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Revising the taxonomic placement of *Laetiporus persicinus* within the Laetiporaceae

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ABSTRACT

The fungus currently known as *Laetiporus persicinus* is a recognizable brown-rot decayer that is widespread on oak hosts in the southeastern United States. This species was first described as *Polyporus persicinus* in 1872 based on collections by Henry W. Ravenel from South Carolina. In this study, we elucidate the phylogenetic relationships of *Laetiporus persicinus* based on maximum likelihood and Bayesian inference analyses of a four-locus data set (18S, 28S, *rpb2*, and *tef1*) from taxa within the Fomitopsidaceae and Laetiporaceae. The internal transcribed spacer (ITS) region was analyzed separately because it was not possible to align this locus across a diverse data set that included taxa from multiple families. Our analysis and previous studies indicate that *Laetiporus persicinus* does not belong to *Laetiporus* sensu stricto, and we found a strongly supported relationship between *Laetiporus persicinus* and the African species *Kusaghiporia usambarensis*, despite the fact that the 28S phylogeny resolved a different (but unsupported) topology. Here, we propose *Kusaghiporia persicinus*, comb. nov., based on a combination of morphological and molecular data. *Laetiporus persicinus* shares many morphological features with *K. usambarensis* that are missing in other *Laetiporus* species, including centrally stipitate basidiomata, a brown to pinkish pileus surface, and a pore layer that bruises when touched. However, *K. usambarensis* and *L. persicinus* differ in basidiospore size and shape as well as their geographic distributions. We provide a revised taxonomic treatment for this common wood-decay fungus.

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Brown-rot decay; *Kusaghiporia*; *Laetiporus persicinus*; taxonomy; 1 new taxon

INTRODUCTION

Laetiporus (Polyporales) is a genus containing wood-decay fungi with worldwide distribution that was described by Murrill (1904). There are currently 21 recognized species in the genus, which are distributed in both temperate and tropical zones (Banik et al. 2012; Burdsall and Banik 2001; Gilbertson 1981; Ota et al. 2009; Pires et al. 2016; Song et al. 2018; Tomsovsky and Jankovský 2008). All *Laetiporus* species are considered either saprobes or secondary pathogens of trees and known to cause brown-rot decay (Arora 1986; Arya and Perelló 2010).

The type species of the genus, *L. sulphureus* (Bull.) Murrill, is characterized by its bright orange color and annual, sessile fruiting bodies with a yellow, bright creamy yellow, or white pore surface. In fact, the genus name refers to the bright-colored pores (Murrill 1904). Members of the genus *Laetiporus* are also characterized by thin-walled tubes, smooth, hyaline, ovoid to ellipsoid basidiospores, dimitic-binding hyphae that lack clamp connections, and the absence of cystidia in the hymenium (Gilbertson 1981; Lindner and Banik 2008; Murrill 1904).

Recent studies have demonstrated that most *Laetiporus* species share morphological similarities and constitute a monophyletic group (Lindner and Banik 2008). However, several species that have traditionally been treated in the genus *Laetiporus*, such as *Laetiporus portentosus* (Berk.) Rajchenb. and *Laetiporus persicinus* (Berk & M.A. Curtis) Gilbertson, are phylogenetically and morphologically divergent (Lindner and Banik 2008). This paper focuses on the taxonomy and phylogeny of the common and widespread eastern North American fungus *Laetiporus persicinus*.

Laetiporus persicinus was first described as *Polyporus persicinus* by Berkeley and Curtis (1853), based on collections by Henry W. Ravenel from South Carolina (USA). Gilbertson (1981) transferred *Polyporus persicinus* to *Laetiporus persicinus* based on its ecology (brown-rot decay) and microscopic characteristics, such as spore

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(ovoid to ellipsoid, hyaline, and smooth) and hyphal (dimitic with binding and generative hyphae) morphologies. This species has a rich and convoluted taxonomic history (see Discussion) but has been generally accepted in the genus *Laetiporus* since 1981 (Bessette et al. 2019; Gilbertson 1981; Gilbertson and Ryvarden 1986). However, *Laetiporus persicinus* is different from the other species of *Laetiporus* based on the morphological features of the basidiomata. *Laetiporus persicinus* forms a medium to very large, brown, centrally stipitate basidioma, which is different than the brightly colored, sessile to slightly stipitate basidiomata produced by most other *Laetiporus* species.

