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FULL PAPER

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Toward resolving family-level relationships in rust fungi (Uredinales)

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Abstract Rust fungi (Basidiomycota, Uredinales) consist of more than 7000 species of obligate plant pathogens that possess some of the most complex life cycles in the Eumycota. Traditionally, a limited number of synapomorphic characters and incomplete life-cycle and host-specificity data have hampered phylogenetic inference within the Uredinales. The application of modern molecular characters to rust systematics has been limited, and current contradictions, especially in the deeper nodes, have not yet been resolved. In this study, two nuclear rDNA genes (18S and 28S) were examined across the breadth of the Uredinales to resolve some systematic conflicts and provide a framework for further studies of the group. Three suborders of rusts are recovered. Of the 13 rust families most widely accepted, 8 are supported in full or in part (Coleosporiaceae, Melampsoraceae, Mikronegeriaceae, Phakopsoraceae p.p., Phragmidiaceae, Pileolariaceae, Pucciniaceae, Raveneliaceae), 3 are redundant (Cronartiaceae, Pucciniastraceae, Pucciniosiraceae), and the status of 2 (Chaconiaceae, Uropyxidaceae) could not be resolved. The Mikronegeriaceae and *Caeoma torreyae* are the most basal rusts sampled. It is concluded that morphology alone is a poor predictor of rust relationships at most levels. Host selection, on the other hand, has played a significant role in rust evolution.

Key words Molecular systematics · Pathogenic fungi · Rust taxonomy · Urediniomycetes

Introduction

The rusts (Uredinales) are the largest group of phytopathogenic fungi (Savile 1976), with at least 7000 described species in the order—one-third of all described basidiomycetes (Kirk et al. 2001). Rusts are phenotypically and genetically plastic organisms that have the most complicated life cycles of any Eumycota (Laundon 1973; Hennen and Buriticá 1980; Cummins and Hiratsuka 2003). The rust life cycle can involve up to five or six different spore types with varying nuclear composition and may require alternation between two unrelated host plants for completion (Hiratsuka and Hiratsuka 1980; Cummins and Hiratsuka 2003). Karyogamy typically occurs in specialized spores termed teliospores that germinate to produce the basidia in which meiosis takes place, but many species have conscripted other spore stages, such as aeciospores or urediniospores, for completion of the sexual cycle (Savile 1976; Cummins and Hiratsuka 2003). Even genome size is quite variable, with haploid size-estimates ranging from 64 to 418 Mbp for some species in the Pucciniaceae alone (Eilam et al. 1994). Rust diseases cause serious economic damage worldwide on agricultural, forest, and ornamental plants. Because of the presumed host-specificity of some species, they also offer a potential source of biological control organisms for noxious and invasive weeds (McCain et al. 1990; Evans 1993). Yet, for the majority of rust species, complete life-cycle data including host range, geographic distribution, cytology, identity of alternate hosts, and/or mode of sexual reproduction are incomplete (Savile 1976; Ono and Hennen 1983; McCain et al. 1990; Hennen and McCain 1993), and even family-level classification is contentious (Hennen and Buriticá 1980; Ono and Hennen 1983) and "requires further investigation" (Kirk et al. 2001).

Rust taxonomy has been almost entirely informed by morphology, despite known phenotypic variability of some species. For instance, in two studied species urediniospore morphology was found to be dependent on which alternate host was utilized (Long 1914). Family-level classifications for the rusts have undergone numerous changes since

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Dietel (1900), with Uredinales typically divided into anywhere from 2 (Dietel 1928) to 14 (Cummins and Hiratsuka 1983; Kirk et al. 2001) different families (see Hennen and Buriticá 1980 and Hart 1988 for a summary). Different morphological characters have been emphasized during different periods in rust taxonomy (Ono and Hennen 1983). For example, early classifications emphasized teliospore (Dietel 1928; Thirumalachar and Cummins 1949; Thirumalachar and Mundkur 1949a) and telium (Thirumalachar and Cummins 1949) morphology as of primary importance. Cummins and Hiratsuka (1983, 2003) revised rust taxonomy and developed the systematic treatment most widely used today by deemphasizing telial state morphology and emphasizing spermogonial structure, based on the work of Hiratsuka and Cummins (1963) and Hiratsuka and Hiratsuka (1980). Researchers have often deemphasized or cautioned against using host associations in the formation of rust classifications (Thirumalachar and Mundkur 1949b). The primary exception is in the treatment of the "fern rusts" – those genera of rusts that form their telia on ferns – which were widely believed to be the most primitive rusts because they parasitize a primitive group of plants (Arthur 1924; Savile 1976), although alternate hypotheses regarding which group of rusts are the most primitive exist (Ono and Hennen 1983).

Cladistic analysis of 28 rust characters challenged the hypothesis that the fern rusts represented the most primitive extant Uredinales (Hart 1988). DNA sequence-based phylogenetic analyses of the rusts have not been as widely applied as for other fungi, largely because they are obligate biotrophs that are generally impossible to maintain in pure culture. However, the first such study to broadly examine the rusts at a suprageneric level provided conclusive evidence that two fern rusts, *Uredinopsis* Magnus and *Hyalopsora* Magnus, did not hold a basal position in the order (Sjamsuridzal et al. 1999). Two subsequent phylogenetic studies have confirmed these findings as well as the monophyly of the rusts but provide conflicting topologies (Maier et al. 2003; Wingfield et al. 2004). Sequence data from ~600 bp of the 5′-end of the large subunit (28S) nuclear rDNA place *Melampsora* Castagne in the basalmost position for the Uredinales (Maier et al. 2003). Sequence data from nuclear rDNA encoding the entire small subunit (18S) RNA place *Racospermyces* J. Walker in the basal-most position and show *Melampsora* in a derived lineage (Wingfield et al. 2004). In both cases, neither the 28S nor 18S rDNA alone was capable of full resolution, although the 28S provided better support for groupings than did the 18S. The purpose of the present study is to use a two-gene analysis of combined 18S and 28S sequence data for exemplars from all 13 most widely accepted rust families fide Cummins and Hiratsuka (2003) toward resolving subordinal relationships in the rusts. Discussion of the families in a phylogenetic context is provided with emphasis on which rusts hold promise as being representative of the most primitive extant Uredinales.

