus*, *Neopuccinia*, and *Nyssopsora* within *Urediniaceae*. SplitsTree analysis of *Raveneliineae* recovered a star-shaped pattern of reticulate edges indicative of multiple competing hypotheses of evolution for this lineage (Fig. S2).

Taxonomy

Families and sub-orders treated here show strong support at their most recent common ancestor, with the exception of *Pucciniastraceae* and *Raveneliaceae* (Figs 1–3). We propose four new suborders (*Araucariomycetinae*, *Raveneliineae*, *Rogerpetersoniineae*, and *Skierkineae*), seven new families (*Araucariomycetaceae*, *Crossopsoraceae*, *Milesinaceae*, *Ochropsoraceae*, *Rogerpetersoniaceae*, *Skierkaceae*, and *Tranzscheliaceae*) and four new genera (*Araucariomyces*, *Neoolivea*, *Rogerpetersonia*, and *Rossmatomyces*); 21 new combinations and one new name are made for species. Suborders and families are arranged from earliest diverging to more recently derived (Fig. 1). We use the terms gametothallus and sporothallus as applied by Berndt (2018) and use the notation 0-I [for spermogonial (0) and aecial (I) stages] to denote the gametothallus, and II-III [for uredinial (II) and telial (III) stages] to denote the sporothallus. We follow the ontogenic system for sorus terminology, which emphasizes function in the life cycle and the nuclear cycle over morphology, as refined by Hiratsuka (1973). Morphological terms for spermogonia follow Hiratsuka & Cummins (1963); terms for aecial and uredinial sori follow the descriptions for asexual genera in Cummins & Hiratsuka (2003) but are indicated in lowercase, non-italics, to delineate use as descriptive terms from generic names.

Rogerpetersoniineae Aime & McTaggart, *subord. nov.* MycoBank MB836604.

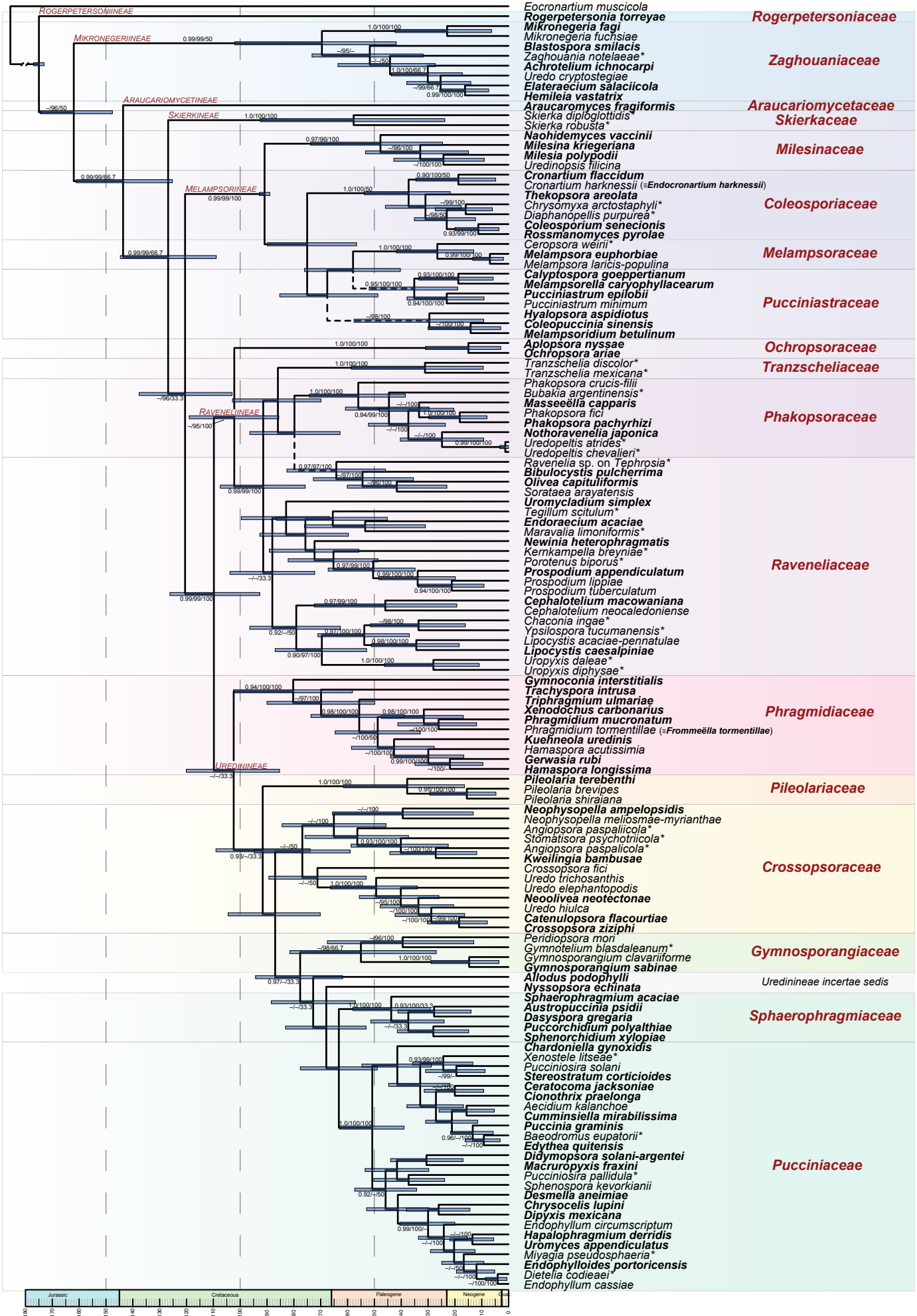
Type family: *Rogerpetersoniaceae* Aime & McTaggart, this paper.

Diagnosis: Differs from all other *Pucciniales* in that gametothalli are formed on *Taxaceae*.

Description: With the characteristics of *Rogerpetersoniaceae*.

Included family: *Rogerpetersoniaceae*.

Fig. 1. *Pucciniales*. Phylogram obtained from BEAST constrained to a ML topology from three concatenated loci (28S, 18S, and CO3). The tree is rooted with *Eocronartium muscicola*. Families are indicated by coloured blocks; dashed lines indicate uncertainty at the referenced nodes. Genera represented by types are indicated in bold; genera represented by type proxies (as explained in methods) are indicated by *. Support for nodes is provided from an approximate likelihood ratio test (≥ 0.90), ultrafast bootstraps ($\geq 95\%$) and genealogical concordance factors for the three loci at each node as aLRT/UFBoot/gCF.



Rogerpetersoniaceae Aime & McTaggart, *fam. nov.* MycoBank MB836605.

Type genus: *Rogerpetersonia* Aime & McTaggart, this paper.

Diagnosis: Differs from all other *Pucciniales* in that gametothalli are formed on *Taxaceae*.

Description: With the characteristics of *Rogerpetersonia*.

Included genus: *Rogerpetersonia*.

Host family: *Taxaceae* (0-I); II-III unknown.

Rogerpetersonia Aime & McTaggart, *gen. nov.* MycoBank MB836606.

Type species: *Rogerpetersonia torreyae* (Bonar) Aime & McTaggart, this paper.

Etymology: In honour of Roger Peterson, botanist, ecologist, mycologist and plant pathologist, who pioneered studies on Southern Hemisphere conifer rusts.

Diagnosis: Differs from all other rust fungi in forming gametothalli on *Taxaceae* (*Torreya*).

Description: With the characteristics of *Rogerpetersonia torreyae*.

Rogerpetersonia torreyae (Bonar) Aime & McTaggart, *comb. nov.* MycoBank MB836608.

Basionym: *Caeoma torreyae* Bonar, *Mycologia* **43**: 62. 1951.

Description: *Rogerpetersonia torreyae* is described and illustrated as *C. torreyae* in Peterson (1974). Spermogonia are deep-seated, periphysate, otherwise similar to Group III (type 12). Aecia petersonia-like, *i.e.*, without peridium or intercalary cells. Sporothallus unknown.

Notes: *Caeoma*, as typified by *C. berberidis*, is a synonym of *Puccinia* (Aime *et al.* 2018b), necessitating a new name for the only known rust fungus that infects *Torreya*. Peterson (1974) hypothesized that *R. torreyae* belonged to an undescribed early diverging lineage of *Pucciniales*. Subsequent analyses have shown that *R. torreyae* is the earliest diverging extant rust sequenced to date and holds an isolated position within *Pucciniales* (Aime 2006, Aime *et al.* 2018a) (Fig. 1). No alternate host is known for this rust and it is likely that *R. torreyae* has adapted to cause systemic infections in the gametothallus host in order to compensate for loss of a sporothallus.

Mikronegeriineae Aime, *Mycoscience* **47**: 120. 2006.

Description: With the characteristics of the family.

Included family: *Zaghouaniaceae*.

Zaghouaniaceae P. Syd. & Syd., *Monogr. Uredin.* (Lipsiae) **3**(3): 586. 1915. *emend.* Aime & McTaggart

Synonyms: *Hemileieae* Dietel, *Uredinales* in Engler and Prantl., *Naturl.*: 51. 1928.

Mikronegeriaceae Cummins & Y. Hirats. (as '*Mikronegeriaceae*'), *Illustr. Gen. Rust Fungi*, rev. Edn (St. Paul): 13. 1983.

Type genus: *Zaghouania* Pat., *Bull. Soc. mycol. Fr.* **17**: 187. 1901.

Description: Spermogonia most often Group III (type 12) (deep seated and non-periphysate), but periphyses noted for some; aecia most commonly of the petersonia-type, *i.e.*, without peridium or intercalary cells, however in *Elateraecium* accompanied with specialized elaters; uredinia most often uredo-type, in *Elateraecium* with a weakly developed peridium in young sori; teliospores without dormancy, germinating externally by apical growth, or internally (*Achrotelium*). *Blastospora* and *Mikronegeria* are heteroecious and macrocyclic, *Elateraecium* and *Zaghouania* are autoecious and macro- or demi-cyclic; complete life cycles unknown for *Achrotelium*, *Botryorhiza* and *Hemileia*.

Included genera: *Achrotelium*, *Blastospora*, *Botryorhiza*, *Elateraecium* (= *Hiratsukamyces*), *Hemileia*, *Mikronegeria*, *Zaghouania* (= *Cystopsora*); likely includes *Desmosorus*.

Host families: *Araucariaceae*, *Betulaceae* (0-I heteroecious species); *Apocynaceae*, *Araliaceae*, *Capparidaceae*, *Celastraceae*, *Cupressaceae*, *Dioscoreaceae*, *Euphorbiaceae*, *Fagaceae*, *Oleaceae*, *Orchidaceae*, *Rubiaceae*, *Smilacaceae*, *Verbenaceae* (II-III and autoecious species).

Notes: The family *Mikronegeriaceae* accommodated the heteroecious rust genera *Mikronegeria*, *Blastospora*, and *Chrysocelis*, which have thin-walled basidia that germinate externally without dormancy (Cummins & Hiratsuka 2003). *Hemileia* and some *Maravalia* species formerly placed in *Chaconiaceae* that share the feature of substomatal sori without paraphyses or peridium, also belong here (Aime 2006). Two additional genera, *Achrotelium* and *Zaghouania* (as *Cystopsora*), were included by McTaggart *et al.* (2016). *Zaghouaniaceae*, long considered a synonym for *Pucciniaceae* (*e.g.*, Kirk *et al.* 2008), has priority over *Mikronegeriaceae* and the family is now referred to by the earlier name. The current study adds *Elateraecium* (syn. *Hiratsukamyces*; Aime *et al.* 2018b), whereas *Chrysocelis* is resolved within the *Pucciniaceae* (Fig. 4). The formation of basidia is primarily external by apical growth and spermogonia are primarily deep-seated Group III (type 12), or if periphysate, similar to Group V (type 4).