Laetiporus persicinus is typically found near various hardwoods in the southeastern United States, especially *Quercus* (oak) species (https://mycoportal.org/), although the type specimen was apparently found in a pine-dominated forest (Berkeley and Curtis 1853). Nevertheless, oak trees are ubiquitous throughout most habitats in the southeastern United States (Harms 1990), and this species is consistently found with oaks. Basidiomata are often attached to decayed roots at the base of the tree or sometimes away from the base of the tree, but they generally do not fruit on the trunk (Burdsall and Banik 2001; Lindner and Banik 2008). This is an unusual fruiting location for *Laetiporus*; most other species in the genus typically fruit directly on the trunk, with the exception of *L. cincinnatus*, which is stipitate and fruits in clusters at the base of its tree hosts (although this taxon is otherwise quite similar to other species of *Laetiporus* sensu stricto) (Burdsall and Banik 2001; Ortiz-Santana et al. 2013). Another unique feature in *L. persicinus* is that the pore surface of fresh *L. persicinus* bruises rapidly from whitish to reddish brown when damaged (Gilbertson 1981; Lindner and Banik 2008).

Laetiporus persicinus has also been shown to be divergent from other taxa in the genus based on molecular data. Molecular studies using restriction fragment length polymorphism (RFLP) of the internal transcribed spacer (ITS) rDNA indicated that *Laetiporus persicinus* should be placed in another genus (Burdsall and Banik 2001). This hypothesis was further corroborated by Lindner and Banik (2008) who sequenced and analyzed ITS and large subunit (28S) rDNA data for the genus *Laetiporus* and related fungi. Their studies concluded that *Laetiporus persicinus* is not a member of *Laetiporus* sensu stricto clade, but the placement of this taxon was unresolved in the *Antrodia* clade. Due to the taxonomic confusion about the placement of *L. persicinus* within the *Antrodia* clade, the phylogenetic relationship has remained unresolved for this species and *L. persicinus* has remained in the genus *Laetiporus* despite the fact that it is not a part of *Laetiporus* sensu stricto.

The aims of this study are to (i) use five phylogenetically informative regions to determine the phylogenetic placement of *L. persicinus*, namely, the nuclear large subunit rDNA (28S), the internal transcribed spacer region (ITS), the nuclear small subunit rDNA (18S), the translation elongation factor (*tef1*), and the second largest subunit of RNA polymerase II (*rpb2*); (ii) determine morphologically diagnostic characters; and (iii) determine the geographic distribution of *L. persicinus* based on fresh collections and herbarium records.

MATERIALS AND METHODS

Sample collection and isolation.—Fresh fruiting bodies of *L. persicinus* were collected in Florida from 2016 to 2019. The Köppen climate classification of the general location is *Cfa* (humid subtropical), with average annual precipitation of 1202–1658 mm and average temperature of 20.5–22.9 C (NOAA, 2021). Basidiomata observed on the ground near the bases of oak trees were collected in both urban and forested areas. Fresh specimens were photographed and then placed in a paper bag for transport to the laboratory. To obtain axenic cultures, a small piece of fresh tissue from inside the context of the basidiocarp was placed on sterile plates of malt extract yeast extract agar (MEYE) (3 g malt extract, 3 g yeast extract, 5 g peptone, 10 g dextrose, and 1 L distilled water, with the addition of chloramphenicol at 10 mg/L and streptomycin at 100 mg/L). Isolates were maintained in MEYE to obtain pure cultures and plugs were added to sterile deionized water (diH_2O) for long-term storage. After culturing, the remaining portion of each specimen was dried using a forced-air dehydrator for 24 h and then placed in a new plastic bag with silica gel.