Materials and methods

Specimens

Materials were obtained as dried field collections or herbarium specimens, or previously accessioned DNA sequences from GenBank (http://www.ncbi.nlm.nih.gov/). Field collections were dried using a standard plant press. Origin and voucher deposition of all collections are provided in Table 1.

DNA extraction, polymerase chain reaction, and cycle sequencing

Sori were excised from the dried host material, placed in 2 ml Bead Solution tubes of the UltraClean Plant DNA Isolation Kit, and extracted per the manufacturer's instructions (MoBio Laboratories, Solana Beach, CA, USA).

Polymerase chain reactions (PCRs) were performed in 25-μl reaction volumes with 12.5 μl PCR Master Mix (Promega, Madison, WI, USA), 1.25 μl each 10 μM primers (upstream and downstream), and 10 μl diluted (10- to 100 fold) DNA template. Approximately 1400 bp of a region of the ribosomal repeat spanning the 5.8S subunit, the internal transcribed spacer region 2 (ITS-2), and the large subunit (28S) was amplified with rust-specific primer Rust2inv (5′-GATGAAGAACACAGTGAAA, based on the reverse-complement of Rust2 from Kropp et al. 1997) and LR6 (Vilgalys and Hester 1990), and sequenced with Rust2inv, LR6, LR0R (Moncalvo et al. 1995), and LR3 (Vilgalys and Hester 1990). The complete 18S rDNA (~1750 bp) was amplified with rust-specific primer Rust18S-R (5′-ACCTTGTTACGACTTTTACTTC) and NS1 (White et al. 1990) and sequenced with NS1, NS3, NS4, NS5, NS6 (White et al. 1990), and Rust18S-R. Amplification of both regions was achieved with an initial denaturation step of 2 min at 94°C; 40 cycles of 30 s at 94°C, 1 min at 57°C, and 1.5 min at 72°C, and a final extension of 7 min at 72°C.

PCR products were cleaned by one of two methods. The majority were cleaned with Montage PCR Centrifugal Filter Devices (Millipore, Billerica, MA, USA) according to the manufacturer's protocol. If more than one PCR product was produced during amplification, then the band of the correct size was excised from a 1% agarose gel and cleaned with the MinElute PCR Gel Extraction Kit (Qiagen, Valencia, CA, USA). Cleaned PCR products were sequenced with BigDye Terminator sequencing enzyme v.3.1 (Applied Biosystems, Foster City, CA, USA) in the reaction: 2 μl diluted BigDye in a 1 : 3 or 1 : 1 dilution of BigDye : dilution buffer (400 mM Tris pH 8.0, 10 mM $MgCl_2$), 0.3 μl 10 μM primer, 10–20 ng cleaned PCR template, and H_2O to 5 μl total reaction volume. Cycle sequencing parameters consisted of a 2-min denaturation step at 94°C, then 35 cycles of 94°C for 39 s, 50°C for 15 s, and 60°C for 4 min. Sequencing reactions were cleaned by ethanol precipitation and sequenced on an ABI 3100 Genetic Analyzer (Applied Biosystems). DNA sequences have been deposited in GenBank, accessions DQ354508–569 (see Table 1).

Table 1. Origin of materials used for sequence analyses

Species	Host	Location	Collection no.	Voucher no.[a]	GenBank LSU[b]	GenBank SSU[b]
Aecidium kalanchoe J.R. Hern.	*Kalanchoe blossfeldiana* Poelln. (Crassulaceae)	USA: ID	E.K. Vavrika s.n. (U-18)	BPI 843633	AY463163*	DQ354524
Batistopsora crucis-filii Dianese, R.B. Medeiros & L.T.P. Santos	*Annona* sp. (Annonaceae)	Guyana	J. Hernandez 2003-085	BPI 863563	DQ354539	DQ354538
Blastospora smilacis Dietel	*Smilax sieboldii* Hort. Bog ex Hassk. (Smilacaceae)	Japan	Y. Ono 3179	PUR N270	DQ354568	DQ354567
Caeoma torreyae Bonar					AF522183*	AY123284*
Coleosporium asterum (Dietel) Syd. & P. Syd.	*Solidago* sp. (Asteraceae)	USA: TN	M.C. Aime 2600	BPI 863448	DQ354559	DQ354558
Cronartium ribicola J.C. Fisch.	*Ribes* sp. (Grossulariaceae)	USA: VA	D.E. Farr & E. Farr s.n. (U-396)	BPI 871660	DQ354560	M94338*
Cumminsiella mirabilissima (Peck) Nannf.	*Mahonia aquifolium* Pursh (Berberidaceae)	Germany	G. Arnold s.n. (U-480)	BPI 871101	DQ354531	DQ354530
Dietelia portoricensis (Whetzel & L.S. Olive) Buriticá & J.F. Hennen	*Mikania micrantha* Kunth (Asteraceae)	Costa Rica	H. Evans s.n. (U-322)	BPI 844288	DQ354516	AY125414*
Endoraecium acaciae Hodges & D.E. Gardner	*Acacia koa* A. Gray (Fabaceae)	USA: HI	D.E. Farr & E. Farr, MCA2957	BPI 871098	DQ323916	DQ323917
Eocronartium musicola (Pers.) Fitzp.					AY512844*	AY123323*
Frommeëlla mexicana (Mains) J.W. McCain & J.F. Hennen	*Duchesnea* sp. (Rosaceae)	USA: MD	J. Hernandez & M.C. Aime, U-3	BPI 843392	DQ354553	DQ354552
Gymnosporangium clavipes (Cooke & Peck) Cooke & Peck	*Amelanchier canadensis* Medik. (Rosaceae)	USA: VA	M. Sogonov, MCA2568B	BPI 871102	DQ354545	DQ354546
Gymnosporangium juniperi-virginianae Schwein.	*Malus domestica* Borkh. (Rosaceae)	USA: VA	D.E. Aime & M.C. Aime 2776	BPI 871103	DQ354547	AY123289*
Helicobasidium purpureum Pat.					AY512846*	D85648*
Hemileia vastatrix Berk. & Broome	*Coffea arabica* L. (Rubiaceae)	Mexico	J. Hernandez 2002-004	BPI 843642	DQ354566	DQ354565
Kuehneola uredinis (Link) Arthur	*Rubus argutus* Link (Rosaceae)	USA: NC	M.C. Aime 2830	BPI 871104	DQ354551	AY123310*
Kweilingia divina (Syd.) Buriticá	*Bambusa* sp. (Poaceae)	Costa Rica	M.C. Aime 2887	BPI 871105	DQ354554	AY123288* (as *Dasturella*)
Maravalia cryptostegiae (Cummins) Y. Ono					n/a	AY125404*
Melampsora epitea Thüm.	*Salix* sp. (Salicaceae)	USA: WA	L. Roberts s.n. (U-563)	BPI 871106	DQ354564	AY123293*
Melampsora euphorbiae Castagne	*Euphorbia heterophylla* L. (Euphorbiaceae)	Oman	M. Deadman s.n. (U-681)	BPI 871135	DQ351722	AY123294*
Melampsoridium betulinum Kleb.	*Alnus* sp. (Betulaceae)	Costa Rica	M.C. Aime 2884	BPI 871107	DQ354561	AY125391*
Mikronegeria alba Oehrens & R.S. Peterson	*Nothofagus nervosa* Phil. (Fagaceae)	Argentina	detr. Havrilenko	PUR N1122	DQ354569	n/a
Miyagia pseudosphaeria (Mont.) Jørst.	*Sonchus oleraceus* L. (Asteraceae)	USA: CA	S.T. Koike s.n. (U-63)	BPI 842230	DQ354517	AY125411*
Naohidemyces vaccinii (G. Winter) Jørst.	*Vaccinium ovatum* Pursh (Ericaceae)	USA: WA	A.Y. Rossman, D. Feuillet, & M. Bair, MCA2780	BPI 871754	DQ354563	DQ354562
Olivea scitula Syd.	*Vitex doniana* Sweet (Lamiaceae)	Zambia	R.G. Kapooria s.n. (U-668)	BPI 871108	DQ354541	DQ354540
Phakopsora pachyrhizi Syd. & P. Syd.	*Glycine max* Merr. (Fabaceae)	Zimbabwe	O. Mhembere s.n. (U-644)	BPI 871755	DQ354537	DQ354536
Phakopsora tecta H. Jacks. & Holw.	*Commelina diffusa* Burm. f. (Commelinaceae)	Costa Rica	J. Hernandez 2003-137	BPI 843896	DQ354535	AY125397* (as *Physopella*)