Uredo cryptostegiae (syn. *Maravalia cryptostegiae*; *Scopella cryptostegiae*), which has been used as a biocontrol agent for rubber-vine (*Cryptostegia grandiflora*) is placed in *Zaghouaniaceae* (Fig. 1). Cummins (1950) transferred *M. cryptostegiae* to *Scopella*, while hypothesizing that the rust might belong to *Hemileia*. Most later workers considered *Scopella* and *Maravalia* congeneric and *Scopella* fell out of use. The type of *Maravalia*, *M. pallida* occurs on *Fabaceae* and is now placed in *Raveneliineae*. The type of *Scopella*, *S. echinulata*, is a subepidermal rust on *Sapotaceae* (Mains 1939a). *Uredo cryptostegiae*, which is not congeneric with *Maravalia* (as represented by *M. limoniformis*, Fig. 1), is most appropriately retained in *Uredo* until type data from *S. echinulata* is obtained.

Zaghouania notelaeae (Syd.) Aime & McTaggart, *comb. nov.* MycoBank MB836655.

Basionym: *Cystopsora notelaeae* Syd., *Annls mycol.* **35**: 351. 1937.

Notes: *Zaghouania* contains two other species of rust fungi on *Oleaceae* with pale-walled teliospores that germinate without dormancy (Cummins & Hiratsuka 2003). There is little to differentiate *Cystopsora* and *Zaghouania* (Thirumalachar 1945, Cummins & Hiratsuka 2003) and we treat *Cystopsora* as a synonym of *Zaghouania*.

Araucariomycetinae Aime & McTaggart, **subord. nov.** MycoBank MB836623.

Type family: *Araucariomycetaceae* Aime & McTaggart, this paper.

Diagnosis: Differs from all other *Pucciniales* in forming gametothalli on *Agathis*.

Description: With the characteristics of *Araucariomycetaceae*.

Included family: *Araucariomycetaceae*.

Araucariomycetaceae Aime & McTaggart, **fam. nov.** MycoBank MB836624.

Type genus: *Araucariomyces* Aime & McTaggart, this paper.

Diagnosis: Differs from all other *Pucciniales* in forming gametothalli on *Agathis*.

Description: With the characteristics of *Araucariomyces*.

Included genus: *Araucariomyces*.

Host family: *Araucariaceae* (0-I); II-III unknown.

Araucariomyces Aime & McTaggart, **gen. nov.** MycoBank MB836625.

Type species: *Araucariomyces fragiformis* (Ces.) McTaggart, R.G. Shivas & Aime, this paper.

Entomology: From the host family, *Araucariaceae*.

Diagnosis: Differs from all other rust genera in forming the gametothallus on species of *Agathis* (*Araucariaceae*).

Description: These species are described and illustrated in Peterson (1966). Spermogonia amphigenous, intra-epidermal becoming sub-epidermal as they break through host walls, convex hymenium; similar to Group 1 (type 1) but with scant periphyses not visible in all mounts, similar to *Rogerpetersonia*. Aecia peridiate, aecidium-type, deep-set within swollen host tissues. Sporothallus unknown. On leaves of *Agathis* (*Araucariaceae*). Two known species.

Notes: Two rust fungi with cupulate aecia on *Agathis* spp., formerly placed in the form-genus *Aecidium*, belong here. Our analyses consistently place these in a lineage separate from all other sequenced *Pucciniales* (Fig. 1). Despite over a decade of sampling rust fungi from Australia and Southeast Asia on hosts co-distributed with *Agathis* species, we have been unable to locate a telial state for these rusts. Peterson (1968) ruled out the possibility that *Araucariomyces* represents an endocyclic form, because aeciospores of *Ar. balansae* germinate to produce germ tubes rather than basidia. As is conjectured with

Rogerpetersonia, the life cycle may not produce a sporothallus, and instead has adapted to systemically infect their hosts possibly including a cryptic sexual or parasexual cycle.

Araucariomyces balansae (Cornu) McTaggart, R.G. Shivas & Aime, **comb. nov.** MycoBank MB836626.

Basionym: *Aecidium balansae* Cornu., *Bull. Soc. mycol. Fr.* **3**: 173. 1887.

Synonym: *Peridermium balansae* (Cornu) Sacc., *Syll. Fung.* **9**: 326. 1891.

Araucariomyces fragiformis (Ces.) McTaggart, R.G. Shivas & Aime, **comb. nov.** MycoBank MB836627.

Basionym: *Aecidium fragiforme* Ces., *Atti Accad. Sci. fis. mat. Napoli* **8**: 26. 1879.

Skierkineae Aime & McTaggart, **subord. nov.** MycoBank MB836628.

Type family: *Skierkaceae* Aime & McTaggart, this paper.

Diagnosis: Differs from all other rust fungi in that sporothalli sori are deep-seated and subepidermal with mature uredinio- and teliospores single-celled and non-catenulate, these forced through a narrow sorus opening by the production of new spores from sporogenous cells from which they are detached before extrusion.

Description: With the characters of *Skierkaceae*.

Included family: *Skierkaceae*.

Skierkaceae (Arthur) Aime & McTaggart, **fam. & stat. nov.** MycoBank MB836629.

Basionym: *Skierkatae* Arthur, *North American Flora* **7**(10): 704. 1926.

Type genus: *Skierka* Racib., *Parasit. Alg. Pilze Javas* (Jakarta) **2**: 30. 1900.

Diagnosis: Differs from all other rust fungi in that sporothalli sori are deep-seated and subepidermal with mature uredinio- and teliospores single-celled and non-catenulate, these forced through a narrow sorus opening by the production of new spores from sporogenous cells from which they are detached before extrusion.

Description: With the characteristics of *Skierka* as described and illustrated in Mains (1939b). Spermogonia deep-seated with convex hymenium, subepidermal, periphysate; aecia and uredinia uredo-type; teliospores strongly adherent, extruded in hair-like columns, germination external, without dormancy. Autoecious and macrocyclic.

Included genus: *Skierka*.

Host families: *Burseraceae*, *Euphorbiaceae*, *Sapindaceae*.

Notes: *Skierka* species are tropical and autoecious (Mains 1939c, Cummins & Hiratsuka 2003). All sori are subepidermal and deep-seated; non-catenulate teliospores are extruded in hair-like columns. *Skierka* has long held an isolated placement

within *Pucciniales*. Arthur (1907–1931) and Dietel (1928) placed *Skierka* in a separate subfamily or tribe, respectively, in the *Pucciniaceae*; Cummins & Hiratsuka (2003) treat it as *incertae sedis* within the rusts. Mains (1939c) hypothesised that *Skierka* represented an intermediate taxon between the *Melampsoraceae* and *Pucciniaceae* (equivalent to the subordinal ranks *Melampsorineae* and *Raveneliineae/Urediniineae*, under the present classification), a position largely congruent with our placement (Fig. 1).

Melampsorineae Aime, *Mycoscience* **47**: 120. 2006.

Type family: *Melampsoraceae* Dietel, in Engler & Prantl, *Nat. Pflanzenfam.* **1**(1): 38. 1897.

Description: Mostly macrocyclic and heteroecious, forming the gametothallus on species of *Pinaceae*. Teliospores germinate after a period of dormancy.

Included families: *Coleosporiaceae*, *Melampsoraceae*, *Milesinaceae*, *Pucciniastraceae*.

Milesinaceae Aime & McTaggart, *fam. nov.* MycoBank MB836630.

Type genus: *Milesina* Magnus, *Ber. Deutsch. Bot. Ges.* **27**: 325. 1909.

Diagnosis: Similar to other *Melampsorineae*, differing in either production of colourless urediniospores in species that infect ferns, or in production of milesia-type aecia in species that infect *Ericaceae*.

Description: With typically colourless sori, although urediniospores of *Naohidemyces* are orange, otherwise similar to *Pucciniastraceae*. Spermogonia Group I (mostly type 1, also type 2 and 3); aecia peridermium-type, milesia-type in *Naohidemyces*; uredinia milesia-type. Teliospores with dormant germination, 1- to many-celled, barely differentiated, sometimes laterally adherent, typically formed within host epidermal cells. Most species macrocyclic and heteroecious with sporothalli on ferns (excepting *Naohidemyces* on *Ericaceae*), and gametothalli on *Pinaceae*.

Included genera: *Milesia*, *Milesina*, *Naohidemyces*, *Uredinopsis*.

Host families: *Pinaceae* (*Abies*, *Tsuga*) (0-I); *Ericaceae* and some ferns in *Polypodiales* and *Lygodium* (II-III).

Notes: Early workers considered rust fungi on early diverging plant hosts (*i.e.*, ferns) to be the “ancestral” *Pucciniales*. Several molecular phylogenetic studies have shown this not to be the case (*e.g.*, Sjamsuridzal *et al.* 1999). However, the fern rusts are among the earliest diverging members of *Melampsorineae* (Fig. 2), the second major radiation of the rust fungi, and belong to the two earliest families in this suborder (*Milesinaceae* and *Pucciniastraceae*). Most of the species in *Milesinaceae* form sporothalli on fern species, except for *Naohidemyces*, which alternates between *Tsuga* and *Vaccinium*.

Aime *et al.* (2018b) recommended protecting the name *Milesina* Magnus over *Milesia* F.B. White. However, our data show that the type of *Milesina*, *M. kriegiana* (Magnus)

is not congeneric with the type of *Milesia*, *M. polypodii* F.B. White (Fig. 2), thus we recommend retaining both genera at this time. Should future work demonstrate that *Uredinopsis* is polyphyletic, then disposition of these taxa will need revision.

Coleosporiaceae Dietel, In: Engler & Prantl, *Nat. Pflanzenfam.*, Teil. I (Leipzig) **1**: 548. 1900. **emend.** Aime & McTaggart
Synonym: *Cronartiaceae* Dietel, in Engler and Prantl, *Nat. Pflanzenfam.* **1**(1) (Suppl.): 548. 1900.

Type genus: *Coleosporium* Lév., *Ann. Sci. Nat. Bot.* III, Ser. **8**: 373. 1847.

Description: Spermogonia Group I (type 2 or 3) (but Group II, type 9 in *Cronartium*); aecia of peridermium-type; uredinia either of caeoma-type or milesia-type. Teliospores packed to loosely adherent, often extruded in columns and/or gelatinous; not dormant, with external germination. Most are heteroecious and macrocyclic, with some derived microcyclic or endocyclic species.

Included genera: *Chrysomyxa*, *Coleosporium*, *Cronartium*, *Diaphanopellis*, *Rossmatomyces*, *Thekopsora* (= *Quasi-pucciniastrum*).

Host families: *Pinaceae* (primarily *Pinus*) (0-I); various, including *Apocynaceae*, *Asteraceae*, *Campanulaceae*, *Convolvulaceae*, *Ericaceae*, *Lamiaceae*, *Ranunculaceae*, *Rosaceae*, *Rutaceae*, *Violaceae* (II-III).

Notes: *Coleosporiaceae* was shown to include *Cronartiaceae* (Aime 2006) as well as *Thekopsora s.s.* (Aime *et al.* 2018a). Aecia are peridermium-type in contrast to most *Milesinaceae*. Telial states show variable morphology but tend to form the sporothallus on herbaceous rather than woody plants (*cf.* *Pucciniastraceae*) or ferns. Dietel (1900) established both *Coleosporiaceae* and *Cronartiaceae* in the same publication. We follow Sydow & Sydow (1915) in applying *Coleosporiaceae* over *Cronartiaceae*, which is discussed in Aime (2006). *Endocronartium* is a later synonym of *Cronartium* (Aime *et al.* 2018b).