Dried specimens were obtained as loans from the Larry F. Grand Mycological Herbarium at North Carolina State University Herbarium (NCSLG) and the U.S. National Fungus Collections, U.S. Department of Agriculture Agricultural Research Service (BPI). We also studied dried specimens deposited at the Fungal Herbarium of the Florida Museum of Natural History (FLAS) in the United States.

In order to estimate the distribution of *L. persicinus*, we plotted known occurrences of this species on a map of the continental United States. We included well-documented records of *L. persicinus* based on data from MycoPortal (https://mycoportal.org/) (MyCoPortal 2022), iNaturalist (https://www.inaturalist.org/) (iNaturalist 2022), and Mushroom Observer (https://mushroomobserver.org/). We included only

L. persicinus records that we verified using either DNA sequences, morphological examination of specimens, or high-quality photos (FIG. 1). To be conservative, occurrence records that could not be verified via sequences, morphological examinations, or high-quality photos were excluded.

Morphological characteristics.— Morphological characteristics were determined based on recently collected samples and herbarium material by placing sectioned context or pore tissues on a slide containing water, 3% KOH, or Melzer's reagent. Microscopic features were observed with a Zeiss Axio Imager A2 light microscope, and images were obtained using a AxioCam 305 digital camera (Carl Zeiss Microscopy, New York). Hyphal characteristics were observed, and at least 10 spores were measured per specimen. Microscopic features of newly obtained specimens and herbarium samples were directly compared with the type specimen of *L. persicinus* (BPI 216927), which was originally collected from South Carolina by Ravenel (Gilbertson 1981).

DNA analysis, PCR amplification, and DNA sequencing.— We used two different DNA extraction methods. For fresh basidiomata or living axenic cultures growing on agar, we extracted DNA from fresh tissues using the Extract-N-Amp rapid DNA extraction kit using the manufacturer's protocol (Sigma-Aldrich, St. Louis, Missouri). For dried herbarium specimens,

