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Taxonomy of mayapple rust: the genus *Allodus* resurrected

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Abstract: Mayapple rust is a common, disfiguring disease that is widespread in temperate eastern North America wherever the host, *Podophyllum peltatum*, occurs. *Puccinia podophylli*, the etiological agent of this rust, has been shown to be distantly related to both *Puccinia* and *Uromyces* as exemplified by their types. A systematic study was made to determine the generic classification of *P. podophylli*. Phylogenetic analyses of two rDNA loci from multiple specimens support the recognition of this taxon as a separate genus of Pucciniaceae. Based on historical literature and type material, *P. podophylli* was found to represent the type of the forgotten genus *Allodus* and it is correctly named *Allodus podophylli*. A neotype is designated for *Puccinia podophylli* Schwein. (≡ *Allodus podophylli*) and a lectotype is designated for *Aecidium podophylli*.

Key words: autoecious rust fungi, Berberidaceae, fungal taxonomy, Pucciniales, rDNA systematics, Uredinales

INTRODUCTION

The fungus that causes mayapple rust, known as *Puccinia podophylli*, is widespread (Farr and Rossman 2011) and well known in eastern parts of Canada and the United States. This species is easily recognized in the field (FIG. 1), and several works have provided excellent descriptive accounts (e.g. Arthur 1921, 1934; Parmelee and de Carteret 1984).

Recent progress toward an understanding of the phylogeny of rust fungi has shown that parts of the current classification of rusts are artificial (Aime 2006). The two largest genera, *Puccinia* Pers. and *Uromyces* (Link) Unger (Cummins and Hiratsuka 2003), have proven to be especially problematic in this regard because these two genera do not consist of discrete, well defined clades as presently circumscribed (e.g. Aime 2006, Merwe et al. 2007, Zuluaga et al. 2011). Cummins and Hiratsuka (2003) recognized that the generic circumscription for these most likely delimited artificial groups, but they nonetheless advocated the separation of *Puccinia* and *Uromyces* based on morphology of the teliospores due to convenience and historical reasons. Even with a better understanding of rust phylogeny, not much has changed for these genera in current taxonomic practice because no one has produced a phylogeny-based classification for *Puccinia* and *Uromyces* that addresses the problem of artificial groups.

Puccinia podophylli is distantly related to the large clades containing most species of *Puccinia* and *Uromyces* (Aime 2006, Zuluaga et al. 2011). These large clades include the type species of these genera, *P. graminis* Pers. and *U. appendiculatus* F. Strauss (Merwe et al. 2007). Thus, this study was conducted to determine the generic placement of *P. podophylli*. It included examination of type specimens and a phylogenetic analysis of 56 rust taxa using two nuclear rDNA loci. Based on the results, it appears that *Allodus* is an appropriate genus for this species that is now accepted as *Allodus podophylli*.

MATERIALS AND METHODS

Taxon sampling.—New specimens were collected, dried in a plant press and deposited at the U.S. National Fungus Collections (BPI). Additional historical material that was studied is housed at BPI. Herbarium acronyms are those of Thiers (2011).

Morphology.—Microscopic characters were observed by light microscopy. Herbarium materials were rehydrated and viewed in 3% KOH. Whenever possible, a minimum of 20 structures per collection were measured.

DNA extraction, amplification and sequencing.—DNA was extracted according to the protocol outlined by Aime (2006) using the UltraClean Plant DNA Isolation Kit (MoBio Laboratories, Solana Beach, California). Portions of the ITS2 and LSU rDNA region were amplified with Rust2inv/LR6 (Aime 2006, Vilgalys and Hester 1990). Unpurified PCR product was sent to Beckman Coulter