Rossmatomyces Aime & McTaggart, *gen. nov.* MycoBank MB836632.

Type species: *Rossmatomyces pyrolae* (Rostr.) Aime & McTaggart, this paper.

Etymology: In honour of Amy Rossmann, biologist, mycologist, plant pathologist, and mentor.

Diagnosis: Similar to *Chrysomyxa* but differs in forming a systemic sporothallus; differs from all other rust fungi in forming sporothalli on *Moneses* and *Orthilia* (*Ericaceae*).

Description: See Saville (1950) and Feau *et al.* (2011). Gametothalli systemic in cones of *Picea* species; sporothalli systemic in *Moneses*, *Orthilia*, and *Pyrola* species.

Rossmatomyces monesis (Ziller) Aime & McTaggart, *comb. nov.* MycoBank MB836633.

Basionym: *Chrysomyxa monesis* Ziller, *Canad. J. Bot.* **32**: 435. 1954.

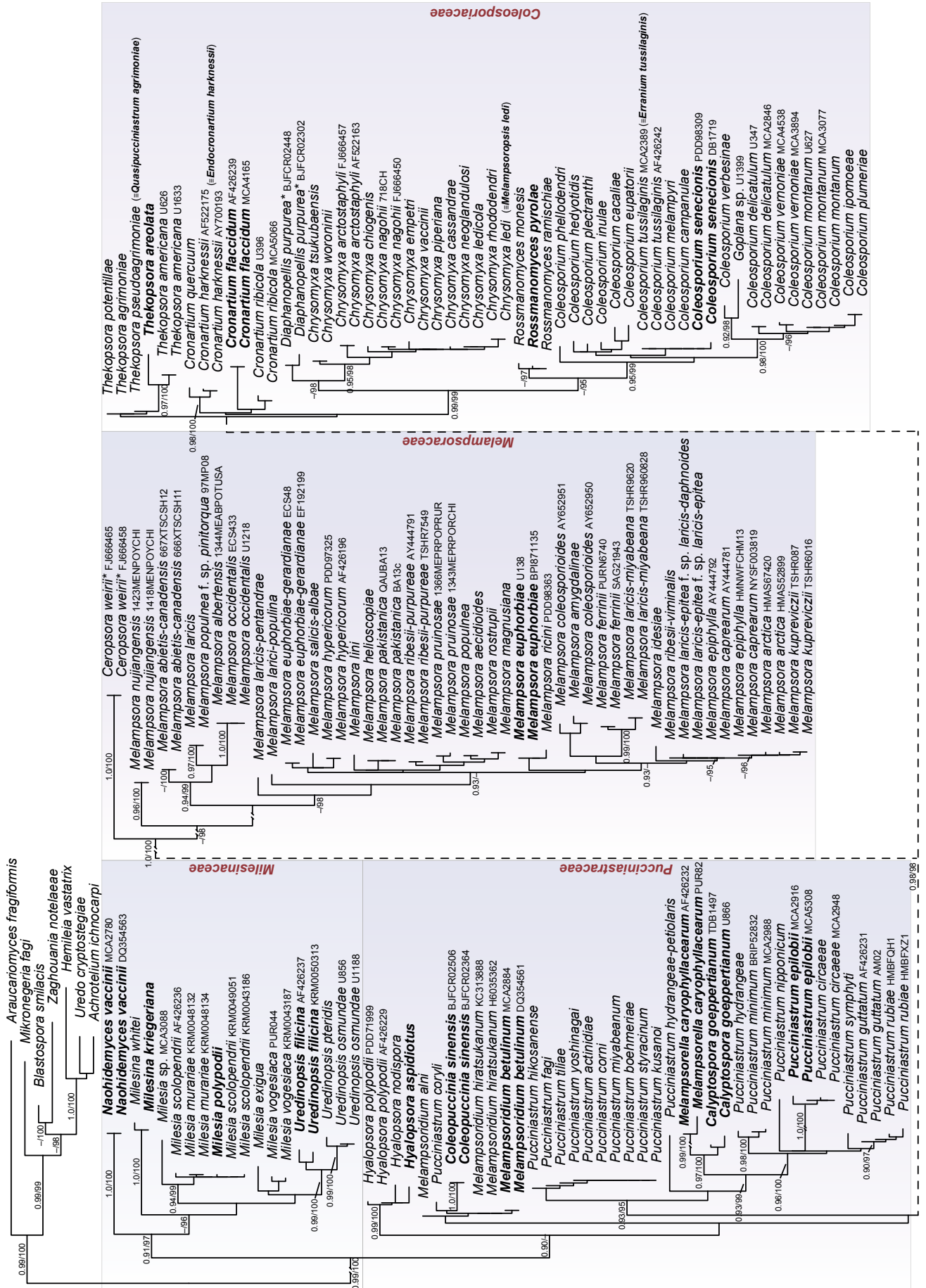


Fig. 2. *Melamporsorineae*. ML topology generated from three concatenated loci (28S, 18S, and CO3) with expanded taxon sampling. The tree is rooted with *Araucariomyces fragiformis* and *Zaghouania notelaeae*. Families are indicated by coloured blocks; *Pucciniastraceae* is recovered as a grade in these analyses. Genera represented by bold; genera represented by type proxies (as explained in methods) are indicated by *. Support for nodes is provided from an approximate likelihood ratio test (≥ 0.90) and ultrafast bootstrap ($\geq 95\%$) as aLRT/UFBoot.

Rossmatomyces pyrolae (Rostr.) Aime & McTaggart, **comb. nov.** MycoBank MB836634.

Basionym: *Chrysomyxa pyrolae* Rostr., *Botan. Zbl.* **5**: 127. 1881.

Rossmatomyces ramischiae (Lagerh.) Aime & McTaggart, **comb. nov.** MycoBank MB836635.

Basionym: *Chrysomyxa ramischiae* Lagerh., *Svensk bot. Tidskr.* **3**: 26. 1909.

Notes: *Chrysomyxa* is typified by *C. abietis*, a microcyclic species for which there are no sequence data. In our analyses (Fig. 2) most species of *Chrysomyxa* were monophyletic, excluding *C. weirii* now placed in *Ceropsora*, and species that infect wintergreens, now placed in *Rossmatomyces*. The species of *Rossmatomyces* are the only known rust species that form sporothalli on species of *Moneses* and *Orthilia*, and the only *Coleosporiaceae* that form sporothalli on species of *Pyrola*. The gametothalli are produced on *Picea* and are systemic within the cones, in contrast to gametothalli of *Chrysomyxa* species, which infect needles.

Thekopsora americana (Farl.) Aime & McTaggart, **comb. et stat. nov.** MycoBank MB836637.

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

Synonym: *Pucciniastrum americanum* (Farl.) Arthur, *Bull. Torrey bot. Club* **47**: 468. 1920.

Thekopsora potentillae (Korn.) Aime & McTaggart, **comb. nov.** MycoBank MB836636.

Basionym: *Pucciniastrum potentillae* Korn., in Jaczewski *et al.*, *Fungi Rossiae Exsicc. fasc.* **7**: 327. 1900 [1899].

Notes: Delimitation between *Thekopsora* and *Pucciniastrum* has never been satisfactory (e.g., Hiratsuka 1958, Sato *et al.* 1993). While prior works mostly consider these confamilial or even congeneric, *Thekopsora s.s.*, as typified by *T. areolata*, belongs to *Coleosporiaceae* (Aime *et al.* 2018a; Fig. 2). New combinations are proposed for ex-*Pucciniastrum* species. Other former *Thekopsora* species, such as *P. minima* and *P. rubiae* are placed in *Pucciniastraceae* (Fig. 2).

Thekopsora pseudoagrimoniae Aime & McTaggart, **nom. nov.** MycoBank MB836638.

Basionym: *Quasipucciniastrum agrimoniae* X.H. Qi *et al.*, *Mycology* **10**(3): 145. 2019.

Description: See Qi *et al.* (2019).

Notes: The recently described monotypic *Quasipucciniastrum* based on *Q. agrimoniae* is congeneric with *Thekopsora* (Fig. 2). In addition to the phylogenetic data, *Quasipucciniastrum* shares key morphological features, ecology, and hosts with *Thekopsora*. This paper highlights the importance of including type species and adequate sampling in phylogenetic studies of known polyphyletic genera. The name *Thekopsora agrimoniae* Dietel is already in use, thus a new name is proposed for this taxon. However, there is little to differentiate *T. pseudoagrimoniae* from *T. agrimoniae* and the two may be conspecific.

Pucciniastraceae Gäum. ex Leppik, *Ann. bot. fenn.* **9**: 139. 1972. **emend.** Aime & McTaggart

Type genus: *Pucciniastrum* G.H. Otth, *Mitt. Naturforsch. Ges. Bern* **1861**: 71. 1861.

Description: Similar to *Milesiaceae*, but most species with cytoplasmic pigmentation, at least within urediniospores. Spermogonia Group I (type 2 or 3). Aecia peridermium-type; uredinia milesia-type. Telia undergo dormancy with external germination; either formed within epidermal cells, or as a subepidermal crust, which is gelatinous in *Coleopuccinia*. Most species heteroecious, macrocyclic; *Calyptospora* is demicyclic, *Coleopuccinia* is microcyclic, producing only teliospores.

Included genera: *Calyptospora*, *Coleopuccinia*, *Hyalopsora*, *Melampsorella*, *Melampsidium*, *Pucciniastrum*.

Host families: *Pinaceae* (*Abies*, *Larix*, *Picea*, *Tsuga*) (0-I); *Aceraceae*, *Betulaceae*, *Caryophyllaceae*, *Ericaceae*, *Fagaceae*, *Onagraceae*, *Rosaceae*, *Rubiaceae* and some ferns in the *Polypodiales* (II-III).

Notes: Most species of *Pucciniastraceae* produce spores with pigmented cytoplasm and telia that may be subepidermal, in contrast to *Milesiaceae*. *Hyalopsora* is the only genus in *Pucciniastraceae* that infects ferns. *Coleopuccinia* is known only from teliospores (Cao *et al.* 2018). *Pucciniastraceae s.l.* has been difficult to resolve and appears polyphyletic with varying degrees of support in earlier studies (e.g., Maier *et al.* 2003, Aime 2006, Aime *et al.* 2016a, Ji *et al.* 2019). In this work, we find weak support for *Pucciniastraceae* in some analyses (data not shown) but not all (e.g., Fig. 1). In nearly all analyses *Pucciniastraceae* is resolved into two groups: (i) *Calyptospora*, *Melampsorella*, and *Pucciniastrum*; and (ii) *Coleopuccinia*, *Hyalopsora*, and *Melampsidium*. These often form a grade (Fig. 2) and may or may not represent separate family-rank lineages. Pending additional analyses, we broadly define *Pucciniastraceae* to include both groups. *Pucciniastrum* is also difficult to resolve with confidence, and is most likely paraphyletic, even after removing the ex-*Pucciniastrum* elements that were reassigned to *Thekopsora* (Fig. 2). We retain *Coleopuccinia*, *Calyptospora*, and *Melampsorella* at this time, although future work may show that the latter two are synonyms for *Pucciniastrum*.

Melampsoraceae Dietel, in Engler & Prantl, *Nat. Pflanzenfam.*, Teil. I (Leipzig) **1**: 38. 1897.

Type genus: *Melampsora* Castagne, *Obs. Plantes Acotylédonées Fam. Urédinié* **2**: 18. 1843.