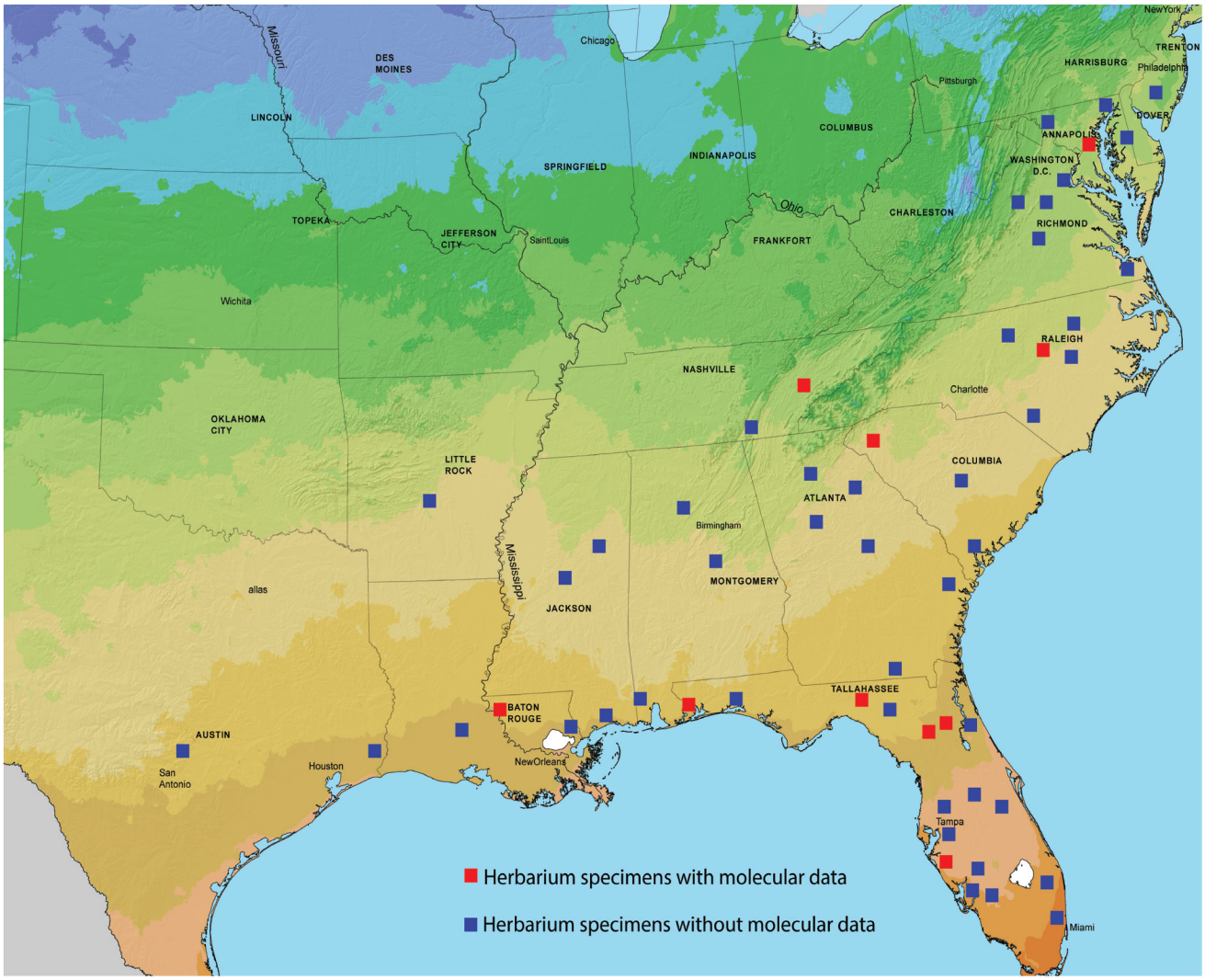

Figure 1. Distribution of *Kusaghiporia persicinus*. Red squares represent locations for which we obtained *K. persicinus* herbarium specimens that were confirmed by ITS sequences (TABLE 1; SUPPLEMENTARY FIG. 1). Blue squares represent locations for which specimens were identified based on the distinctive macroscopic morphology using MyCoPortal (Mycoportal.org), Mushroom Observer (MushroomObserver.org), and iNaturalist but were not confirmed with molecular data.

fungal tissue was taken from inside of basidiomata and DNA extraction was performed using a modified cetyltrimethylammonium bromide (CTAB) method (Gardes and Bruns 1993). Polymerase chain reaction (PCR) of the ITS region was performed using primers ITSIF (Gardes and Bruns 1993) and ITS4 (White et al. 1990). PCR of the 28S rDNA was performed using primers LROR and LR5 (Hopple and Vilgalys 1994; Tedersoo et al. 2008). PCR of the 18S rDNA was performed using primers NS1 and NS4 (White et al. 1990). PCR for the three regions ITS, 28S, and 18S were performed following the protocols of White et al. (1990). *rpb2* was amplified using Phusion Hot Start Flex DNA Polymerase standard protocol (New England Biolabs, Ipswich, Massachusetts) with forward primer fRPB2-5 F and reverse primer bRPB2-7.1 R (Matheny 2005) using a modified (annealing temperature 65 C) touchdown PCR protocol from Bonito et al. (2013). Translation elongation factor 1-alpha (*tef1*) was amplified using primers EF1-983 F and EF1-1567 R using the protocol of Rehner and Buckley (2005).