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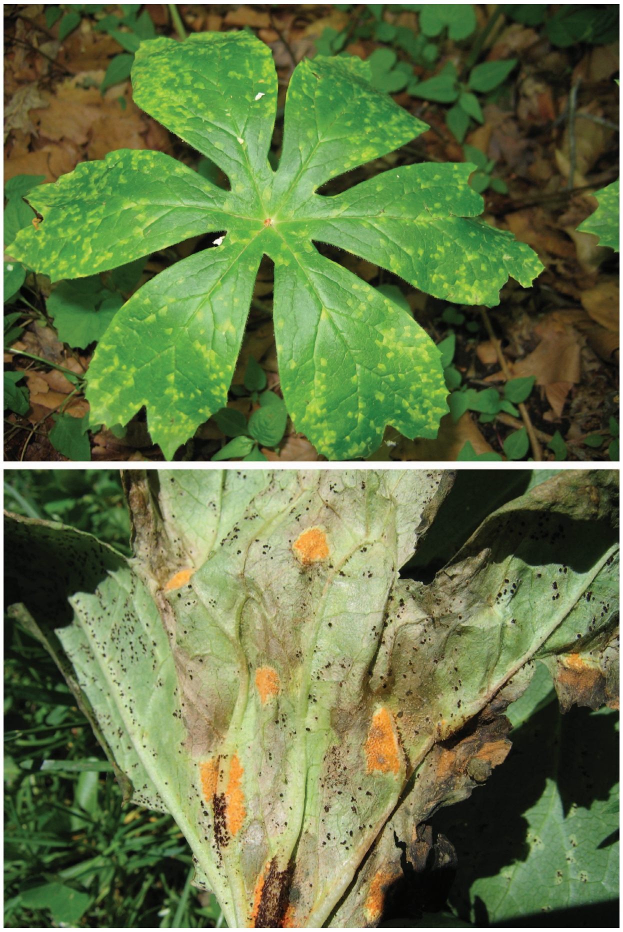

FIG. 1. *Allodus podophylli* on *Podophyllum peltatum* in the field (BPI 871630).

sequencing (Danvers, California) and sequenced with the same primers used for amplification. Sequence data were deposited in GenBank (TABLE I).

Phylogenetic analyses.—Sequence alignment and editing was undertaken in the MEGA software package (Kumar et al. 2008) using the MUSCLE algorithm (Edgar 2004). The nucleotide alignments were deposited as Nexus files in TreeBASE (S12008). The final dataset consisted of 56 rust taxa with *Helicobasidium purpureum* (Helicobasidiales) and *Eocronartium musicola* (Platygloeales) selected as outgroups because these have been shown to be the sister groups of the rusts (Aime et al. 2006). Rust taxa were selected to represent every major lineage within the Pucciniales recovered in phylogenetic analyses (e.g. Aime 2006, Dixon et al. 2010). The supermatrix consisted of 3010 characters, including LSU sequences for all taxa (1303 nucleotides) and SSU sequences for 45 of the taxa (1706 nucleotides) (TABLE I).

RAxML (Stamatakis 2006) was used to search for the best-scoring likelihood tree with a rapid bootstrap analysis (command -f a). The model of evolution specified was GTRMIX, which uses an accelerated algorithm to calculate maximum likelihood bootstrap values and uses a GTRGAMMA model of evolution to calculate the final tree topology (Stamatakis et al. 2008). The analyses were run with a random starting tree and with 1000 maximum likelihood bootstrap replicates.

A parsimony analysis was implemented with PAUP* 4.0b10 (Swofford 2000) using a heuristic search with 1000 random additions and TBR branch swapping. Bootstrap support was determined with 500 replicates using a heuristic search and TBR branch swapping, with the MAXTREES option set at 5000.

RESULTS

Data matrix and phylogenetic analysis.—The four sequenced isolates of *Puccinia podophylli* had identical sequences in the ITS2-LSU region. Phylogenetic analyses of the combined LSU and SSU data using maximum likelihood and parsimony criteria consistently recovered a strongly supported Pucciniaceae, consisting of three major clades (FIG. 2), a result similarly recovered by Dixon et al. (2010). The genus *Puccinia* is polyphyletic, with the type species of *Puccinia*, *P. graminis*, belonging to Pucciniaceae group II (FIG. 2). Although not supported, *P. podophylli* appears to hold a basal position within the suborder Uredinineae Aime, related only distantly to other Pucciniaceae (FIG. 2).

TAXONOMY

Allodus Arthur, Résultats Scientifiques du Congrès International de Botanique Vienne 1905:345. 1906.

Typus genericus: Allodus podophylli (Schwein.) Arthur

Allodus podophylli (Schwein.) Arthur, Résultats Scientifiques du Congrès International de Botanique Vienne 1905:345. 1906. FIG. 3

≡ *Puccinia podophylli* Schwein., Schriften Naturf. Ges. Leipzig 1:72. 1822.

Neotypus of *Puccinia podophylli* Schwein. (hic designatus): USA. MARYLAND: Catoctin Mountains, Cunningham Falls, on *Podophyllum peltatum*, 30 Apr 2003, leg. *M.C. Aime* and *J.R. Hernández*, *JRH-2003-001*, U-00002 (BPI 842277, ITS2-LSU: DQ354453, SSU: DQ354544).