Pileolaria brevipes Berk. & Ravenel	*Toxicodendron* sp. (Anacardiaceae)	USA: MN	R.W. Stack s.n. (U-607)	BPI 871761	DQ323924	AY123314*
Platygloea vestita Bourdot & Galzin					AY512872*	AY124480*
Prospodium lippiae (Speg.) Arthur	*Aloysia polystachya* (Griseb.) Moldenke (Verbenaceae)	Argentina	J. Hernandez 2001-015	BPI 843901	DQ354555	n/a
Puccinia caricis (Schumach.) Rebenh.	*Grossularia* sp. (Grossulariaceae)	USA: ND	R.W. Stack s.n. (U-193)	BPI 871515	DQ354514	DQ354515
Puccinia convolvuli Castagne	*Calystegia sepium* (L.) R. Br. (Convolvulaceae)	USA: MD	M.C. Aime 2778	BPI 871465	DQ354512	DQ354511
Puccinia coronata Corda	*Rhamnus cathartica* L. (Rhamnaceae)	USA: ND	R.W. Stack s.n. (U-244)	BPI 84300	DQ354526	DQ354525
Puccinia hemerocallidis Thüm.	*Hemerocallis* sp. (Hemerocallidaceae)	USA: AL	J. Olive s.n. (U-73)	BPI 843967	DQ354519	DQ354518
Puccinia hordei G.H. Otth	undetr. Poaceae	USA: CA	M.C. Aime 2391	BPI 871109	DQ354527	n/a
Puccinia menthae Pers. ex Pers.	*Cunila origanoides* (L.) Britton (Lamiaceae)	USA: MD	C. Park & M.C. Aime 2989	BPI 871110	DQ354513	AY123315*
Puccinia physalidis Peck	*Physalis lanceolata* Michx. (Solanaceae)	USA: ND	R.W. Stack s.n. (U-189)	BPI 844306	DQ354522	DQ354523
Puccinia podophylli Schwein.	*Podophyllum peltatum* L. (Berberidaceae)	USA: MD	J. Hernandez & M.C. Aime, U-2	BPI 842277	DQ354543	DQ354544
Puccinia smilacis Arthur	*Smilax rotundifolia* L. (Smilacaceae)	USA: MD	L. Castlebury s.n. (U-393)	BPI 871784	DQ354533	DQ354532
Puccinia violae (Schumach.) DC.	*Viola cucullata* Aiton (Violaceae)	USA: MD	J. Hernandez & M.C. Aime, U-4	BPI 842321	DQ354509	DQ354508
Pucciniosira pallidula (Speg.) Pers. Lagerh.	*Triumfetta semitriloba* Jacq. (Malvaceae)	Venezuela	R. Urtiaga 18	BPI 863541	DQ354534	n/a
Racospermyces koae (Arthur) J. Walker	*Acacia koa* A. Gray (Fabaceae)	USA: HI	M. Scholler & M.C. Aime 2961	BPI 871071	DQ323918	DQ323919
Ravenelia havanensis Arthur	*Enterolobium contortisiliquum* Morong. (Fabaceae)	Argentina	R. Berndt 5788	Z+ZT RB5788	DQ354557	DQ354556
Sphenospora kevorkianii Linder	*Stanhopea candida* Bab. Rodr. (Orchidaceae)	Peru	H. Ruiz, MIA 223837	BPI 863558	DQ354521	DQ354520
Trachyspora intrusa (Grev.) Arthur	*Alchemilla vulgaris* L. (Rosaceae)	Switzerland	L. Castlebury, MCA2384	BPI 843828	DQ354550	DQ354549
Tranzschelia discolor (Fuckel) Tranzschel & Litv.	*Prunus domestica* L. (Rosaceae)	Iran	R. Zare s.n. (U-510)	KR-0010966	DQ354542	AY125403*
Uromyces appendiculatus (Pers. ex Pers.) Unger	*Phaseolus vulgaris* L. (Fabaceae)	USA	J.R. Stavely #39	SBML & VL	AF522182*	DQ354510
Uromyces ari-triphylli (Schwein.) Seeler	*Arisaema triphyllum* (L.) Schott (Araceae)	USA: MD	D.E. Farr & E. Farr s.n. (U-637)	BPI 871111	DQ354529	DQ354528
Uromycladium fusisporum (Cooke & Massee) Savile	*Acacia salicina* Lindl. (Fabaceae)	Australia	R. Shivas s.n.	BRIP 27608	DQ323921	DQ354548