PCR amplicons were visualized using SYBR Green I stain (Molecular Probes, Eugene, Oregon), separated by electrophoresis on 1.5% agarose gel in sodium boric acid buffer and photographed under ultraviolet (UV) light. PCR amplicons were purified for sequencing with 2 µL of exonuclease I (EXO) and Antarctic Phosphatase (AnP) enzymes (New England Biolabs) (Werle et al. 1994). Sanger sequencing was performed using the same forward and reverse primers as above at Eurofins Genomics (Louisville, Kentucky). Sequence chromatograms were trimmed and aligned in Geneious 11.0.6 (Biomatters, San Diego, California). Sequences generated in this study were deposited in the National Center for Biotechnology Information (NCBI) database (TABLE 1); alignments and trees were submitted to the Open Science Framework (OSF) at https://osf.io/8f3q5/?view_only=16089235b5e64f6983f4cc7ec3f8259.

Phylogenetic analysis.— Additional sequences (TABLE 1) from *L. persicinus* and other members of Laetiporaceae and Fomitopsidaceae were downloaded from the NCBI database (Lindner and Banik 2008; Tibuhwa et al. 2020). Nucleotide sequences of the five loci were edited manually in Geneious 11.0.6 (Biomatters), and individual loci were aligned using MUSCLE 3.8.425 (Edgar 2004). The individual alignments for each of the loci were modified by manually trimming sequences and removing gaps using Geneious 11.0.6. Each locus was analyzed separately to ensure that there was no supported incongruence among the loci. For the individual analyses of all of the loci (ITS, 18S, 28S, *rpb2*, and *tef1*), the GTRGAMMA model was used with 1000 bootstrap iterations and midpoint-rooted (FIG. 2; SUPPLEMENTARY FIGS. 1, 2, 3, and 4).

For the analysis of the ITS region, we selected all sequences of *L. persicinus* available in GenBank and from our study to cover all available geographic regions of the world. Sequences of the ITS region were not alignable for all of the same taxa that were used in the multilocus analysis, so the ITS region was excluded from the multilocus analysis.

For the four loci (18S, 28S, *rpb2*, and *tef1*), we were able to obtain sequences for 48 specimens in total; all four loci are available from 22 specimens, three loci were available from four specimens, two loci were available for two specimens, and only one locus was available for 20 specimens (TABLE 1). However, at least three loci are available for each of the species that are included in the multilocus analysis. All four loci were concatenated using a custom Perl script, superaligner (Mujic et al. 2019). The concatenated alignment was partitioned into 18S rDNA, 28S rDNA, the 1st, 2nd, and 3rd codon positions of both *rpb2* and *tef1*, and the *tef1* intron region. Optimal evolutionary models were estimated independently for each partition with PartitionFinder (Guindon et al. 2010; Lanfear et al. 2012, 2016) and chosen based on Akaike information criterion (AIC) scores. The concatenated alignment and 28S rDNA were analyzed with maximum likelihood (ML) and Bayesian inference (BI) methods. ML bootstrap was performed in Cyberinfrastructure for Phylogenetic Research Science Gateway (CIPRES) 3.3 (Miller et al. 2010) and executed using RAxML 8.2.12 (Stamatakis 2014) under the GTRGAMMA evolutionary model. Bayesian posterior probability calculations were performed on the HiperGator supercomputer at the University of Florida. Bootstrap analyses were conducted using 1000 iterations. For BI analyses, the GTR+I+G model was the best fit for the 18S, 28S, and the 1st and 3rd positions of *rpb2*. The TVMEF+I+G model was the best fit for the 2nd position of *rpb2*, whereas the TIMEF+I+G model was the best fit for both *tef1* and the *tef1* intron. However, those models are not available for RAxML 8.2.12 (Stamatakis 2014) and MrBayes 3.2.6 (Ronquist et al. 2012); therefore, we chose the GTR+I+G model as recommended by PatitionFinder (Guindon et al. 2010; Lanfear et al. 2012, 2016). Two runs were performed with four chains for 10 million generations with sampling every 1000 generations, and the first 25% of trees sampled were discarded as the burn-in. All other parameters were set to default. To verify the appropriate effective sample size, run convergence and stationarity were confirmed with Tracer 1.7.1 (Rambaut et al. 2018). Phylogenetic trees for ML and BI were visualized in FigTree 1.4.4 (Rambaut 2018). Nodes with bootstrap support ≥70% and posterior probability

Table 1. Collections used in this study, with collection (ID) numbers, GenBank accession numbers, and references.