Description: Spermogonia Group I (type 2 or 3). Aecia mostly caeoma-type; uredinia uredo-type. Teliospores subepidermal, laterally adherent in crusts, 1-celled, often with a sterile basal cell; germination external or semi-external (*Ceropsora*). Most species heteroecious, macrocyclic; *Ceropsora* species are microcyclic.

Included genera: *Melampsora*; likely includes *Ceropsora*.

Host families: Primarily *Pinaceae* (0-I); primarily *Salicaceae*, also *Apocynaceae*, *Asteraceae*, *Euphorbiaceae*, *Flacourtiaceae*, *Hypericaceae*, *Linaceae*, *Passifloraceae*, *Saxifragaceae*, *Scrophulariaceae*, *Thymelaeaceae* (II-III)

Ceropsora weirii (H.S. Jacks.) Aime & McTaggart, **comb. nov.** MycoBank MB836631.

Basionym: *Chrysomyxa weirii* H.S. Jacks., *Phytopathology* **7**: 353. 1917.

Notes: Most of the ca. 30 species of *Chrysomyxa* are heteroecious with gametothalli on *Pinaceae* and are allied within *Coleosporiaceae* (Fig. 2). *Chrysomyxa weirii*, an autoecious microcyclic pathogen of *Picea* species, is unique among described *Chrysomyxa* in forming laterally adherent teliospores that act as diaspores, are adapted for dispersal in water, and germinate to produce 2-celled basidia (Crane 2000, Crane *et al.* 2000). Crane *et al.* (2000) conjectured that *Ch. weirii* is not a true *Chrysomyxa*, which is supported with molecular data (Feau *et al.* 2011, Aime *et al.* 2018a, Fig. 2). The type and only other species of *Ceropsora*, *C. picea*, is a teliospore-only species infecting *Picea* in India (Bakshi & Singh 1960). While we have been unable to sequence a representative of the type species, *C. weirii* and *C. picea* are both microcyclic producing telia on *Picea* species. In both species, the telia contain some thin-walled sterile cells on the sides that have been interpreted as remnants of a peridermium. And in both, teliospores are subtended by sterile basal cells forming initially adherent crusts that separate at dispersal; germination is semi-external (Bakshi & Singh 1960, Crane *et al.* 2000).

Raveneliineae Aime & McTaggart **subord. nov.** MycoBank MB836639.

Type family: *Raveneliaceae* Leppik, *Ann. Bot. Fenn.* **9**(3): 139. 1972.

Diagnosis: Similar to *Uredinineae* differing in that the majority of species form Group VI spermogonia whereas the majority of *Uredinineae* form Group V spermogonia.

Description: With the characteristics of the included families. Most species form Group VI spermogonia; many species form elaborate, multi-celled teliospores.

Included families: *Ochropsoraceae*, *Phakopsoraceae*, *Raveneliaceae*, *Tranzscheliaceae*.

Notes: The *Raveneliineae* is the most challenging suborder in which to resolve families due to: (i) a pattern of multiple, parallel radiations in this lineage (Fig. S2); (ii) multiple instances of convergent morphologies; (iii) polyphyly; and (iv) incomplete sampling and missing data in our analyses. *Raveneliineae* is the second richest suborder in terms of taxonomic diversity, with ca. 45 accepted genera, of which we were only able to sample representatives from about half and most of these with incomplete locus data.

Host range may be an informative character to place taxa of *Raveneliineae* in families. For example, Savile (1989) predicted *Maravalia sensu* Ono (1984) was polyphyletic, and hypothesised that species on *Fabaceae* belonged to *Raveneliaceae*, supported here with the placement of the *Fabaceae*-infecting *M. limoniformis* within *Raveneliineae* (Figs 1, 3) and the *Apocynaceae*-infecting *U. cryptostegiae* (syn. *M. cryptostegiae*) within *Zaghouaniaceae* (Fig. 1). Likewise, *Triphragmium* Link has evolved elaborate teliospores similar to those in some *Raveneliaceae* where it has been allied in the past

(e.g., Cummins & Hiratsuka 2003); *Triphragmium* species are now known to belong to *Phragmidiaceae* with other *Rosaceae*-infecting rusts (Aime 2006).

We treat four families within *Raveneliineae*, taking into account life cycle and host data, and have taken a conservative approach to assigning genera within families and species to genera until data from type species and/or exemplars from key missing taxa as well as additional loci can be obtained.

Ochropsoraceae (Arthur) Aime & McTaggart, **fam. & stat. nov.** MycoBank MB836640.

Basionym: *Ochropsoratae* Arthur, *Rés. Sci. Congr. Int. Bot. Vienne*: 336. 1906.

Type genus: *Ochropsora* Dietel, *Ber. Dtsch. Bot. Ges.* **13**: 401. 1895.

Description: Spermogonia Group VI (type 7). Aecia aecidium-type; uredinia malupa-type; aecial states systemic overwintering as mycelium; telia forming crusts, 1-cell deep, at first subepidermal, then erumpent; teliospores germinate without dormancy, either internally (*Ochropsora*) or externally (*Aplopsora*). Species likely macrocyclic and heteroecious, although gametothallus not known for *Aplopsora*.

Included genera: *Aplopsora*, *Ochropsora*; likely includes *Ceraceopsora*.

Host families: *Ranunculaceae* (0-I); *Rosaceae*, *Cornaceae* (II-III)

Notes: A monophyletic *Ochropsoraceae* as the earliest diverging lineage of *Raveneliineae* was recovered in all of our analyses. *Aplopsora* and *Ochropsora* were previously treated within the artificial *Chaconiaceae* (Cummins & Hiratsuka 2003) where they shared the convergent character of teliospore germination without dormancy.

Tranzscheliaceae (Arthur) Aime & McTaggart, **fam. & stat. nov.** MycoBank MB836641.

Basionym: *Tranzschelieae* Arthur, *Rés. Sci. Congr. Int. Bot. Vienne*: 340. 1906.

Type genus: *Tranzschelia* Arthur, *Rés. Sci. Congr. Int. Vienne*: 340. 1906.

Description: Spermogonia Group VI (type 7). Aecia aecidium-type; uredinia uredo-type. Teliospores 2-celled, pedicellate, produced from sterile basal cells. Species are macrocyclic and heteroecious, with some derived microcyclic species.

Included genera: *Leucotelium*, *Tranzschelia*.

Host families: *Ranunculaceae* (0-I and autoecious species); *Rosaceae* (II-III in heteroecious species).

Notes: *Tranzschelia* has held an isolated position within *Pucciniales* in prior molecular studies (Aime 2006) and appears as an independent lineage of *Raveneliineae* in this work (Fig. 1). *Leucotelium* has been treated as a synonym of *Sorataea* (Cummins & Hiratsuka 2003) but retained by Thirumalachar & Cummins (1940) due to the presence of a sterile basal cell layer from which the teliospores develop that is lacking in *Sorataea*.

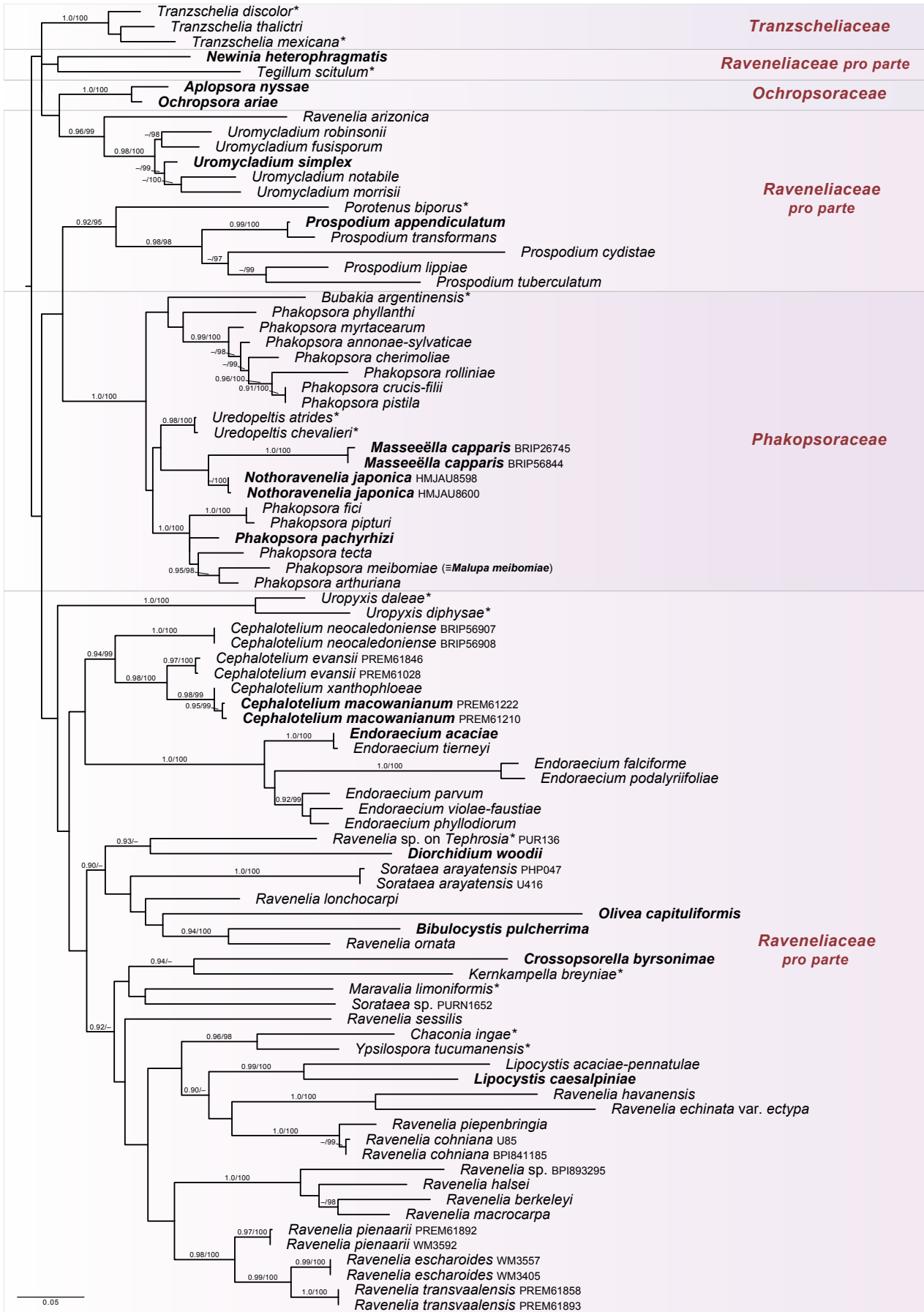


Fig. 3. *Raveneliaceae*. ML topography generated from 28S with expanded taxon sampling. The tree is mid-point rooted. Families are indicated by colour blocks; *Raveneliaceae* is not resolved. Only 26 of the estimated 45+ genera in this suborder are represented by types (indicated in bold) and type proxies (indicated by *), and poor resolution may be attributable to missing data (both locus and taxon sampling), combined with long branch lengths (Fig. S2) in this lineage. Support for nodes is provided from an approximate likelihood ratio test (≥ 0.90) and ultrafast bootstraps ($\geq 95\%$) as aLRT/UFBoot.

Two non-type species of *Sorataea* were included in our analyses and are referable to *Raveneliaceae* (Fig. 3). *Leucotelium* is the sister genus to *Tranzschelia* (Scholler *et al.* 2019), with which it shares a similar host range and teliospore production from sterile sporogenous cells (Thirumalachar & Cummins 1940, López-Franco & Hennen 1990). Many species of *Tranzschelia* are microcyclic on *Ranunculaceae* in accordance with Tranzschel's Law (Scholler *et al.* 2019).