LSU, large subunit; SSU, small subunit

[a] BPI, US National Fungus Collections, Beltsville, MD, USA; BRIP, Plant Pathology Herbarium, Indooroopilly, Australia; KR, Staatliches Museum Für Naturkunde Karlsruhe, Karlsruhe, Germany; PUR, Arthur Herbarium, Purdue University, West Lafayette, IN, USA; SBML & VL, collection housed as frozen urediniospores at the Systematic Botany & Mycology Laboratory and Vegetable Laboratory, USDA-ARS, Beltsville, MD, USA; Z+ZT, Geobotanisches Institut, Zurich, Switzerland

[b] An asterisk (*) denotes sequence obtained from GenBank

Sampling strategy and sequence analyses

Sequencing reactions were edited and contiguous sequences were assembled in Sequencher v.4.1.4 (Gene Codes, Ann Arbor, MI, USA). An initial dataset of 630 sequences aligned across the first 500 bp of the 5′-region of the 28S were assembled into a single dataset. Sequence alignments were constructed by eye in Se-Al v2.0a11 (Andrew Rambaut, Zoology Department, University of Oxford, UK; http://evolve.zoo.ox.ac.uk/); these include representative taxa from all 13 Uredinales families fide Cummins and Hiratsuka (2003), representative taxa from 58 of 128 rust genera fide Cummins and Hiratsuka (2003), and ~500 rust species (duplicate sequences were obtained from additional collections for many taxa to confirm derived sequences and phylogenetic placements). Bootstrapping analyses using maximum-parsimony (MP) and neighbor-joining (NJ) were conducted in PAUP* version 4.0b10 (Swofford 2002).

Based on the results from the primary 28S dataset (trees not shown), 49 taxa were selected from across the breadth of the 28S-derived phylogenetic tree for combined 18S and 28S analyses. These included at least one representative of each of the 13 families fide Cummins and Hiratsuka (2003). Preference was given to include type taxa for families and genera wherever possible. Outgroups [*Helicobasidium purpureum* Pat., *Eocronartium muscicola* (Pers.) Fitzp., *Platygloea vestita* Bourdot & Galzin] were chosen from Urediniomycete taxa believed to be closely related to the rusts (Leppik 1955; Hiratsuka 1990; Cummins and Hiratsuka 2003). Approximately 1150 bp of 28S sequence data, covering divergent domains D1–D3 (Hopple and Vilgalys 1999) and all ~1750 bp of 18S for each exemplar taxon were combined into a single dataset, aligned in Se-Al, and analyzed in PAUP. A total of 317 bp (305 bp of the 28S and 12 bp of 18S) were too ambiguous to confidently align and were excluded from further analyses.

MP analyses were conducted in PAUP as heuristic searches with 100 random addition replicates and TBR branch swapping. Support for MP branching topologies was evaluated by bootstrap analysis derived from 10 000 replicates with 10 random addition replicates each. Maximum-likelihood (ML) analyses were conducted by the quartet puzzling method (Strimmer and von Haeseler 1996) in PAUP with 10 000 puzzling steps; transition/transversion ratio = 2.