		GenBank accession numbers					
Taxon name	Collection (ID) number	ITS	28S	18S	*tef1*	*rpb2*	Reference
Amyloporia xantha	Cui 1154	KR605817	KR605756	KR605918	KR610746	KR610836	Han et al. 2016
Antrodia serialis	Cui 1051	KP715307	KP715323	KR605911	KP715337	KR610830	Han et al. 2016
Antrodia serpens	Dai 7465	KR605813	KR605752	KR605913	KR610742	KR610832	Han et al. 2016
Daedalea circularis	Cui 10134	—	KP171221	KR605876	KR610709	KR610800	Han et al. 2016
Daedalea quercina	Dai 2260	KR605792	KR605731	KR605885	KR610718	KR610808	Han et al. 2016
Fibroporia albicans	Cui 9464	KC456250	KR605758	KR605920	KR610748	KR610838	Han et al. 2016
Fibroporia radiculosa	Cui 2970	—	KR605761	KR605923	—	—	Han et al. 2016
Fomitopsis cystidiata	Cui 5481	KF937288	KF937291	KR605832	KR610667	KR610765	Han et al. 2016
Fomitopsis durescens	O 10796	—	—	KR605834	KR610669	KR610766	Han et al. 2016
Fomitopsis palustris	Cui-7597	KP171213	KP171236	KR605854	KR610687	KR610778	Han et al. 2016
Fomitopsis pinicola	Cui-1031	KR605781	KR605720	KR605856	KR610689	KR610780	Han et al. 2016
Kusaghiporia usambarensis	JMH-02	—	MH010045	—	MH048869	—	Hussein et al. 2018
Kusaghiporia usambarensis	JMH-01	—	MH010044	MH010046	MH048871	MH048870	Hussein et al. 2018
Kusaghiporia persicinus	FLAS-F-67997	—	OK623377	—	—	—	This study
Kusaghiporia persicinus	FLAS-F-67998	OK623489	OK623378	OK663112	OK648489	OK669055	This study
Kusaghiporia persicinus	FLAS-F-67996	OK623490	OK623376	OK663111	OK648488	OK669054	This study
Kusaghiporia persicinus	FLAS-F-68000	OK623487	—	OK663114	—	—	This study
Kusaghiporia persicinus	FLAS-F-67995	—	OK623375	OK663110	OK648487	OK669053	This study
Kusaghiporia persicinus	FLAS-F-67999	OK623488	—	OK663113	—	OK669056	This study
Kusaghiporia persicinus	FLAS-F-61002	MH211690	—	—	—	—	Kaminsky and Smith unpublished
Kusaghiporia persicinus	FLAS-F-60416	MF153094	—	—	—	—	Kaminsky and Smith unpublished
Kusaghiporia persicinus	RLG-14739	EU402582	—	—	—	—	Lindner and Banik 2008
Kusaghiporia persicinus	RLG-14725	EU402581	EU402512	EU402502	—	—	Lindner and Banik 2008
Kusaghiporia persicinus	NCSLG-18429	OK623493	—	—	—	—	This study
Kusaghiporia persicinus	HHB-9564	KU668961	EU402513	EU402579	—	—	Lindner and Banik 2008
Kusaghiporia persicinus	FLAS-F-68088	OK623492	—	—	—	—	This study
Kusaghiporia persicinus	FLAS-F-68089	OK623491	—	—	—	—	This study
Kusaghiporia persicinus	PBM4263	MT196945	—	—	—	—	Matheny and Swenie unpublished
Kusaghiporia persicinus	MVC-620b	MW795373	—	—	—	—	Caiafa and Smith 2022
Kusaghiporia persicinus	F LAS-F-60939	MH211687	—	—	—	—	Kaminsky and Smith unpublished
Laetiporus sulphureus	Dai-12 826	KR605819	KR605762	KR605925	KR610753	KR610842	Han et al. 2016
Laetiporus sulphureus	GR-12	EU402561	EU402534	—	—	—	Lindner and Banik 2008
Laetiporus sulphureus	DA-41	EU402566	EU402533	—	—	—	Lindner and Banik 2008
Laetiporus sulphureus	Cui 12 389	KR187106	KX354487	KX354519	KX354608	KX354653	Song et al. 2018
Laetiporus cincinnatus	Dai-12 811	KF951291	KF951304	KX354516	KX354605	KT894788	Song et al. 2018
Laetiporus cincinnatus	FP-140120	KY886728	KY886754	—	KY886787	KY886801	Song and Cui 2017
Laetiporus conifericola	JAM-1-12	AB472632	—	—	AB472664	—	Ota et al. 2009
Laetiporus conifericola	CA-8	EU402575	EU402523	—	—	—	Lindner and Banik 2008
Laetiporus conifericola	JV 0709/81 J	KF951292	KF951327	KX354531	—	KX354683	Lindner and Banik 2008
Laetiporus gilbertsonii	CA-13	EU402549	EU402527	—	—	—	Lindner and Banik 2008
Laetiporus gilbertsonii	JV 1109/31	KF951293	KF951306	KX354542	KX354630	KX354671	Song and Cui 2017
Laetiporus gilbertsonii var. *pallidus*	TJV2000-101	EU402553	EU402528	—	—	—	Lindner and Banik 2008
Laetiporus huroniensis	HMC-3	EU402571	EU402540	—	—	—	Lindner and Banik 2008
Laetiporus huroniensis	MI-14	EU402573	EU402539	—	—	—	Lindner and Banik 2008
Phaeolus schweinitzii	OKM-4435-T	KC585370	KC585199	—	—	—	Ortiz-Santana et al. 2013
Phaeolus schweinitzii	AFTOL-ID 702	-	AY629319	AY705961	DQ028602	DQ408119	Matheny et al. 2007
Phaeolus schweinitzii	DA-38	EU402585	EU402514	—	—	—	Lindner and Banik 2008
Phaeolus schweinitzii	HHB-18924	EU402586	EU402515	—	—	—	Lindner and Banik 2008
Phaeolus schweinitzii	Dai-8025	KX354457	KX354511	KX354553	KX354686	DQ408119	Song and Cui 2017
Piptoporellus baudonii	JMH-01/19	MT447066	MT447069	MT447063	MT452549	-	Tibuhwa et al. 2020
Piptoporellus soloniensis	Dai-1187	KR605804	KR605743	KR605902	KR610731	KR610823	Han et al. 2016
Polyporus cf. talpae	PR-2	—	EU402543	—	—	—	Lindner and Banik 2008