≡ *Dicaeoma podophylli* (Schwein.) Kuntze, Revisio Generum Plantarum 3:470. 1898.

≡ *Puccinia aculeata* Link, Species Plantarum 6:79. 1825. Note: This is nom. illeg. via superfluous (McNeill et al. 2006, ICBN Art. 52). The epithet '*podophylli*' should have been maintained in *Puccinia*.

Anamorph names:

Aecidium podophylli Schwein., Schriften Naturf. Ges. Leipzig 1:66. 1822.

TABLE I. Taxa used in phylogenetic analysis, voucher number, GenBank number and source. Author citations follow Index Fungorum. Source of LSU followed by source of SSU when sources differ

Name	GenBank LSU	GenBank SSU	Source
Aecidium kalanchoe J.R. Hern.	AY463163	DQ354524	Hernandez et al. (2004), Aime (2006)
Allodus podophylli (Schwein.) Arthur (BPI 844307)	JQ423258	N/A	This study
Allodus podophylli (BPI 844308)	JQ423259	N/A	This study
Allodus podophylli (BPI 878056)	JQ423260	N/A	This study
Allodus podophylli (BPI 842277)	DQ354543	DQ354544	Aime (2006)
Batistopsora crucis-filii Dianese, R.B. Medeiros & L.T.P. Santos	DQ354539	DQ354538	Aime (2006)
Blastospora smilacis Dietel	DQ354568	DQ354567	Aime (2006)
Caeoma torreyae Bonar	AF522183	AY123284	Szaro and Bruns unpubl., Wingfield et al. (2004)
Chrysomyxa arctostaphyli Dietel	AF522163	AY123285	Szaro and Bruns unpubl., Wingfield et al. (2004)
Coleosporium asterum (Dietel) Syd. & P. Syd.	DQ354559	DQ354558	Aime (2006)
Cronartium ribicola A. Dietr.	DQ354560	M94338	Aime (2006), Bruns et al. (1992)
Cumminsiella mirabilissima (Peck) Nannf.	DQ354531	DQ354530	Aime (2006)
Dietelia portoricensis (Whetzel & L.S. Olive) Buriticá & J.F. Hennen	DQ354516	AY125414	Aime (2006), Wingfield et al. (2004)
Endocronartium harknessii (J.P. Moore) Hirats.	AF522175	M94339	Szaro and Bruns unpubl., Bruns et al. (1992)
Endoraecium hawaiiense Hodges & D.E. Gardner	DQ323916	DQ323917	Scholler and Aime (2006)
Endoraecium koae (Arthur) M. Scholler & Aime	DQ323918	DQ323919	Scholler and Aime (2006)
Eocronartium muscicola (Pers.) Fitzp.	AY512844	DQ241438	Begerow et al. unpubl., Henk and Vilgalys (2007)
Gymnoconia peckiana (Howe) Trotter	GU058010	N/A	Dixon et al. (2010)
Helicobasidium purpureum (Tul.) Pat.	AY885168	D85648	Matheny and Hibbet unpubl., Kuninaga unpubl.
Hemileia vastatrix Berk. & Broome	DQ354566	DQ354565	Aime (2006)
Hyalopsora polypodii (Pers.) Magnus	AF426229	AB011016	Maier et al. (2003), Sjamsuridzal et al. (1999)
Kuehneola uredinis (Link) Arthur	DQ354551	DQ092919	Aime (2006), Matheny and Hibbet unpubl.
Melampsora euphorbiae (Ficinus & C. Schub.) Castagne	DQ437504	DQ789986	Aime (2006), Matheny et al. (2006)
Melampsoridium betulinum (Pers.) Kleb.	DQ354561	AY125391	Aime (2006), Wingfield et al. (2004)
Miyagia pseudosphaeria (Mont.) Jørst.	DQ354517	AY125411	Aime (2006), Wingfield et al. (2004)
Naohidemyces vaccinii (Jørst.) S. Sato, Katsuya & Y. Hirats.	DQ354563	DQ354562	Aime (2006)
Olivea scitula Syd.	DQ354541	DQ354540	Aime (2006)
Phakopsora pachyrhizi Syd. & P. Syd.	DQ354537	DQ354536	Aime (2006)
Phakopsora tecta H.S. Jacks. & Holw.	DQ354535	N/A	Aime (2006)
Phragmidium rubi-idaei (DC.) P. Karst.	AF426215	AY125405	Maier et al. (2003), Wingfield et al. (2004)
Phragmidium tormentillae Fuckel	DQ354553	DQ354552	Aime (2006)
Pileolaria toxicodendri (Berk. & Ravenel) Arthur	DQ323924	AY123314	Scholler and Aime (2006), Wingfield et al. (2004)
Puccinia caricis (Schumach.) Rebent.	DQ354514	DQ354515	Aime (2006)
Puccinia convolvuli (Pers.) Castagne	GU058018	DQ354511	Dixon et al. (2010), Aime (2006)
Puccinia coronata Corda	DQ354526	DQ354525	Aime (2006)
Puccinia graminis Pers.	AF522177	N/A	Bruns et al. (1992)
Puccinia hemerocallidis Thüm.	GU058020	DQ354518	Dixon et al. (2010), Aime (2006)
Puccinia heucherae (Schwein.) Dietel	DQ359702	N/A	Henricot et al. (2006)
Puccinia hordei G.H. Otth	DQ354527	DQ831030	Aime (2006), Matheny et al. (2006)
Puccinia menthae Pers.	DQ354513	AY123315	Aime (2006), Wingfield et al. (2004)
Puccinia poarum E. Nielsen	DQ831028	DQ831029	Matheny et al. (2006)
Puccinia polysora Underw.	GU058024	N/A	Dixon et al. (2010)
Puccinia smilacis Schwein.	DQ354533	DQ354532	Aime (2006)
Puccinia sp. MCA2969	GU058025	N/A	Dixon et al. (2010)
Puccinia sp. MCA3259	GU058026	N/A	Dixon et al. (2010)
Puccinia triticina Eriks.	DQ664194	N/A	Deadman et al. (2007)
Puccinia violae (Schumach.) DC.	DQ354509	DQ354508	Aime (2006)
Puccinia windsoriae Schwein.	GU057995	N/A	Dixon et al. (2010)
Pucciniastrum epilobii G.H. Otth	AF522178	AY123303	Szaro and Bruns unpubl., Wingfield et al. (2004)
Pucciniosira solani Lagerh.	EU851137	N/A	Zuluaga et al. (2011)