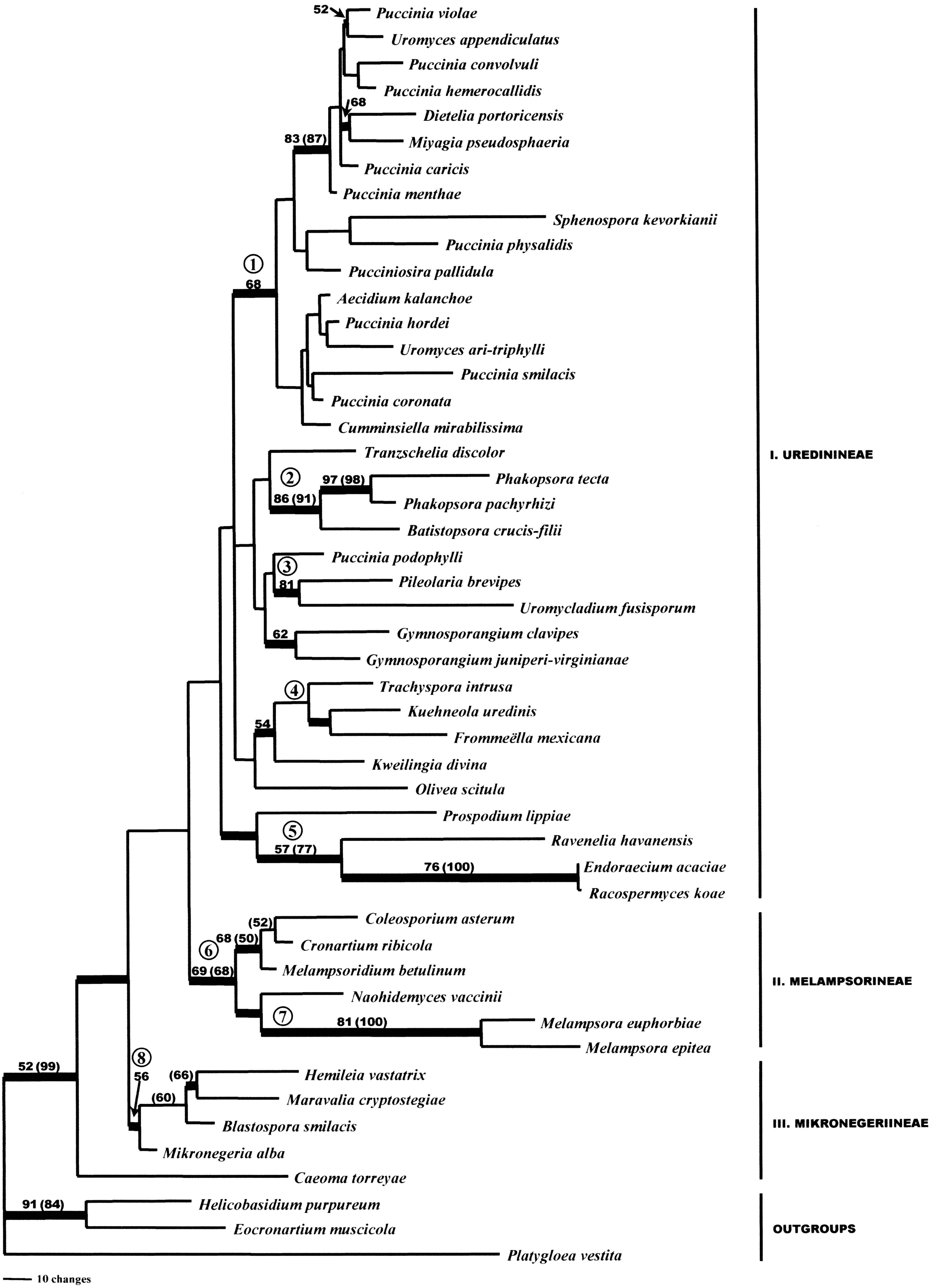
Results

Forty-six rust taxa from 34 genera representing all 13 families fide Cummins and Hiratsuka (2003) were sampled and analyzed for two rDNA genes (Fig. 1). A total of 2562 characters were included in the combined 18S and 28S analysis, of which 389 were parsimony informative and 312 were variable but parsimony uninformative. A single most parsimonious tree of length 1806 was found by MP; consistency index (CI) = 0.52; retention index (RI) = 0.55. The Uredinales appear monophyletic with three major rust lineages recovered (Fig. 1, I–III). Support was found for components of 8 established families, indicated by encircled numbers (in Fig. 1), with some revision. A few genera, *Tranzschelia* Arthur, *Gymnosporangium* R. Hedwig, and *Olivea* Arthur, could not be confidently assigned to any of the supported families with these data (Fig. 1). The position of *Olivea scitula* Syd. is conflicted: in MP analyses it is an unsupported member of crown lineage I; in ML analyses it forms a sister to the Mikronegeriaceae (Fig. 1, no. 8) in basal lineage III. When *O. scitula* is removed from this dataset, all three major lineages are strongly supported (not shown). In all cases, *Caeoma torreyae* Bonar is the most basal rust sampled (see Fig. 1).

Discussion

Many hypotheses regarding which may be the most primitive rusts have been proposed. The molecular study of Sjamsuridzal et al. (1999) refuted the fern rust hypothesis of Arthur (1924) and others, but sampling was too limited to determine the true ancestral rusts. Durrieu (1980) proposed *Melampsora* to be ancestral, and some support for this hypothesis was found with 28S sequence data (Maier et al. 2003). Alternatively, the short-cycled tropical members of the Chaconiaceae sensu Ono and Hennen (1983) (*Goplana* Racib., *Chrysocelis* Lagerh. & Dietel, *Chaconia* Juel, and *Olivea* Arthur) have been proposed as the most primitive rusts (Ono and Hennen 1983; Hart 1988). In earlier works, Leppik (e.g., 1955) proposed that the primitive rust genera were those he termed “stomatosporous,” i.e., short-cycled rusts with telia that emerge through the host stomata, such as *Desmella* H. & P. Syd. (Uropyxidaceae fide Cummins and Hiratsuka 2003), *Hemileia* Berk. & Broome (Chaconiaceae fide Cummins and Hiratsuka 2003), and *Gerwasia* Racib. (Phragmidiaceae fide Cummins and Hiratsuka 2003). In the present study, the anamorphic rust *Caeoma torreyae* was found to be the most basal rust sampled, with the Mikronegeriaceae, *Hemileia*, and *Maravalia cryptostegiae* (Cummins) Y. Ono (Chaconiaceae fide Cummins and Hiratsuka 2003), forming the remainder of basal lineage III (see Fig. 1, no. 8). Thus lineage III, herein defined as suborder Mikronegeriineae, contains an assemblage of rusts that have not been allied in any previous classification; these are discussed further under the Mikronegeriaceae below.

Fig. 1. The single most parsimonious tree recovered from combined 28S and 18S sequence data. A *thickened branch* indicates a node recovered by both maximum-likelihood (ML) and maximum-parsimony (MP) methods. *Numbers above a branch* represent support >50% for those nodes: the *first number* represents the quartet puzzling reliability score; bootstrapping values for MP are shown in *parentheses*. *Circled numbers* indicate lineages referred to in the text


52
Puccinia violae
Uromyces appendiculatus
Puccinia convolvuli
Puccinia hemerocallidis
68
Dietelia portoricensis
Miyagia pseudosphaeria
83 (87)
Puccinia caricis
Puccinia menthae
Sphenospora kevorkianii
Puccinia physalidis
①
68
Pucciniosira pallidula
Aecidium kalanchoe
Puccinia hordei
Uromyces ari-triphylli
Puccinia smilacis
Puccinia coronata
Cumminsiella mirabilissima
Tranzschelia discolor
②
97 (98)
Phakopsora tecta
86 (91)
Phakopsora pachyrhizi
Batistopsora crucis-filii
Puccinia podophylli
③
81
Pileolaria brevipes
Uromycladium fusisporum
62
Gymnosporangium clavipes
Gymnosporangium juniperi-virginianae
④
Trachyspora intrusa
54
Kuehneola uredinis
Frommeëlla mexicana
Kweilingia divina
Olivea scitula
Prospodium lippiae
⑤
57 (77)
Ravenelia havanensis
76 (100)
Endoraecium acaciae
Racospermyces koae
(52)
Coleosporium asterum
68 (50)
Cronartium ribicola
⑥
69 (68)
Melampsoridium betulinum
Naohidemyces vaccinii
⑦
81 (100)
Melampsora euphorbiae
Melampsora epitea
⑧
52 (99)
56
(66)
Hemileia vastatrix
(60)
Maravalia cryptostegiae
Blastospora smilacis
Mikronegeria alba
Caeoma torreyae
91 (84)
Helicobasidium purpureum
Eocronartium muscicola
Platygloea vestita
10 changes
I. UREDININEAE
II. MELAMPSORINEAE
III. MIKRONEGERIINEAE
OUTGROUPS