Phakopsoraceae Cummins & Y. Hirats., *Illustr. Gen. Rust Fungi, rev. Edn* (St. Paul): 13. 1983. **emend.** Aime & McTaggart

Type genus: Phakopsora Dietel, *Ber. Deutsch. Bot. Ges.* **13**: 333. 1895.

Description: Spermogonia Group VI (type 7). Aecia caeoma-type, some *Masseëlla* with aecidium-type aecia; uredinia lecythea- or uredo-type. Teliospores 1-celled. *Bubakia*, *Masseëlla* and *Nothoravenelia* species are autoecious and macrocyclic. The majority of *Phakopsora* and *Uredopeltis* species are only known from the sporothallus.

Included genera: *Bubakia*, *Masseëlla*, *Nothoravenelia*, *Phakopsora*, *Uredopeltis*; likely includes *Arthuria*, *Cerotelium*, *Dicheirinia*, *Monosporidium*, *Phragmidiella*, *Pucciniostele*, *Scalarispora*.

Host families: *Annonaceae*, *Bignoniaceae*, *Burseraceae*, *Commelinaceae*, *Euphorbiaceae*, *Fabaceae*, *Myrtaceae*, *Rubiaceae*, *Urticaceae* (0-III).

Notes: Both *Phakopsora* and the *Phakopsoraceae* are known to be polyphyletic (e.g., Aime 2006), with more than 100 species currently classified in *Phakopsora s.l.* However, lack of data and differing interpretations of the type have hampered taxonomic progress. The recent designation of a new type species for *Phakopsora*, *P. pachyrhizi* (Aime *et al.* 2019a, b), has stabilized use of the name as applied here, for those genera and species that share a common ancestor with *P. pachyrhizi*. *Phakopsora* remains poorly resolved with our data and consists of two supported clades, one containing *P. pachyrhizi* and its allies and the other containing most of the *Annonaceae*-infecting species, which may represent a separate genus, but were recovered as monophyletic in some analyses (not shown).

The name *Bubakia* is often treated as a synonym of *Phakopsora* (e.g., Cummins & Hiratsuka 2003). Our study shows that *Bubakia argentinensis* belongs to a distinct lineage within *Phakopsoraceae* (Figs 1, 3). Further, *B. argentinensis* shares similar hosts (*Croton* spp.) and characteristics with the type, *B. crotonis*, and we accept *Bubakia* for these species (Mundkur 1943). *Masseëlla* has previously been treated as *incertae sedis* within *Pucciniales* (Cummins & Hiratsuka 2003), but our data place it within *Phakopsoraceae* (Figs 1, 3).

The majority of *Phakopsora* and *Uredopeltis* species are known only from sporothalli. It is unknown whether gametothalli occur on an alternate host, or whether these species are autoecious. Sporothalli have been described for a few *Phakopsora* species, i.e., *P. breyniae*, *P. innata*, *P. phyllanthidiscoidei*, and *P. stratosata*, which are all autoecious (Berndt & Wood 2012, Ono 2015b), although it is unclear whether these should be retained in *Phakopsora s.s.* or are allied with one of the segregate ex-*Phakopsora* genera.

Phakopsora pipturi (Syd.) Aime & McTaggart, **comb. nov.** MycoBank MB836642.

Basionym: *Pucciniastrum pipturi* Syd., *Annls mycol.* **29**(3/4):171. 1931.

Synonym: *Uredo pipturi* (Syd.) Hirats. f., *Trans. Mycol. Soc. Japan* **5**: 4. 1957.

Raveneliaceae Leppik, *Ann. bot. fenn.* **9**: 139. 1972. **emend.** Aime & McTaggart

Synonyms: *Chaconiaceae* Cummins & Y. Hirats., *Illustr. Gen. Rust Fungi, rev. Edn* (St. Paul): 14. 1983.

Uropyxidaceae Cummins & Y. Hirats., *Illustr. Gen. Rust Fungi, rev. Edn* (St. Paul): 14. 1983.

Type genus: Ravenelia Berk., *Gard. Chron.* **13**:132. 1853.

Description: Spermogonia Group VI (type 5 or 7); aecia uredo- (rarely aecidium-, caeoma-, or lecythea-) type; uredinia uredo-type. Teliospores 1- to many-celled, some species with elaborate compound or multi-celled teliospores. Majority of species autoecious and macrocyclic, with a few derived microcyclic species; many species on mimosoid (*Caesalpinioideae*) hosts.

Included genera: *Bibulocystis*, *Cephalotelium*, *Crossospora*, *Diorchidium*, *Endoraecium*, *Kernkampella*, *Lipocystis*, *Newinia*, *Olivea*, *Porotenus*, *Prospodium*, *Ravenelia*, *Sorataea*, *Uromycladium*, *Uropyxis*, *Ypsilospora*; likely includes *Allotelium*, *Anthomyces*, *Anthomycetella*, *Apra*, *Atelocauda*, *Chaconia*, *Cystomyces*, *Diabole*, *Diochordiella*, *Esalque*, *Hennenia*, *Maravalia*, *Mimema*, *Phragmopyxis*, *Spumula*, *Tegillum*.

Host families: *Bignoniaceae*, *Euphorbiaceae*, *Fabaceae*, *Ranunculaceae*, *Rosaceae*, *Sapotaceae*, *Verbenaceae* (0-III).

Notes: Leppik (1972) limited *Melampsoraceae* to rust species that are heteroecious and temperate, reassigning the autoecious and tropical species to a new family, *Raveneliaceae*. Savile (1989) provided an in-depth study of *Raveneliaceae* and hypothesised that the most recent common ancestor of *Raveneliaceae* was heteroecious, but that the family diversified as autoecious species on mimosoid (*Caesalpinioideae*) hosts after an environmental event severed their association with the initial sporothallus host. This hypothesis finds support in our work, which shows that the two early diverging families of *Raveneliaceae*, *Ochropsoraceae* and *Tranzscheliaceae* (Fig. 1), are heteroecious with sporothalli hosts in *Ranunculaceae*.

Chaconia, which we place within *Raveneliaceae*, has been placed variously in the *Melampsoraceae* or with other rust genera in the artificial *Chaconiaceae*. This and prior works have shown *Chaconiaceae*, and most of the genera therein, as polyphyletic. The morphological character on which they were based, specifically thin-walled, pale teliospores that germinate without dormancy, was derived multiple times within *Pucciniales* (Aime, 2006, Aime *et al.* 2018a), as a result of convergent morphologies in species adapted to tropical climates that do not need to overwinter (Savile 1989).

Uropyxidaceae consists of an artificial assemblage of rust fungi combining (mostly) 2-celled, transversely septate teliospores and Group VI (type 5) spermogonia (where present). In this study, we sampled nearly all genera of *Uropyxidaceae* as circumscribed by Cummins & Hiratsuka (1983, 2003), most of which had not been previously sequenced; from our results the family is clearly

polyphyletic. Many of the genera placed in *Uropyxidaceae* by Cummins & Hiratsuka (1983, 2003) were once considered allied within *Pucciniaceae* due to similarities in teliospore morphology. Our analysis shows that several of these, *i.e.*, *Desmella*, *Dipyxis*, *Edythea*, *Macruropyxis*, belong to *Pucciniaceae* (Fig. 4). *Dasyospora* is allied in *Sphaerophragmiaceae* and *Tranzschelia* in *Tranzscheliaceae* (Fig. 1). The remaining genera – *Newinia*, *Porotenus*, *Prospodium*, *Sorataea*, and *Uropyxis* – are included within a broadly defined *Raveneliaceae* (Fig. 3).

Raveneliaceae is not resolved in our analyses, with strong support for some genera with multiple sampling, but almost no support for infra-familial nodes (Figs 1, 3, S2). Branch lengths for species of *Raveneliaceae* are comparatively long (Figs 3, S2) and may indicate an accelerated evolutionary rate in this family. 28S data alone can be informative for other *Puccinales* lineages (*e.g.*, Ji *et al.* 2019), but are inadequate for resolving relationships of genera, and in many cases even species, within *Raveneliaceae* (Fig. S2).

No sequence data are available for the generic type, *R. glandulosa*, a Western Hemisphere rust of *Tephrosia*. *Ravenelia* sp. (PUR F19717, Fig. 3) shares a host with *R. glandulosa* and may be congeneric with the type. *Maravalia s.s.* as represented by *M. limoniformis* (Figs 1, 3) is likely to belong here.

The genus *Olivea*, as circumscribed in the past, contains a polyphyletic assemblage of species that form a hymenial layer of probasidia that germinate via apical extension. Three species formerly placed in *Olivea* were included in our analyses: (i) *O. capituliformis*, the type for the genus; (ii) *O. scitula*; and (iii) *O. tectonae*, none of which are related to each other (Figs 3 & S2). *Neolivea tectonae* (syn. *O. tectonae*) is placed in the *Crossosporaceae* and discussed there. *Olivea scitula* was considered by Mains (1940) as most similar to *Tegillum fimbriatum*, and we apply the name *T. scitulum* to this species, although further work is necessitated to determine if it is, indeed, congeneric with the type species, *T. fimbriatum*. *Olivea capituliformis* is the only described species in this complex that infects hosts in *Euphorbiaceae*; the ex-*Olivea* species that we treat infect hosts in *Verbenaceae* (Ono & Hennen 1983).

Cephalotelium evansii (Syd. & P. Syd.) Aime & McTaggart, **comb. nov.** MycoBank MB836643.

Basionym: *Ravenelia evansii* Syd. & P. Syd. *Annls mycol.* **10**: 440. 1912.

Synonym: *Dendroecia evansii* (Syd. & P. Syd.) Syd., *Annls mycol.* **19**: 165. 1921.

Cephalotelium neocaledoniense (B. Huguenin) Aime & McTaggart, **comb. nov.** MycoBank MB837616.

Basionym: *Ravenelia neocaledoniensis* B. Huguenin, *Bull. trimest. Soc. mycol. Fr.* **82**: 263 (1966).

Cephalotelium xanthophloeae (M. Ebinghaus *et al.*) Aime & McTaggart, **comb. nov.** MycoBank MB836644.

Basionym: *Ravenelia xanthophloeae* M. Ebinghaus *et al.*, *MycoKeys* **43**: 11. 2018.

Notes: Of the *ca.* 200 species currently placed in *Ravenelia*, our data consistently resolved as congeneric those we now refer to *Cephalotelium* (Figs 3, S2). These species were also strongly supported as one of two monophyletic groups in *Ravenelia s.l.* by Ebinghaus *et al.* (2018b). *Cephalotelium macowanianum* (syn. *Ravenelia macowanianum*) is the type of *Cephalotelium*.

The formation of telial galls is sometimes induced by infection of *Ravenelia* species, but not by *Cephalotelium* species. In contrast, *C. evansii*, *C. macowanianum* and *C. xanthophloeae* induce aecial gall formation in host tissues, which is a trait that appears to be confined to the *Cephalotelium* lineage (Ebinghaus *et al.* 2018a, b). *Cephalotelium* species infect members of *Vachellia* (*Caesalpinioideae*) in the Eastern Hemisphere (Sydow 1921). *Cephalotelium* is possibly a later synonym for *Dendroecium*, however, the type, *D. farlowiana*, occurs on *Senegalia* (*Caesalpinioideae*) species in the Western Hemisphere (Dietel 1894).

Lipocystis acaciae-pennatulae (Dietel) Aime & McTaggart, **comb. nov.** MycoBank MB836645.