TABLE I. Continued

Name	GenBank LSU	GenBank SSU	Source
Ravenelia havanensis Arthur	DQ354557	DQ354556	Aime (2006)
Trachyspora intrusa (Grev.) Arthur	DQ354550	DQ354549	Aime (2006)
Tranzschelia discolor (Fuckel) Tranzschel & M.A. Litv.	DQ995341	AY125403	Aime (2006), Wingfield et al. (2004)
Triphragmium ulmariae (DC.) Link	AF426219	AY125402	Maier et al. (2003), Wingfield et al. (2004)
Uredinopsis filicina (Niessl) Magnus	AF426237	N/A	Maier et al. (2003)
Uromyces acuminatus Arthur	GU058004	N/A	Dixon et al. (2010)
Uromyces appendiculatus F. Strauss	AY745704	DQ354510	Matheny et al. unpubl., Aime (2006)
Uromyces ari-triphylli (Schwein.) Seeler	DQ354529	DQ354528	Aime (2006)
Uromyces viciae-fabae (Pers.) J. Schröt.	AY745695	N/A	Matheny and Hibbet unpubl.
Uromycladium fusisporum (Cooke & Massee) Savile	DQ323921	DQ354548	Scholler and Aime (2006), Aime (2006)
Uromycladium tepperianum (Sacc.) McAlpine	DQ323922	DQ323923	Scholler and Aime (2006)

Lectotypus of *Aecidium podophylli* (hic designatus): USA. NORTH CAROLINA: Salem, on leaves of *Podophyllum peltatum*, Michener Collection (BPI 882441).

≡ *Caeoma* (*Aecidium*) *podophyllatum* Schwein. Trans. Amer. Phil. Soc., n.s. 4:293. 1832.

Note: This is nom. illeg. via superfluous (McNeill et al. 2006, ICBN Art. 52). The epithet '*podophylli*' should have been adopted in *Caeoma*. Schweinitz (1832) discusses a lapsus calami for *A. podophylli* (Schweinitz 1822) where the spores were described as septate. He apparently inadvertently included the description of the teliospores instead of the aeciospores. In all other regards, the protolog of *A. podophylli* describes aecia.