The other two lineages resolved (see Fig. 1; I, II) most closely correspond to the two-meta-family system of Dietel (1928) and others (Arthur 1934; Bessey 1950). Lineage II, Dietel's Melampsoraceae, herein defined as suborder Melampsorineae, contains rusts placed in the Melampsoraceae, Pucciniastraceae, Coleosporiaceae, and Cronartiaceae fide Cummins and Hiratsuka (2003). The Melampsorineae contains the fern rusts and many important pathogens of conifers. A unifying feature of these rusts is that the aecial stage, when present, is typically formed on members of the Pinaceae. Lineage I, herein defined as suborder Uredinineae, contains Dietel's (1928) Pucciniaceae with the exclusion of the rusts that belong to the Mikronegeriineae. Rusts in this suborder that form aecia do so on angiosperms. Many researchers have subdivided the Pucciniaceae *sensu* Dietel into various segregate families (Hennen and Buriticá 1980; Hart 1988). The system of Cummins and Hiratsuka (2003) divides this group into nine families: Mikronegeriaceae, Phakopsoraceae, Chaconiaceae, Uropyxidaceae, Pileolariaceae, Raveneliaceae, Phragmidiaceae, Pucciniaceae, and Pucciniosiraceae, primarily based on spermogonia type. Topology within this lineage is less resolved than for the other two, yet at least five clades are recovered that correspond, with some revision, to the Pucciniaceae, Phakopsoraceae, Pileolariaceae, Phragmidiaceae, and Raveneliaceae fide Cummins and Hiratsuka (2003). The Pucciniosiraceae is found to be confamilial with the Pucciniaceae. Both the Chaconiaceae (represented here by *Olivea*, *Hemileia*, and *Maravalia* Arthur) and Uropyxidaceae (represented by *Tranzschelia*, and *Prospodium* Arthur) appear polyphyletic (see Fig. 1). Preliminary 28S data (not presented) place some members of *Chaconia* within the Raveneliaceae. However, until type genera and species can be studied, the status for both of these families remains unresolved. A discussion of each resolved family follows.

Pucciniaceae Chevall

The Pucciniaceae (Fig. 1, no. 1) forms the crown group of extant rusts and contains ~4000 of the ~7000 described species (Kirk et al. 2001). Fifteen genera are placed here by Cummins and Hiratsuka (2003). These analyses do not confirm the placement of 1 of these, *Gymnosporangium*, within the Pucciniaceae (see Fig. 1). A few species currently placed in *Puccinia* Pers. ex Pers. have affinities elsewhere (e.g., *P. podophylli* Schwein., Fig. 1), but the vast majority belong to this family. Other genera whose placement in the family is confirmed with these data are *Cumminsiella* Arthur, *Miyagia* Miyabe ex H. & P. Syd., and *Uromyces* (Link) Unger. The anamorphic rust *Aecidium kalanchoe* J.R. Hern. belongs to this family, as is expected for most *Aecidium* spp. (Cummins and Hiratsuka 2003). The large genera *Puccinia* and *Uromyces* are not monophyletic, as has been noted elsewhere (Savile 1978; Maier et al. 2003).

Two genera from the Pucciniosiraceae have been sampled (*Dietelia* Henn. and *Pucciniosira* Lagerh.). The Pucciniosiraceae is an artificial family of endocyclic rusts (Cummins and Hiratsuka 2003). Placement of the two species sampled here, including *Pucciniosira pallidula* (Speg.) Lagerh. [=*P. triumfettae* Lagerh., the type of *Pucciniosira* (Buriticá and Hennen 1980)] confirms the hypothesis of Buriticá and Hennen (1980) that most if not all the Pucciniosiraceae will eventually be found to have affinities within the Pucciniaceae. Similar to *Endophyllum* Lév. (Pucciniaceae), these are most likely polyphyletic taxa derived from various Pucciniaceae ancestors, including *Endophyllum*-like forms (Jackson 1931).

The placement of *Sphenospora kevorkianii* Linder (Raveneliaceae fide Cummins and Hiratsuka 2003) within this family was unexpected. *Sphenospora kevorkianii* is a parasite of orchids (Linder 1944). Most taxa currently placed in the genus occur on other monocots (Linder 1944; Cummins and Hiratsuka 2003), whereas most members of the Raveneliaceae parasitize fabaceous hosts in subfamily Mimosoideae. Sampling from the type species *S. pallida* (G. Winter) Dietel is needed to resolve the status of this genus, which most likely is allied with the Pucciniaceae rather than the Raveneliaceae.

In all analyses the genus *Gymnosporangium* is resolved as a monophyletic group separate from the Pucciniaceae, which was also found by Maier et al. (2003) using different taxa. *Gymnosporangium* is unusual in that the members of this genus are the only rusts that form their telia on gymnosperms, on members of the Cupressaceae (Leppik 1973). Thus far, the genus holds a rather isolated position in phylogenetic studies and may represent a separate family-level lineage of rusts within the Uredinineae.

Phakopsoraceae (Arthur) Cummins & Y. Hirats

The Phakopsoraceae contains a morphologically diverse group of 12 (Buriticá and Hennen 1994) to 13 (Cummins and Hiratsuka 2003) different teleomorphic genera and 10 (Buriticá and Hennen 1994) different anamorphic-form genera. Representatives from three of these – *Batistopsora* Dianese, Medeiros & Santos, *Kweilingia* Teng., and *Phakopsora* Dietel – were sampled for this study. Additional species of *Phakopsora* were sampled in the extended 28S analyses (not presented). All analyses to date indicate that the family and the genus *Phakopsora* itself are polyphyletic, divided into two monophyletic but unrelated lineages [Fig. 1, no. 2 and *K. divina* (Syd.) Buriticá]. The genus *Phakopsora* contains at least 90 morphologically variable species (Ono et al. 1992; Cummins and Hiratsuka 2003) and several genera have been segregated from or synonymized with it (Mains 1934; Cummins and Ramachar 1958; Ono et al. 1992; Buriticá and Hennen 1994). The type species of *Phakopsora*, *P. punctiformis* (Barclay & Dietel) Dietel (on Rubiaceae), must be sampled to determine the taxonomic status of these two lineages.

The genus *Angiopsora* Mains was erected to accommodate *Phakopsora*-like species on Poaceae (Mains 1934). Although *Angiopsora* has been synonymized with *Physopella* Arthur (Cummins and Ramachar 1958), which in turn is considered synonymous with *Phakopsora*

(Cummins and Hiratsuka 2003), analysis of the type species is warranted to ascertain whether this genus represents the sister to *Kweilingia*, forming a distinct lineage of *Phakopsora*-like species on grass hosts. However, of the additional species of *Phakopsora* that have been sampled with 28S data, only those on Poaceae thus far are sisters to *K. divina* (also on Poaceae); thus, it is likely that clade no. 2 (see Fig. 1) contains the true Phakopsoraceae.