Basionym: *Ravenelia acaciae-pennatulae* Dietel, *Beih. bot. Zbl., Abt. 2* **20**: 373. 1906.

Notes: *Lipocystis* with the type species *L. caesalpiniae* was described as a monotypic genus for a rust on *Mimosa* from the West Indies. A second species, *Lipocystis acaciae-pennatulae*, infects *Acacia* species in Central America and is congeneric with *L. caesalpiniae* (Figs 1, 3, S2).

Urediniineae Engl., *Syllabus der Vorlesungen über spezielle und medizinisch-pharmazeutische Botanik*: 36. 1892. **emend.** Aime & McTaggart

Synonym: *Pucciniineae* Doweld, *Index Fungorum* **77**: 1. 2014.

Type family: *Pucciniaceae* Chevall.

Description: With the characteristics of the included families. Most species form Group V but also Group VI spermogonia and 1- or 2- celled teliospores but multi-celled telia formed in some or most *Nyssospora*, *Phragmidiaceae*, and *Sphaerophragmiaceae*.

Included families: *Crossosporaceae*, *Gymnosporangiaceae*, *Phragmidiaceae*, *Pileolariaceae*, *Pucciniaceae*, *Sphaerophragmiaceae*.

Notes: *Urediniineae* is the largest suborder in both species numbers and generic diversity. *Pucciniineae* is a superfluous name for the older *Urediniineae*. We were able to sample types or type representatives for 50 of the *ca.* 70 genera placed here as well as several species currently assigned to form-genera.

We were unable to resolve the placement for three genera: *Allodus*, *Neopuccinia*, and *Nyssospora*. *Allodus* was long considered a synonym of *Puccinia* due to its pedicellate, 2-celled teliospores. Minnis *et al.* (2012) resurrected *Allodus* as an orphan genus of uncertain placement. Our analyses occasionally resolved *Allodus* as sister to *Peridiopsora mori* with weak support (not shown). Only a single 28S sequence is available for the newly described *Neopuccinia*, which shares many similarities with *Kimuromyces* (Dianese *et al.* 1995). Connections between *Nyssospora* and *Sphaerophragmium* have been noted by Lohsomboon *et al.* (1994). *Nyssospora* was recovered as sister to *Sphaerophragmiaceae* in some but not all of our analyses (Figs 1, 4) and may represent a separate family lineage.

Phragmidiaceae Corda *Icon. fung.* (Prague) **1**: 6. 1837.

Type genus: *Phragmidium* Link, *Mag. Ges. Naturfr. Freunde Berlin* **7**: 30. 1816.



Fig. 4. Uredineae. ML topography generated from three concatenated loci (28S, 18S, and CO3) with expanded taxon sampling. The tree is rooted with *Melampsorineae*. Six families are resolved and indicated by coloured blocks; three genera are unresolved to family and indicated as *incertae sedis*. Genera represented by types are indicated in bold; genera represented by type proxies (as explained in methods) are indicated by *. Support for nodes is provided from an approximate likelihood ratio test (≥ 0.90), ultrafast bootstraps ($\geq 95\%$) and genealogical concordance factors for the three loci at each node as aLRT/UFBoot/gCF.

Description: Spermogonia of Group IV (various types); aecia variable, caeoma-, petersonia- or uredo-type; uredinia lecythea- or uredo-type. Teliospores mostly multi-celled, usually by transverse septa. Species autoecious on *Rosoideae* subfamily of *Rosaceae*.

Included genera: *Gerwasia*, *Gymnoconia*, *Hamaspora*, *Kuehneola*, *Phragmidium*, *Trachyspora*, *Triphragmium*, *Xenodochus*; likely includes *Joerstadia*.

Host family: *Rosaceae* (0-III).

Notes: Convergence in teliospore morphology between some genera of *Phragmidiaceae* and *Raveneliaceae* has been previously noted (e.g., Cummins & Hiratsuka 2003); Aime (2006) showed that *Phragmidiaceae* species are confined almost

exclusively to the *Rosoideae* in contrast to *Raveneliaceae*.

Pileolariaceae (Arthur) Cummins & Y. Hirats., *Illustr. Gen. Rust Fungi, rev. Edn* (St. Paul): 14. 1983. *emend.* Aime & McTaggart

Type genus: *Pileolaria* Castagne, *Obs. Plantes Acotylédonées Fam. Urédinées* 1: 22. 1842.

Description: Spermogonia Group VI (type 7). Aecia and uredinia uredo-type. Teliospores 1-celled with characteristic sculpted appearance; germination external after dormancy. Species mostly macrocyclic and autoecious.

Included genus: *Pileolaria*.

Host family: *Anacardiaceae* (0-III).

Notes: *Pileolariaceae* was established for autoecious rusts in *Pileolaria*, *Uromykladium* and *Endoraecium* (Arthur 1906, Cummins & Hiratsuka 2003). The latter two have been resolved within *Raveneliaceae*, while *Pileolaria* holds an isolated position within *Pucciniales* (Aime 2006, Scholler & Aime 2006, Figs 1, 4). *Pileolaria* species are autoecious on *Anacardiaceae*, with very characteristic sculpted discoid teliospores.

Crossopsoraceae Aime & McTaggart, **fam. nov.** MycoBank MB836646.

Type genus: *Crossopsora* Syd. & P. Syd., *Annls mycol.* **16**(3/6): 243. 1919.

Diagnosis: Similar to *Phakopsoraceae*, differing in that the majority of sporothalli infect *Poaceae*, *Vitaceae*, *Lamiaceae*, and *Rhamnaceae* with none known on *Annonaceae* and *Euphorbiaceae* and that some species are known to be heteroecious.

Description: Spermogonia Group VI (type 7) where known; aecia aecidium-type where known; uredinia typically paraphysate, malupa-type; teliospores germinate externally, with or without dormancy, 1-celled, compact, often produced in catenulate chains of a few to many cells. Most species only known from the sporothallus; *Neophysopella* is macrocyclic and heteroecious, as may be other species in this family.

Included genera: *Angiopsora*, *Catenulopsora*, *Crossopsora*, *Kweilingia* (= *Dasturella*), *Neolivea*, *Neophysopella*, *Stomatissora*.

Host families: *Papaveraceae*, *Sabiaceae*, *Rubiaceae* (0-I); *Lamiaceae*, *Fabaceae*, *Poaceae*, *Rhamnaceae*, *Rubiaceae*, *Salicaceae*, *Vitaceae* (II-III).

Notes: *Phakopsoraceae sensu* Cummins & Hiratsuka (2003) is a polyphyletic family, with multiple polyphyletic genera (Aime 2006, Aime *et al.* 2018a, 2019a, b, Ji *et al.* 2019). The phakopsoroid fungi share a convergent suite of characters including pale, subepidermal sori, and 1-celled, sessile teliospores with external germination, which have long been the subject of taxonomic debate, especially concerning application of the names *Angiopsora*, *Bubakia*, *Phakopsora*, and *Physopella*. *Phakopsoraceae s.s.* is now confined to species within *Raveneliineae* on various hosts including *Annonaceae*, *Euphorbiaceae* and *Fabaceae*. The remaining ex-*Phakopsoraceae* are now placed in *Crossopsoraceae* (Figs 1, 4), including the species that have radiated on *Poaceae* and *Vitaceae*. Some species in both families form teliospores in extruded columns, but these are produced in catenulate chains in *Crossopsoraceae*, versus tightly packed individual cells in *Phakopsoraceae*. Life cycles are unknown for many species. However, *Neophysopella* is heteroecious, alternating either between *Sabiaceae* and *Vitaceae* species (Ji *et al.* 2019) or *Papaveraceae* and *Fabaceae* (*N. kraunhia*, Hiratsuka & Kaneko 1978); *K. divina* alternates between *Rubiaceae* (gametothallus) and *Poaceae* (sporothallus) (Thirumalachar *et al.* 1947).

Physopella Arthur (1906), although often applied to the species now assigned to *Neophysopella* and others, is a later homonym of *Physopella* G. Poirault (1905) and is therefore an illegitimate name (Xi *et al.* 2019). Our work (Fig. 4) shows that *Kweilingia* (type *K. bambusae*, syn. *Chrysomyxa bambusae*)

and *Dasturella* (type *D. divina*, syn. *Angiopsora divina*) are congeneric; *Kweilingia* (1940) has priority over *Dasturella* (1943) and we retain these species in the former genus.

The phakopsoroid species that form teliospore chains are difficult to diagnose and classify, as exemplified by the complex taxonomic histories of *Crossopsora*, *Cerotelium*, *Catenulopsora*, and *Kuehneola* (*e.g.*, Ono 2015a). In this work, *Crossopsora* and *Catenulopsora* are assigned to *Crossopsoraceae*. *Cerotelium* most likely belongs to *Phakopsoraceae s.s.*; the type, *C. canavaliae* parasitizes *Fabaceae* and the uredinia are peridiate in contrast to *C. fici* with paraphysate uredinia (Cummins 1941). Nonetheless, these genera still appear to be polyphyletic with little support for generic lineages and resolution will require additional taxon and locus sampling (Fig. 4).

Numerous *Uredo* species assigned to *Crossopsoraceae*, especially within the *Crossopsora/Catenulopsora* complex, could not be placed in other genera and we have retained use of names in anamorphic form-genera for these. *Crossopsora fici* and *U. moricola* form a distinct lineage within *Crossopsoraceae* and may require a new genus, pending examination of other critical types including those of *Mehtamyces*, *Phragmidiella*, *Pucciniostele*, and *Scalarispora*.

Neophysopella kraunhia (Dietel) Aime & McTaggart, **comb. nov.** MycoBank MB837747.

Basionym: *Phakopsora kraunhia* Dietel, *Hedwigia* **41**: 178. 1902.

Synonyms: *Ochropsora kraunhia* (Dietel) Dietel., *Bot. Jahrb.* **37**: 106. 1905.

Aecidium corydalinum Syd. & P. Syd., *Monogr. Ured.* **4**: 235.1923.

Notes: *Neophysopella kraunhia* is heteroecious and produces gametothalli on *Corydalis incisa* (*Papaveraceae*) and sporothalli on *Wisteria floribunda* (*Fabaceae*) (Hiratsuka & Kaneko 1978). Our data support its classification in the newly circumscribed *Neophysopella*, a genus that contains most other known heteroecious species in *Crossopsoraceae*.

Neolivea Aime & McTaggart, **gen. nov.** MycoBank MB837748.

Type species: *Neolivea tectonae* (T.S. Ramakr. & K. Ramakr.) Aime & McTaggart, this paper.

Etymology: New genus segregated from *Olivea*.

Diagnosis: Similar to *Olivea* and *Tegillum* but differs in having subglobose to ellipsoid, non-angular urediniospores with inconspicuous germ pores, and waxy telia.

Description: With characteristics of the type species *Neolivea tectonae*.

Neolivea tectonae (Racib.) Aime & McTaggart, **comb. nov.** MycoBank MB837749.

Basionym: *Uredo tectonae* Racib., *Parasit. Alg. Pilze Java's* (Jakarta) **1**: 28. 1900.

Synonyms: *Olivea tectonae* (Racib.) Thirum., *Curr. Sci.* **18**: 176. 1949.

Tegillum tectonae (Racib.) Doweld, *Index Fungorum* **36**: 1. 2013. *Chaonia tectonae* T.S. Ramakr. & K. Ramakr., *Indian Phytopath.* **2**: 19. 1949.