(*Continued*)

Table 1. (Continued).

		GenBank accession numbers					
Taxon name	Collection (ID) number	ITS	28S	18S	*tef1*	*rpb2*	Reference
Polyporus cf. talpae	PR-6326	—	EU402544	—	—	—	Lindner and Banik 2008
Pycnoporellus fulgens	OKM-7608-T	KC585387	KC585220	—	—	—	Ortiz-Santana et al. 2013
Pycnoporellus fulgens	FP101689	EU402592	EU402536	—	—	—	Lindner and Banik 2008
Pycnoporellus fulgens	HHB-17342	EU402593	EU402535	—	—	—	Lindner and Banik 2008
Pycnoporellus fulgens	Cui-1003	—	KX354512	KX354554	KX354687	KX354684	Song and Cui 2017
Wolfiporia dilatohypha	CS-63	EU402555	EU402516	EU402497	—	—	Lindner and Banik 2008
Wolfiporia dilatohypha	FP-72162	KU668959	KC585235	—	—	—	Ortiz-Santana et al. 2013
Wolfiporia hoelen	KCTC6480	MW251876	—	—	—	—	Wu et al. 2020
Wolfiporia hoelen	Dai 2004	—	MW251878	—	—	—	Wu et al. 2020
Wolfiporia hoelen	Dai 2003	—	MW251866	—	—	—	Wu et al. 2020
Wolfiporia cartilaginea	13121	—	KC585405	—	—	—	Ortiz-Santana et al. 2013
Wolfiporia cartilaginea	13122	GU256260	—	—	—	—	Banik et al. 2010
Wolfiporia cocos	CBK-1	KX354453	KX354689	KX354690	KX354688	KX354685	Song and Cui 2017
Wolfiporia cocos	MD-106	EU402594	EU402519	—	—	—	Lindner and Banik 2008
Wolfiporia cocos	MD-275	EU402595	EU402520	—	—	—	Lindner and Banik 2008