[≡ *Puccinia podophylli* (Schwein.) Link, Species Plantarum 6:79. 1825 non *Puccinia podophylli* Schwein., Schriften Naturf. Ges. Leipzig 1:72. 1822.]

Note: This is nom. illeg. because it is a later homonym (ICBN Art. 53). Although Link (1825) was reclassifying this species in *Puccinia* due to the lapsus calami of Schweinitz that was discussed above, this name should have received a nom. nov. designation instead of the same name as the already valid and legitimate *Puccinia podophylli* Schwein.

≡ *Puccinia aurea* Spreng., Systema Vegetabilium 4:568.1827.

Note: This is nom. nov. for *Aecidium podophylli.*

Study of Allodus podophylli *(designated neotype of* Puccinia podophylli *Schwein.):* Leaf spots scattered to gregarious, typically more or less circular to elongate-elliptical, yellow, 3–8 mm diam. Spermogonia of Group V (type 4), epiphyllous on leaf spots, scattered to gregarious, subepidermal and scarcely visible as small raised warts, honey yellow, globoid to depressed globoid, with ostiolar filaments, 130–160 μm diam. Spermatia 8–10.5 × 3–5 μm, ellipsoid to oblong to ovate to reniform, hyaline, walls smooth. Aecia amphigenous on leaf spots but typically hypophyllous, scattered to gregarious, subepidermal, erumpent becoming pulverulent, circular from above, cupulate in cross section with peridium at maturity having margin somewhat recurved, orangish yellow, up to approx. 300 μm diam. Peridial cells 29–35 × 24–30 μm, typically rhomboid, outer walls rugose, inner walls punctate. Aeciospores 25.5–32 × 22.5–29 μm, catenulate, globoid to ellipsoid or somewhat irregularly angular, contents hyaline in aged collections, walls hyaline, smooth becoming slightly verrucose, approx. 1 μm thick, pores conspicuous, typically with five per aeciospore. Uredinia absent. Telia epiphyllous on leaf spots, scattered to gregarious, at times becoming confluent, subepidermal and erumpent becoming pulverulent, circular, dark brown, up to approx. 500 μm diam. Teliospores 37–59 × 16–27 μm, non-catenulate, ellipsoid to clavate, obtuse at apices, obtuse or tapering below at bases, one-septate, walls with or without slight constriction at septa, dark brown, with scattered spines, spines straight to curved, up to 7.5 μm long and widest at bases, walls 1–2 μm thick, pores not visible, pedicels at times persistent, terete, fragile, readily collapsing, hyaline, walls smooth, up to 9.5 μm long.

Study of Aecidium podophylli *(designated lectotype):* Leaf spots scattered to gregarious, at times becoming confluent, typically more or less circular to elongate-elliptical, yellow, 5–10 mm diam. Spermogonia epiphyllous on leaf spots, scattered to gregarious, subepidermal and scarcely visible as small raised warts, honey yellow. Aecia hypophyllous, scattered to gregarious, subepidermal, erumpent