Olivea tectonae (T.S. Ramakr. & K. Ramakr.) R.L. Mulder, *CMI*

Descriptions of Pathogenic Fungi and Bacteria **37**: no. 365. 1973.
Olivea neotectonae Buriticá & Salazar-Yepes, *Revista Fac. Agron. Medellín* **60**(1): 3652. 2007.
Tegillum neotectonae (Buriticá & Salazar-Yepes) Doweld, *Index Fungorum* **36**: 1. 2013.

Notes: *Neolivea tectonae* causes leaf rust on teak (*Tectona grandis*, *Tectoneae*, *Verbenaceae*). It is described in Ono & Hennen (1983) and illustrated in Ramakrishnan & Ramakrishnan (1949). Our data show that *N. tectonae* is unrelated to the type of *Olivea* (*O. capituliformis*), which belongs to the *Raveneliaceae* (Figs 1, 3, 4). *Tegillum* was established for *Olivea*-like species, with the type *T. fimbriatum* (Mains 1940). While no type data exist for *T. fimbriata*, the species is most similar to *T. scitulum* (Mains 1940), sharing characteristics such as lobed or angular urediniospores with germ pores residing in the lobes and hosts in the *Vitex* group of *Verbenaceae* (Ono & Hennen 1983), which is placed in *Raveneliineae* (Fig. 1). *Neolivea tectonae* differs from other described *Olivea* and *Tegillum* species in producing rounded urediniospores with inconspicuous germ pores, as well as waxy, orange telia (Ono & Hennen 1983, Osorio *et al.* 2019).

Angiopsora apoda (Har. & Pat.) Aime & McTaggart, **comb. nov.** MycoBank MB836647.

Basionym: *Puccinia apoda* Har. & Pat., *Bull. Mus. natn. Hist. nat.*, Paris **15**:199. 1909.

Synonym: *Phakopsora apoda* (Har. & Pat.) Mains, *Mycologia* **30**: 45. 1938.

Angiopsora chusqueae (Pardo-Card.) Aime & McTaggart, **comb. nov.** MycoBank MB836648.

Basionym: *Uredo chusqueae* Pardo-Card., *Revta Acad. colomb. cienc. exact. fis. nat.* **20**: 205. 1996.

Angiopsora paspalicola (Henn.) Aime & McTaggart, **comb. nov.** MycoBank MB836649.

Basionym: *Uredo paspalicola* Henn., *Hedwigia* **44**: 57. 1905.

Synonyms: *Puccinia paspalicola* (Henn.) Arthur, *Manual Rusts U.S. & Canada. Purdue Res. Found.*: 127. 1934.

Physopella paspalicola (Henn.) Buriticá & Hennen, *Buriticá Rev. I. C. N. E. (Medellín)* **5**: 179. 1994.

Puccinia compressa Arthur & Holway, *Proc. American Phil. Soc.* **64**:257. 1925.

Angiopsora compressa (Arthur & Holway) Mains, *Mycologia* **26**: 29. 1934.

Physopella compressa (Arthur & Holway) Cummins & Ramachar, *Mycologia* **50**: 742. 1958.

Phakopsora compressa (Arthur & Holway) Buriticá & Hennen, *Buriticá, Rev. I. C. N. E. (Medellín)* **5**: 179. 1994.

Notes: Mains (1934) established *Angiopsora* for *Poaceae*-infecting ex-*Pucciniaceae* species with similarities to *Phakopsora*. Although the name has been considered a synonym for *Phakopsora* (e.g., Cummins & Hiratsuka 2003), we find that it is applicable to numerous former *Phakopsora* species on grasses (Fig. 4).

Gymnosporangiaceae P. Zhou & L. Cai, *Persoonia* **45**: 79. 2020. **emend.** Aime & McTaggart

Synonym: *Gymnosporangieae* Dietel, In: Engler & Prantl, *Naturlichen Pflanzenfamilien Band* **6**: 73. 1938.

Type genus: *Gymnosporangium* R. Hedw. ex DC., In: Lamarck & de Candolle, *Fl. franç.*, *Edn 3* (Paris) **2**: 216. 1805.

Description: Spermogonia Group V (type 4). Aecia roestelia-type (*Gymnosporangium*) or less frequently aecidium-type (*Gymnotelium*). Teliospores mostly 2-celled, germinating without dormancy via external basidia. Life cycles mostly demicyclic and heteroecious (*Gymnosporangium*).

Included genera: *Gymnosporangium*, *Gymnotelium*; likely includes *Peridiopsora*.

Host families: *Rosaceae*, *Hydrangeaceae*, *Myricaceae* (0-I); *Cupressaceae* (II-III); autoecious species on *Berberidaceae*, *Cupressaceae*, *Liliaceae*, *Moraceae*.

Notes: The genus *Gymnosporangium* is unusual in that temperate species form teliospores in the spring and aecia in the summer, in contrast to most other temperate rust species (Kern 1960). Most species of *Gymnosporangium* form sporothalli on *Juniperus* spp. and gametothalli on *Maloideae* (*Rosaceae*). Although traditionally placed in *Pucciniaceae*, *Gymnosporangium* has been treated as an “orphan” genus in molecular phylogenetic studies (Maier 2003, Aime 2006, Aime *et al.* 2018a) and recently established as a monotypic family of unresolved placement (Zhao *et al.* 2020). Although the older name *Gymnosporangieae* Dietel exists for this lineage, priority only applies within rank, thus we retain *Gymnosporangiaceae* P. Zhou & L. Cai for the family. In addition to the puccinioid character of 2-celled, pedicellate teliospores, most species are demicyclic. *Gymnosporangium* has been conserved against the older name *Roestelia* Rebent. (Aime *et al.* 2018b).

Peridiopsora mori (syn. *Caeoma mori*, *Aecidium mori*) causes a well-known disease in mulberries. It is unusual in having a true hemicyclic life cycle, wherein the mitospores appear to function as urediniospores although likely are derived from the aecial part of the life cycle (Mordue 1991). Spermogonia and teliospores are not known. *Peridiopsora* was erected to accommodate an unusual asexual rust that persisted as cyclical urediniospores, producing uredinia in peridiate sori that lack paraphyses, the latter being typical of aecia but rare in uredinia (Kamat & Sathe 1969) and which we interpret as uredinioid aecia. Whether *P. mori* will prove to be congeneric with the type, *P. adelocaryi*, or will be placed within *Gymnotelium*, remains uncertain.

Gymnotelium speciosum (Peck) Aime & McTaggart, **comb. nov.** MycoBank MB836652.

Basionym: *Gymnosporangium speciosum* Peck, *Bot. Gaz.* (Crawfordsville) **4** (10): 217. 1879.

Synonym: *Tremella speciosa* (Peck) Arthur, *Proc. Indiana Acad. Sci.* **1900**: 135. 1901.

Notes: *Gymnotelium* was erected for *Gyt. nootkatense*, a macrocyclic (rather than demicyclic) species with a gametothallus host (*Chamaecyparis*) not within the usual *Maloideae*/*Juniperus* range of *Gymnosporangium*. Arthur (1929) considered the diagnostic character of aecidium-like rather than rostrate aecia as more important than presence of uredinia, transferring an additional two species, *Gyt. blasdaleanum* (syn. *G. libocedri*) and *Gyt. myricatum* (syn. *G. ellisii*) to *Gymnotelium*. In later works Arthur (1934) treated *Gymnotelium* as a subgenus of *Gymnosporangium*, including a fourth species, *G. speciosum*.

Novick (2008) showed that *G. nootkatense*, *G. blasdaleanum* (as *G. libocedri*), *G. myricatum* (as *G. elisii*), and *G. speciosum* are the earliest diverging members of *Gymnosporangium*. The cupulate aecia of *Gymnotelium* bear a strong resemblance to those of *P. mori*, and our work resolves these together as the sister lineage to *Gymnosporangium* (Figs 1, 4). In addition to producing cupulate (rather than rostrate) aecia, *Gymnotelium* species produce their sporothallus on hosts other than *Maloideae* spp., and/or the sporothallus on hosts other than *Juniperus* spp. (Kern 1960).

Sphaerophragmiaceae Cummins & Y. Hirats., *Illustr. Gen. Rust Fungi*, rev. Edn (St. Paul): 15. 1983. **emend.** Aime & McTaggart
Synonym: *Dasysporatae* Arthur, *North American Flora* 7: 807. 1926.

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

Description: Spermogonia mostly lacking, Group V (type 4) in *Sphenorchidium*. Aecia aecidium-type; uredinia resembling aecia, lecythea-type in *Sphenorchidium*. Teliospores 2- to multi-celled. Species autoecious with variable life cycles.

Included genera: *Austropuccinia*, *Dasyspora*, *Puccorchidium*, *Sphaerophragmium*, *Sphenorchidium*.

Host families: *Annonaceae*, *Fabaceae*, *Myrtaceae*.

Notes: *Sphaerophragmium* has been hypothesized as belonging to *Raveneliaceae* based on similarities in teliospores and host (Cummins & Hiratsuka 2003). More recently *Sphaerophragmium* was shown to belong to a monophyletic lineage (Beenken & Wood 2015) for which the oldest available name is *Dasysporatae*, but for which *Sphaerophragmiaceae* has been recently applied (e.g., McTaggart *et al.* 2016, Beenken 2017). Because priority only applies within rank, we retain the more widely used name for this family. *Austropuccinia psidii*, causes an economically important epidemic disease of *Myrtaceae* and was recently demonstrated to be autoecious and macrocyclic but lacking spermogonia (I-IV) and with uredinioid aecia (McTaggart *et al.* 2018, 2020).

Pucciniaceae Chevall., *Fl. gén. env. Paris* (Paris) 1: 413. 1826. **emend.** Aime & McTaggart

Synonyms: *Puccinosiraceae* (Dietel) Cummins & Y. Hirats., *Illustrated Genera of Rust Fungi*: 15. 1983.

Endophyllaceae Dietel, In: Engler & Prantl, *Nat. Pflanzenfam., Teil. I* (Leipzig) 1: 35. 1897.

Type genus: *Puccinia* Pers., *Synopsis methodica fungorum*: 225. 1801.

Description: Spermogonia Group V (type 4). Aecia aecidium-type; uredinia mostly uredo-type. Teliospores borne singly, mostly pedicellate, typically with 1 or 2 cells. Basidia external. Most species macrocyclic but many endocyclic and microcyclic species as well; heteroecious or autoecious.

Included genera: *Baeodromus*, *Ceratocoma*, *Chardonella*, *Chrycozelis*, *Cionothrix*, *Cumminsiella*, *Desmella*, *Didymopsora*, *Dietelia*, *Dipyxis*, *Edythea*, *Endophylloides*, *Endophyllum*,

Hapalophragmium, *Leptopuccinia*, *Macruropyxis*, *Miyagia*, *Puccinia*, *Puccinosira*, *Sphenospora*, *Stereostratum*, *Uromyces*, *Xenosteles*; likely includes *Cerradoa*, *Chrysella*, *Chrysocyclus*, *Chrysopsora*, *Cleptomycetes*, *Corbulopsora*, *Kernella*, *Polioma*, *Trichopsora*.

Host families: various including *Berberidaceae*, *Ranunculaceae* (0-I); various including *Asteraceae*, *Euphorbiaceae*, *Fabaceae*, *Malvaceae*, *Orchidaceae*, *Poaceae*, *Solanaceae* (II-III and autoecious species).