Pileolariaceae (Arthur) Cummins & Y. Hiratsuka

Cummins and Hiratsuka (2003) place four genera in this family: *Atelocauda* Arthur & Cummins, *Pileolaria* Castagne, *Uromycladium* McAlpine, and *Endoraecium* Hodges & D.E. Gardner (an endocyclic genus). A fifth genus, *Racospermyces* J. Walker, has recently been segregated from *Atelocauda* (Walker 2001). All but *Atelocauda* were sampled in this study. Contrary to the findings of Wingfield et al. (2004), these analyses support a monophyletic Pileolariaceae s.s., containing *Pileolaria* and *Uromycladium* (Fig. 1, no. 3). *Racospermyces* and *Endoraecium*, on the other hand, are more closely allied with other mimosoid rusts in the Raveneliaceae, which is discussed in Scholler and Aime (2006).

Phragmidiaceae Corda

This is a well-circumscribed family of nine genera, most or all autoecious on Rosaceae, primarily on subfamily Rosoideae (Cummins and Hiratsuka 2003). Monophyly of the Phragmidiaceae has been established with 28S sequence data for four genera (Maier et al. 2003) and for seven genera (not presented) and with three generic representatives (*Frommeëlla* Cummins & Y. Hirats. and *Kuehneola* Magnus, *Trachyspora* Fuckel) in the two-gene analysis of this study (Fig. 1, no. 4). Also included in this family are at least some species of *Triphragmium* Link (Maier et al. 2004; and unpresented 28S data). *Triphragmium* is currently placed in the Raveneliaceae based on spermogonial characteristics (Cummins and Hiratsuka 2003), and there are two species on Fabaceae that may indeed be allied with that family. However, the type species *T. ulmariae* (DC.) Link and three others parasitize the Rosoideae (Cummins and Hiratsuka 2003) and belong to the Phragmidiaceae as hypothesized by Savile (1968).

Raveneliaceae (Arthur) Leppik

The Raveneliaceae is a large family of 21 genera (Cummins and Hiratsuka 2003) containing many rusts on Mimosoideae (Fabaceae) that have been traditionally circumscribed by morphology. Results show that species from two genera on nonleguminous hosts – *Sphenospora* and *Triphragmium* – should be reassigned to the Pucciniaceae and Phragmidiaceae, respectively, whereas two other genera – *Racospermyces* and *Endoraecium* – both parasitic on mimosoids but currently assigned to the Pileolariaceae, are allied here (Fig. 1, no. 5). This finding is consistent with a reinterpretation of the family to include primarily rusts that have evolved on mimosoid hosts. For instance, preliminary 28S analyses (not presented) indicate that *Chaconia* is polyphyletic, which has been predicted (Thirumalachar and Cummins 1949; Thirumalachar and Mundkur 1949a). Of the species sampled, those that infect legumes are allied with *Ravenelia* Berk. and not with other genera currently placed in the Chaconiaceae. The type, *C. alutacea* Juel, although not sampled, also occurs on a mimosoid host, which might indicate that the Chaconiaceae are confamilial with the Raveneliaceae. Certainly, much additional sampling is required from among the other genera currently placed in both of these families to fully resolve the limits of the Raveneliaceae and deposition of extrafamilial genera and species currently allied here.

Coleosporiaceae Dietel

The rusts in this group have been segregated from Dietel's (1928) Melampsoraceae and subsequently subdivided into as many as four segregate families (Leppik 1972). Currently, they are placed in three families, Coleosporiaceae (three genera), Cronartiaceae (two genera, one endocyclic), and Pucciniastraceae (nine genera), fide Cummins and Hiratsuka (2003). Molecular studies show that these rusts are confamilial (Fig. 1 and unpresented 28S data; Maier et al. 2003).

Of the four (Leppik 1972) family names available for this group, two have priority: Coleosporiaceae Dietel (1900) and Cronartiaceae Dietel (1900). Dietel (1928) later revised his classification, including Coleosporiaceae and Cronartiaceae within the Melampsoraceae. However, the Coleosporiaceae was used by Raciborski (1909, as Coleosporieae) and by Sydow and Sydow (1915), who place members of the Cronartiaceae within the Melampsoraceae, thus giving Coleosporiaceae priority over Cronartiaceae (Greuter et al. 2000). In the present study, the Coleosporiaceae appears paraphyletic (Fig. 1, no. 6) with the Melampsoraceae. Additional studies are needed to confirm the reciprocal monophyly of the Coleosporiaceae and Melampsoraceae.

Melampsoraceae Dietel

This is a monotypic family of mostly heteroecious rusts that form telia on members of the Salicaceae or Euphorbiaceae. This clade (see Fig. 1, no. 7) has been recovered in all analyses, including Maier et al. (2003) and Wingfield et al. (2004).

Mikronegeriaceae Cummins & Hirats

Teliospores of *Mikronegeria alba* Oehrens & R.S. Peterson are so poorly developed and uncharacteristic of Uredinales that they have been interpreted as nonexistent. Instead of forming a distinguishable teliospore, *M. alba* produces metabasidia by apical elongation of simple, clavate probasidia (Peterson and Oehrens 1978). This simple mode of reproduction and the absence of conventional telio-spores has been interpreted as evidence to suggest this taxon shares more affinities with the Auriculariales than Uredinales (Peterson and Oehrens 1978), but other researchers suggest that morphologically simple short-cycled rusts are derived from the convergent influence of a secondarily tropical existence rather than indicative of "primitive" status (Savile 1978). Cummins and Hiratsuka (1983) created the monotypic Mikronegeriaceae to accommodate this unique taxon. The family concept has since expanded to include other rusts that have type 12 spermogonia (Hiratsuka and Hiratsuka 1980), *Blastospora* Dietel and *Chrysocelis* Lagerh. & Dietel (Cummins and Hiratsuka 2003). Molecular data consistently place *M. alba* within a lineage that includes *Blastospora smilacis* Dietel, *Hemileia vastatrix* Berk. & Broome, and *Maravalia cryptostegiae* (Cummins) Y. Ono (Chaconiaceae fide Cummins and Hiratsuka 2003) near the base of the Uredinales (see Fig. 1, no. 8).