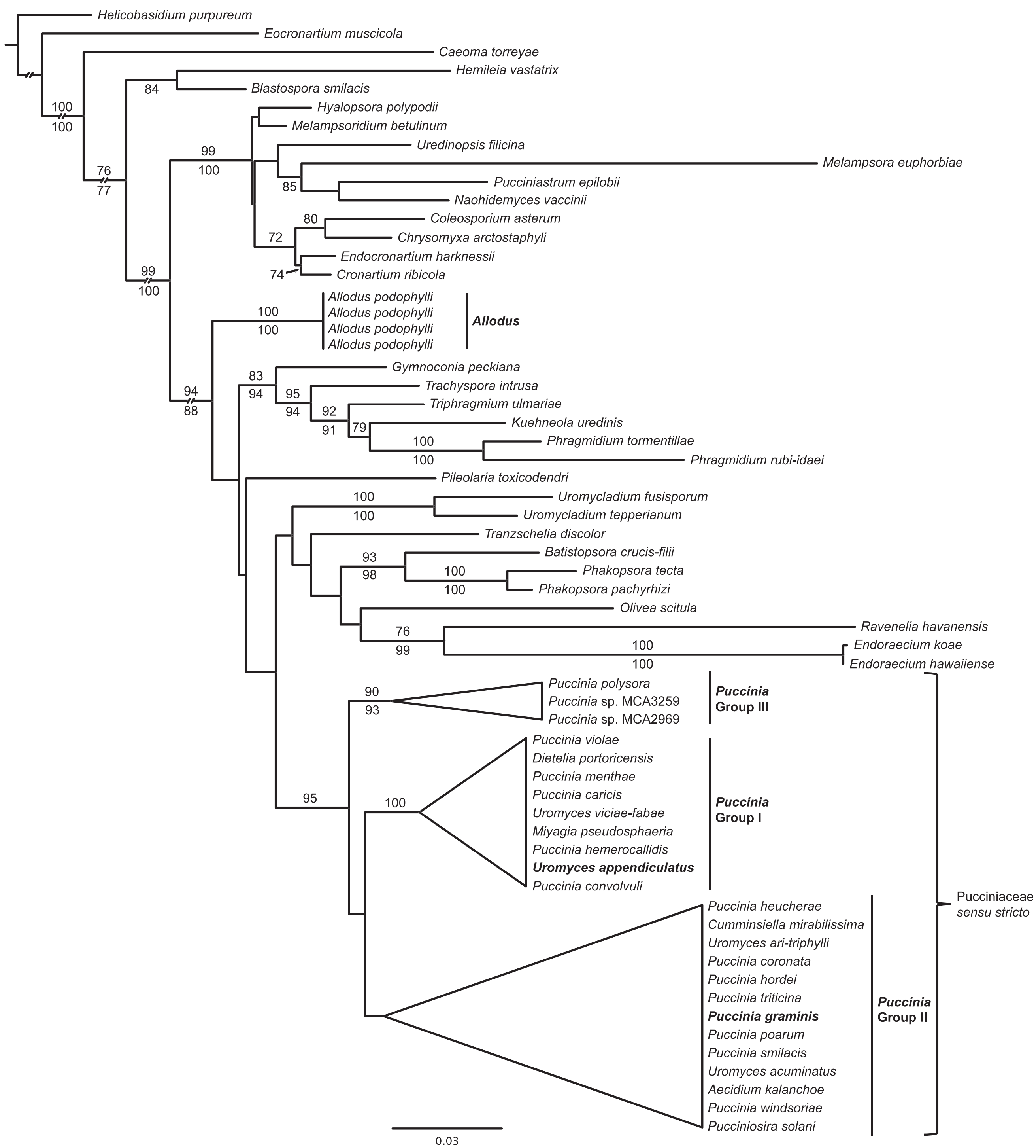

FIG. 2. Phylogram obtained from maximum likelihood analysis of nuclear rDNA loci, LSU and SSU. Bootstrap support values (> 70%) from a maximum likelihood search with 1000 replicates shown above the nodes. Bootstrap support values (> 70%) from parsimony search shown below the nodes.

becoming pulverulent, circular, cupulate, peridium at maturity having margin somewhat recurved, orangish yellow, up to approx. 500 μm diam. Peridial cells 32–37 × 24–32 μm, typically rhomboid, outer walls rugose, inner walls punctate. Aeciospores 24–32 × 21–27 μm, catenulate, globoid