Notes: As with *Raveneliaceae*, infra-familial relationships in *Pucciniaceae* are difficult to resolve at least within the context of currently circumscribed genera (Fig. 4). However, whereas *Raveneliaceae* represents a lineage with multiple parallel radiations and differing rates of evolution, *Pucciniaceae* represents a recent and rapidly radiating lineage that has undergone multiple losses of teliospore septa and morphs. The majority of rust species and the two most speciose genera, *Puccinia* and *Uromyces*, belong here. Taxonomic changes that reflect natural genera will depend on sequencing of additional loci as well as representative types from genera such as *Cerradoa*, *Cleptomycetes*, *Corbulopsora*, *Didymopsora*, *Polioma*, *Kernella*, *Ramakrishnania*, and *Trichopsora*. *Pucciniaceae* includes many endocyclic derivatives, such as those once included in the family *Puccinosiraceae*, as hypothesized by Berndt (2018).

Species of *Pucciniaceae* can be roughly circumscribed into three radiations (Figs 1, 4). One, represented by *P. graminis*, the type of *Puccinia*, includes primarily species with 2-celled teliospores that are macrocyclic and heteroecious, and includes economically important species on *Poaceae* and *Asteraceae*. The second, represented by *U. appendiculatus*, the type of *Uromyces*, includes many species with 1-celled teliospores that have radiated on *Euphorbiaceae* and *Fabaceae*, and are primarily autoecious. A third, weakly supported in Fig. 1, but not in Fig. 4, includes, among others, the fern- and orchid-infecting species of *Pucciniaceae*.

DISCUSSION

The proposed classification of rust fungi includes seven suborders and 18 families. Although we treat approximately the same number of families as Cummins & Hiratsuka (2003), the disposition of many genera varies considerably between our and earlier classifications (Fig. S1). We have excluded demonstrably artificial families such as *Chaconiaceae*, *Puccinosiraceae*, and *Uropyxidaceae*, while establishing new families for cohorts that have been repeatedly shown in our and other works to be strongly supported entities (e.g., *Crossosporaceae*, *Milesiaceae*, *Rogerpetersoniaceae*). While our three-locus approach has enabled resolution of most major lineages of *Puccinales*, providing a stable framework for future studies, resolution remains poor in some areas, especially in the *Pucciniastraceae* and *Raveneliaceae*, which will require additional strategic sampling of both taxa and loci. Additionally, three of our sampled genera – *Allodus*, *Neopuccinia*, and *Nyssopsora* – still cannot be placed to family and remain *incertae sedis* within *Urediniaceae*; placement of these is sensitive to taxon selection within analyses. For example, in our initial analyses (not shown) *Allodus* was weakly supported within *Gymnosporangiaceae*, however, inclusion of *Nyssopsora* (Fig. 1) and *Neopuccinia*

(Fig. 4) results in uncertain placement for all three genera and underscores the need for appropriate taxon selection in reconstructing phylogenetic hypotheses in *Pucciniales*. The necessity of including type species and adequate sampling when dealing with rust taxonomy, especially in polyphyletic and/or convergent genera and families, cannot be overemphasized.

The classification of rust fungi has undergone several epochs, each with emphasis on a different suite of characters including teliospores (e.g., Cunningham 1931) and telia (e.g., Dietel 1928), aecia (e.g., Leppik 1953), and spermogonia (Hiratsuka & Cummins 1963, Hiratsuka & Hiratsuka 1980) in attempts to circumscribe natural groups (Fig. S1). Our work shows that sporothallus characteristics can be useful at the generic and sometimes family ranks. Ontogenic characters, such as the presence of hymenial-like sporogenous cells from which teliospores develop, which distinguishes *Tranzscheliaceae* from *Ochropsoraceae*, may be useful for diagnosing some families. However, in general telial and uredinial characters are among the most homoplasious in rust taxonomy.

The asexual genera – At least 34 generic names for asexual rust morphs have been introduced. Of these, ca. 13 were in wide use (Cummins & Hiratsuka 2003) prior to changes in the nomenclatural code that now eliminate the use of dual nomenclature (McNeill *et al.* 2012, Turland *et al.* 2018). Most of these genera are recognized as later synonyms for sexual-morph genera (e.g., *Canasta* = *Prospodium*, *Endocronartium* = *Cronartium*, *Pelastoma* = *Blastospora*) or in cases where the asexual name has priority, the sexual name has been conserved (e.g., *Gymnosporangium* over *Roestelia*; *Melampsorella* over *Peridermium*) (Aime *et al.* 2018b). In many cases, species only known from an asexual morph can be recombined into sexual genera by a combination of host, morphology, and/or DNA sequence data. But for the largest asexual genera, *Aecidium* and *Uredo*, there remain hundreds of species that cannot reliably be recombined at this time, and the process to place these within natural genera will take painstaking work, even with DNA data. In this paper we were unable to assign several species (e.g., *A. kalanchoes*, *U. cryptostegiae*, *U. elephantopodis*, *U. hiulca* Cummins, *U. trichosanthes*) to sexual genera and recommend use of form-genera names for these species until they can be confidently reassigned.

The endocyclic rusts—Species with endocyclic life cycles, *i.e.*, reduced autoecious life cycles in which the aeciospores function as teliospores, were once treated collectively in heterogeneous families such as *Puccinosiraceae* and *Endophyllaceae* (Cummins & Hiratsuka 2003, Buriticá 1991). Perhaps not surprisingly we find that these are derived multiple times within *Pucciniales* as predicted by Berndt (2018) (e.g., *Baeodromus*, *Ceratocoma*, *Chardonella*, *Cionothrix*, *Didymopsisora*, *Dietelia*, *Endophyllum* and *Puccinosira*, Fig. 4). Interestingly, we see little evidence for expanded radiations of endocyclic rusts. Coupled with the fact that the majority of these species are found within the most recent radiation (*Pucciniaceae*), this life history strategy may represent an evolutionary dead-end for *Pucciniales*.

The chaconiaceous rusts—Classification of the primarily tropical rust species that produce thin-walled teliospores and germinate without dormancy has not received consensus in the past. Genera such as *Chaconia*, *Goplana*, *Hemileia*, *Maravalia*, *Ochropsora*, and *Olivea* were often treated as a single family, *Chaconiaceae*, hypothesized to represent the earliest diverging lineage of rusts by some urediniologists (e.g., Cummins & Hiratsuka 1983, Hiratsuka 1983). Our and prior works (e.g., Aime

2006, Aime *et al.* 2018a) show that these characters represent a syndrome, most likely as an adaptive response to tropical climates where teliospore dormancy or overwintering is not necessary, and that even the species within genera (with the probable exception of *Hemileia*) do not share a common recent ancestor (Figs 1–4).

Rust evolution—The study of rust fungi has been fertile ground for evolutionary theory. Researchers have posited co-evolution to explain rust success (Savile 1971, McTaggart *et al.* 2015), or alternatively host jumps (Hart 1988, McTaggart *et al.* 2016). However, most studies fail to take the heteroecious nature of many rust species into account. The most likely explanation for the success, in terms of species, of *Pucciniales* proposes a combination of both factors in a more complex interplay between the forces of biological specialization and biogenic radiation (Leppik 1953, van der Merwe *et al.* 2008, Aime *et al.* 2018a). A pattern of host jumps followed by rapid radiation to related or ecologically co-distributed host species, or biogenic radiation, is the best explanation for the relationship between rusts and their sporothallus hosts (van der Merwe *et al.* 2008, Aime *et al.* 2018). In contrast, a pattern of co-evolution or biological specialization, best explains the relationship between rust fungi and their gametothallus hosts (Aime *et al.* 2018a). This pattern becomes more evident in light of spermogonial evolution. The earliest rusts (*Rogerpetersoniaceae* and *Zaghouaniaceae*) produce spermogonia of Group III, deep-seated with an exit canal, convex hymenium, and indeterminate growth. Loss of the exit canal occurred approximately 145 mya coinciding with a gametothallus jump to *Pinaceae* hosts. These initially produced subepidermal convex hymenia [Group I (type 1); *Araucariomyces* and *Skierkaceae*], becoming flat and eventually subcuticular [Group I (types 2 & 3)] within the *Melampsorineae*. Well-developed periphyses (Group VI) are apparent approximately 115 mya, coinciding with a gametothallus jump to angiosperms. Group VI spermogonia have a flat hymenium and are retained in *Raveneliineae* and the earlier diverging *Urediniineae*. A well-defined bounding structure surrounding a convex hymenium (Group V) evolved last, ca. 85–90 mya, coinciding with the major angiosperm radiation, in the crown rust radiation that includes *Gymnosporangiaceae*, *Sphaerophragmiaceae*, and *Pucciniaceae*.

The complexities of the macrocyclic rust life cycle and its derivations is difficult to explain in an evolutionary context. One explanation, Tranzschel's law (Arthur 1929, Jackson 1931), posits that autoecious-microcyclic rusts are derived from heteroecious-macrocyclic life cycles that have been restricted to the gametothallus host. Evidence of this has been found at the scale of recently diverging, correlated species (Scholler *et al.* 2019). The authors posit that this plasticity of life cycle provides the template for multiple avenues of speciation, not just on the gametothallus host as demonstrated, but hypothetically from the sporothallus host as well (Scholler *et al.* 2019). At a larger scale, *Raveneliineae* is hypothesized as an initially heteroecious and macrocyclic lineage (Savile 1989) and the earliest diverging families in the suborder, *Ochropsoraceae* and *Tranzscheliaceae*, share this strategy, with gametothallus hosts in *Ranunculaceae*. Loss of the original gametothallus host may have occurred ca. 80 mya, driving the evolution of autoecious and macrocyclic lineages on the sporothallus hosts, with several contemporaneous radiations into what are now recognizable as the *Phakopsoraceae* and *Raveneliaceae* (Fig. 1).

Lineages restricted due to extinction or other forces to

gametothallus hosts compensate by becoming microcyclic (e.g., microcyclic *Tranzschelia* species), endocyclic (e.g., endocronartium-type species of *Cronartium*) or systemic infections (as hypothesized for *Rogerpetersonia* and *Araucariomyces*), but these show constraints, at least in terms of species diversification on that host and seem incapable of regaining all five spore stages. In contrast, lineages that have been restricted on the sporothallus hosts, e.g., *Raveneliaceae*, appear capable of more expansive radiation and in recovering lost spore stages.

In conclusion – We provide a rust tree of life resolved at the deeper nodes and use this framework to redefine the higher rank (suborder and family) classification for *Pucciniales*. The complexities of rust fungal biology that includes alternation of generations, heteroecism, and five developmental stages is mirrored in the taxonomic complexities encountered in this group. Taxonomy is often confounded by multiple parallel radiations, convergent morphologies, and the previous application of dual nomenclature making the necessity of consulting type species in taxonomic revision an imperative.

Our data support a model of rust evolution in which: 1) heteroecism favours diversity by allowing different speciation processes to act on different parts of the life cycle (biogenic radiation on the sporothallus, biologic specialization on the gametothallus); 2) the five developmental stages of a macrocyclic rust provide the templates for multiple avenues of speciation; and, 3) both unique features were present in the earliest extant rust radiation (*Mikronegeriineae*). There is evidence that the highly reduced endocyclic rusts on gametothallus hosts may represent an evolutionary dead-end but that rusts confined to the sporothallus host can regain lost spore stages. The heteroecious macrocyclic strategy is unique to *Pucciniales* and may help to explain the tremendous diversity in form and in species found in the rusts.

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Table S1. Collection and accession data for additional sequences used in *Melampsorineae*, *Raveneliineae*, and *Uredinineae* analyses (Figs 2-4 & S2).

Fig. S1. Alluvial plot tracking generic placement at familial and subfamilial rank. Each colour represents the taxonomic hypotheses of an author. Tracks for genera with conflicting familial and subfamilial placement from multiple authors are dashed. The plot was made in R with the *ggalluvial* package.

Fig. S2. *Raveneliineae*. Network analysis generated with SplitsTree from 28S data. Generic types are indicated in bold, type proxies by *.