The classification of *Hemileia* has been difficult, but it has recently been allied with the Chaconiaceae (Cummins and Hiratsuka 2003). Ono et al. (1986) recognized affinities of this taxon with *B. smilacis*, including similar modes of spore production within the sori. Thirumalachar and Mundkur (1949a) suggested *Blastospora* was related to Dietel's (1928) tribe Hemileiae of the Pucciniaceae. The members of *Hemileia* produce unusual urediniospores, termed "hunchback" (Cummins and Hiratsuka 2003), that probably indicate its monophyly. No spermogonial stages have been discovered for any of the ~50 known species of *Hemileia* (Cummins and Hiratsuka 2003), or for *Maravalia cryptostegiae*, which has a similar life cycle to *H. vastatrix* (Evans 1993). The classification for *Maravalia* has been equally problematic, and the genus has been formally transferred from the Raveneliaceae to the Chaconiaceae, although its true affinities remain obscure (Ono 1984), and it is potentially a polyphyletic genus (Cummins and Hiratsuka 2003). This study strongly supports the placement of *Hemileia* and *M. cryptostegiae* within the Mikronegeriaceae (Fig. 1, no. 8). The newly described monotypic genus *Desmosorus* A. Ritschel, Oberw. & Berndt (2005), a Central and South American orchid rust with suprastomatal sori and *Hemileia*-like urediniospores and no known spermogonial stage, is probably also allied within the Mikronegeriaceae. *Olivea scitula*, another chaconiaceous rust for which the spermogonial stage is unknown (Ono and Hennen 1983), forms part of this lineage in ML analyses but not in MP analyses.

All analyses consistently place *Caeoma torreyae* as the most basal of the Uredinales sampled (Fig. 1). No telial stage is known for *C. torreyae*, which produces spermogonia on *Torreya californica* Torr. (Taxales: Taxaceae) (Bonar 1951). Two known teleomorphic rusts produce spermogonia on non-Pinaceae gymnosperms: *Mikronegeria alba* (Cupressaceae) and *M. fagi* (Dietel & Neger) Dietel (Araucariaceae) (Peterson and Oehrens 1978). Similarities in the simple spermogonia of these three taxa have been previously noted (Peterson and Oehrens 1978).

In conclusion, the data presented in this study indicate that rust phylogeny, at least at the family level, has been strongly influenced by host associations, and that morphological characters typically emphasized in rust taxonomy are often the result of convergent evolution coupled with the plastic life cycles typical of the order. The findings that the Mikronegeriaceae along with some short-cycled chaconiaceous species and *C. torreyae* represent the most basal rusts sampled suggests that the ancestors to the extant rusts may have been tropical species with simple teliospores. The earliest probable fossil record for a rust spore dates to ~300 mya (Tiffney and Barghoorn 1974), which is considerably older than molecular clock-based estimates of ~150 mya (Wingfield et al. 2004). The association between the basalmost rusts in these analyses and gymnosperm lineages suggest an estimate for the extant rusts of radiation in the Triassic (~250 mya) concurrent with the rise of the Araucariaceae and Taxales, and predating the breakup of Pangaea.

Taxonomy

Uredinineae Aime, subord. nov.

Familia typica: Pucciniaceae Chevall. [as "Puccinieae"], Flore Gén. Env. Paris 413 (1826).

Biologia variabilis. Spermogonia e turma VI (typis 5, 7), V (4), et IV (6, 8, 10, 11). Aecia heteroecia in angiospermas. Aeciosporae variabiles. Uredinia variabilia. Urediniosporae variabiles. Telia variabilia. Teliosporae typice pedicellatae, 1 multicellulares.

Life cycle variable. Spermogonia Group VI (type 5, 7), Group V (type 4), and Group IV (6, 8, 10, 11). Aecia of heteroecious species on angiosperms. Aeciospores, uredinia, urediniospores, and telia variable. Teliospores typically pedicellate, 1- to multicelled.

Melampsorineae Aime, subord. nov.

Familia typica: Melampsoraceae Dietel, in Engler and Prantl, Nat. Pflanzenfam. 1(1**): 38 (1897).

Plerumque heterociae et macrocyclicae. Spermogonia e turma 1 (typis 1,2,3) vel II (9). Aecia heteroecia in Pinaceas, pro parte maxima in *Peridermium* typo vel *Caeoma* typo (interdum Milesia typo). Uredinia-variabilia. Urediniosporae typice echinulatae. Telia variabilia. Teliosprae typice sessiles non quiescentes, basidiis externis.

Mostly heteroecious and macrocyclic. Spermogonia Group I (type 1, 2, 3) or Group II (type 9). Aecia of heteroecious species on Pinaceae, mostly *Peridermium* type or *Caeoma* type (occasionally *Milesia* type). Uredinia variable. Urediniospores typically echinulate. Telia variable. Teliospores typically sessile; basidia usually external and germinating without dormancy.

Mikronegeriineae Aime, subord. nov.

Familia typica: Mikronegeriaceae Cummins & Hirats., Illus. Genera Rust Fungi. Rev. ed.: 13 (1983).

Biologia vulgo maxima ignota. Spermogonia e turma III typo 12 (et fortasse V 4) ubi cognita. Aecia ubi cognita typice, sed non semper, in arboribus coniferis non-Pinaceis. Aeciosporae catenulatae. Uredinia pro parte maxima e *Uredo* wel *Wardia* typis. Urediniosporae vulgo asymmetricae, typice supra stomata, pori obscure. Telia typice similia urediniis. Teliosporae sessiles vel brevipedicellatae, 1-cellulares, pallidae, tenuibus parietibus, typice supra stomata; basidia externa vel semiinterna, typicenon quiescentes, germinantes per apicalem extensionem.

Life cycles incompletely known for many. Spermogonia Group III type 12 (and possibly Group V, type 4) where known. Aecia where known typically, but not always, on non-Pinaceae conifers. Aeciospores catenulate. Uredinia mostly *Uredo*- or *Wardia* type. Urediniospores usually asymmetrical, typically suprastomatal, pores obscure. Telia typically as uredinia. Teliospores sessile or short-pedicillate, 1-celled, pale, thin-walled, typically suprastomatal; basidia external or semi-internal, typically germinating without dormancy by apical extension.

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