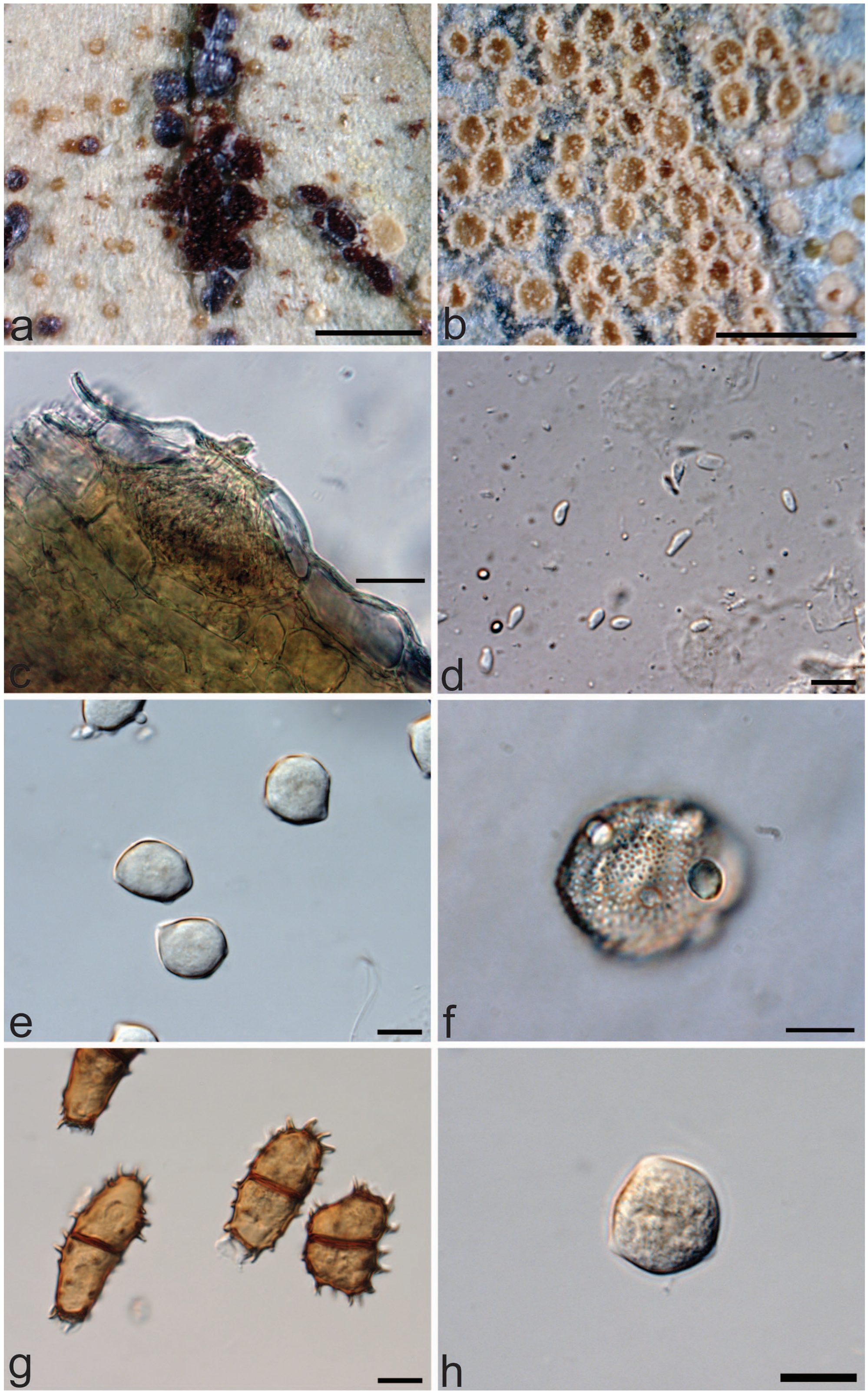

FIG. 3. *Allodus podophylli*. a–g. Designated neotype of *Puccinia podophylli* Schwein. (BPI 842277). a. Aecia (orangish yellow), spermogonia (honey yellow) and telia (dark brown) on upper leaf surface. b. Aecia on lower leaf surface. c. Cross section of spermogonium. d. Spermatia. e. Aeciospores. f. Surface view of aeciospore. g. Teliospores. h. Designated lectotype of *Aecidium podophylli* (BPI 882441), aeciospore. Bars: a–b = approx 1 mm; c = approx 50 μm; d–e, g–h = approx 20 μm; f = approx 10 μm.

to ellipsoid or somewhat irregularly angular, contents hyaline in aged collections, walls hyaline, smooth becoming slightly verrucose, approx. 1 μm thick, pores conspicuous, typically with five per aeciospore. Uredinia and telia absent.

Habitat and distribution.—Known from *Podophyllum peltatum* L. (Berberidaceae). This rust species occurs throughout the range of the host (Farr and Rossman 2011) in eastern parts of Canada and USA (USDA 2011). It also has been reported from *Diphylleia sinensis* H.L. Li (Berberidaceae) in China (Farr and Rossman 2011), but we have not confirmed the accuracy of these reports.

Collections examined: USA. ILLINOIS: Hancock County, on leaves and stems of *Podophyllum peltatum*, 30 Apr 2004, leg. *L. Castlebury*, U-00272 (BPI 844307, ITS2-LSU: JQ423258); 01 May 2004, leg. *L. Castlebury*, U-00273 (BPI 844308, ITS2-LSU: JQ423259). MARYLAND: Beltsville, BARC, along Beaver Dam Road, on *P. peltatum*, 21 Apr 2002, leg. *J.R. Hernández, JRH 2002-221*, U-00013 (BPI 842275); Catoctin Furnace Trail, Catoctin Mountain National Park, on *P. peltatum*, 26 May 2005, leg. *M.C. Aime, C. Park,* and *A. Kennedy, MCA 2945* (BPI 871630), Catoctin Mountains, Cunningham Falls, on *P. peltatum*, 30 Apr 2003, leg. *M.C. Aime* and *J.R. Hernández, JRH-2003-001*, U-00002 (BPI 842277, designated neotype of *Puccinia podophylli* Schwein., ITS2-LSU: DQ354453, SSU: DQ354544). NORTH CAROLINA: Haywood County, Great Smoky Mountains National Park, Baxter Creek Trail, on *P. peltatum*, 30 Apr 2005, leg. *E.B. Lickey*, U-00803 (BPI 878056, LSU: JQ423260); Salem, on leaves of *P. peltatum*, Michener Collection (BPI 882441, designated lectotype of *Aecidium podophylli*). TENNESSEE: Sevier County, Great Smoky Mountains National Park, the sinks at Meigs Creek, on *P. peltatum*, 18 May 2006, leg. *E.B. Lickey*, U-01202 (BPI 878057).

Notes.—We were unable to locate any original material of *Puccinia podophylli* Schwein. This included a search of the Schweinitz herbarium at the Academy of Sciences (PH). Arthur and Bisby (1918) also did not note any existing original material. Hence, we designate a neotype associated with DNA sequence data. Original material of *Aecidium podophylli* was found in the Michener Collection at BPI. The Michener label included an abbreviated and indirect reference to Synopsis Fungorum (Schweinitz 1822) with the name *Aecidum podophyllatum* and the confusing locality Salem-Beth. See Arthur and Bisby (1918) for clarification on Schweinitz's collections that have localities added to the original specimen and label of where a fungus was later collected. This material did not include telia. Herein, we designate this specimen as the lectotype of *Aecidium podophylli*. Although the protolog of *Aecidium podophylli* (Schweinitz 1822) described the aecial state of the life cycle, the spores were described as having two cells. Schweinitz (1832) admitted to this error. Considerable nomenclatural and taxonomic confusion has resulted from the works of other authors who attempted to deal with Schweinitz's error and interpret how many fungi may occur on *Podophyllum*. The designated neotype and lectotype represent the same rust species.

DISCUSSION

Allodus podophylli is phylogenetically distinct from the Pucciniaceae sensu stricto including *Puccinia* and *Uromyces* (FIG. 2). *Dicaeoma* Gray, typified by *D. persicariae* Gray (=*Puccinia polygoni-amphibii* Pers., ≡ *D. polygoni-amphibii* [Pers.] Arthur) (Sydow 1922), is the only other teleomorphic genus in which the mayapple rust has been classified, but it is not an appropriate generic name for this species because the type species of *Dicaeoma* is part of the Pucciniaceae sensu stricto (Maier et al. 2007). *Allodus* was erected by Arthur (1906) as a genus with these characters: subepidermal spermogonia, aecia and telia; pigmented and two-celled teliospores, aecia with peridia, uredinia lacking, and autoecious (Arthur 1906, 1921). The type species of *Allodus* is *A. podophylli* (Arthur 1906). Arthur did not place as much emphasis on missing life cycle stages in later works and considered *Allodus* to be a synonym of *Puccinia* (Arthur 1934, Cummins and Hiratsuka 1983), given the shared diagnostic characters of two-celled, pedicellate, teliospores and Group V (type 4) spermogonia. Our study highlights the homoplasious morphology of these characters in rust fungi and the taxonomic challenges to be faced in developing a systematic classification for members of the Pucciniaceae sensu lato.

It is unknown whether other species that have been classified in *Allodus* will form a monophyletic group or whether any of the other 41 names that at one time have been applied in *Allodus* (Index Fungorum, http://www.indexfungorum.org/) are congeneric with *A. podophylli*. *Allodus podophylli* has been an intriguing fungus to rust scholars due to its unusual life history, which was discussed in detail by Whetzel et al. (1925) and Jackson (1931), and it appears to be a frequent host of mycophagous fly larvae in the genus *Mycodiplosis* (Henk et al. 2011). The autodemicyclic life cycle wherein aeciospores cause infections that give rise to telia without a uredinial stage or host alternation seem to distinguish *Allodus* from the majority of *Puccinia* species and may prove to be diagnostic for the genus.

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