values ≥0.95 were considered strongly supported and are shown in FIGS. 2 and 3. Taxa in the family Fomitopsidaceae were selected as the outgroup for the concatenated and 28S analysis based on the results of Tibuhwa et al. (2020) and Justo et al. (2017). Final phylogenetic trees were formatted in Adobe Illustrator 24.3 (San Jose, California).

RESULTS

Molecular phylogenetic analyses.— The phylogenetic position of *Laetiporus persicinus* was inferred using data sets from 28S rDNA, *rpb2*, 18S rDNA, and *tef1* using both ML and BI analyses (FIG. 3). The concatenated multilocus alignment contains 48 species (TABLE 1) with 2270 characters, in which 34 specimens represent the Laetiporaceae and 14 represent the sister family Fomitopsidaceae. Due to the lack of longer sequences available in GenBank for members of Laetiporaceae and Fomitopsidaceae, alignments of *rpb2* (650 bp) and *tef1* (493 bp) were shorter than expected.

The multilocus phylogenetic analysis revealed that six of the seven *Laetiporus* species included in the analyses (*L. huroniensis, L. conifericola, L. gilbertsonii, L. gilbertsonii* var. *pallidus, L. sulphureus*, and *L. cincinnatus*) fell into *Laetiporus* senus stricto, whereas *Laetiporus persicinus* was resolved outside of this *Laetiporus* core clade. All *Laetiporus persicinus* specimens were recovered as a sister lineage of *Kusaghiporia usambarensis*. Furthermore, the clade that includes *K. usambarensis* and *L. persicinus* is sister to the *Laetiporus* core clade with high statistical support (FIG. 3). Results of the individual phylogenetic analyses for each of the four loci used in the multilocus analysis are shown in SUPPLEMENTARY FIGS. 2, 3, and 4 (18S, *tef1*, and *rpb2* regions) and in FIG. 2 (28S region).

The 28S rDNA large subunit alignment included 756 characters and was generated from a total of 44 specimens. The maximum likelihood analysis with 28S data produced four terminal clades with statistical support (≥70% bootstrap) for the *Laetiporus* core clade. However, *Laetiporus persicinus* fell outside of the *Laetiporus* core clade, whereas *Wolfiporia dilatohypha* Ryvarden & Gilb. and *Wolfiporia cartilaginea* Ryvarden form a sister group to this core *Laetiporus* clade. Similar results were found by Lindner and Banik (2008). Another interesting observation is that *Laetiporus persicinus* does not cluster in a supported clade with *K. usambarensis* in the 28S phylogenetic analysis. However, there was no statistical support for any placement for *L. persicinus* in the 28S. *Kusaghiporia usambarensis* is resolved as the sister taxon to *Polyporus* cf. *talpae* with statistical support for a shared common ancestor (FIG. 2), but due to lack of sequences of other genes for *Polyporus* cf. *talpae*, this taxon was not included in the multilocus analysis.

The alignment of ITS rDNA sequences included 708 characters and included 36 sequences (including nine sequences generated in this study) representing Laetiporaceae and Fomitopsidaceae (SUPPLEMENTARY FIG. 1). The ITS region was analyzed separately because it was not possible to align this locus across the diverse taxa that we used in the multilocus analyses and also because ITS sequences were not available for *K. usambarensis*. However, the ITS rDNA was nonetheless useful because it shows the

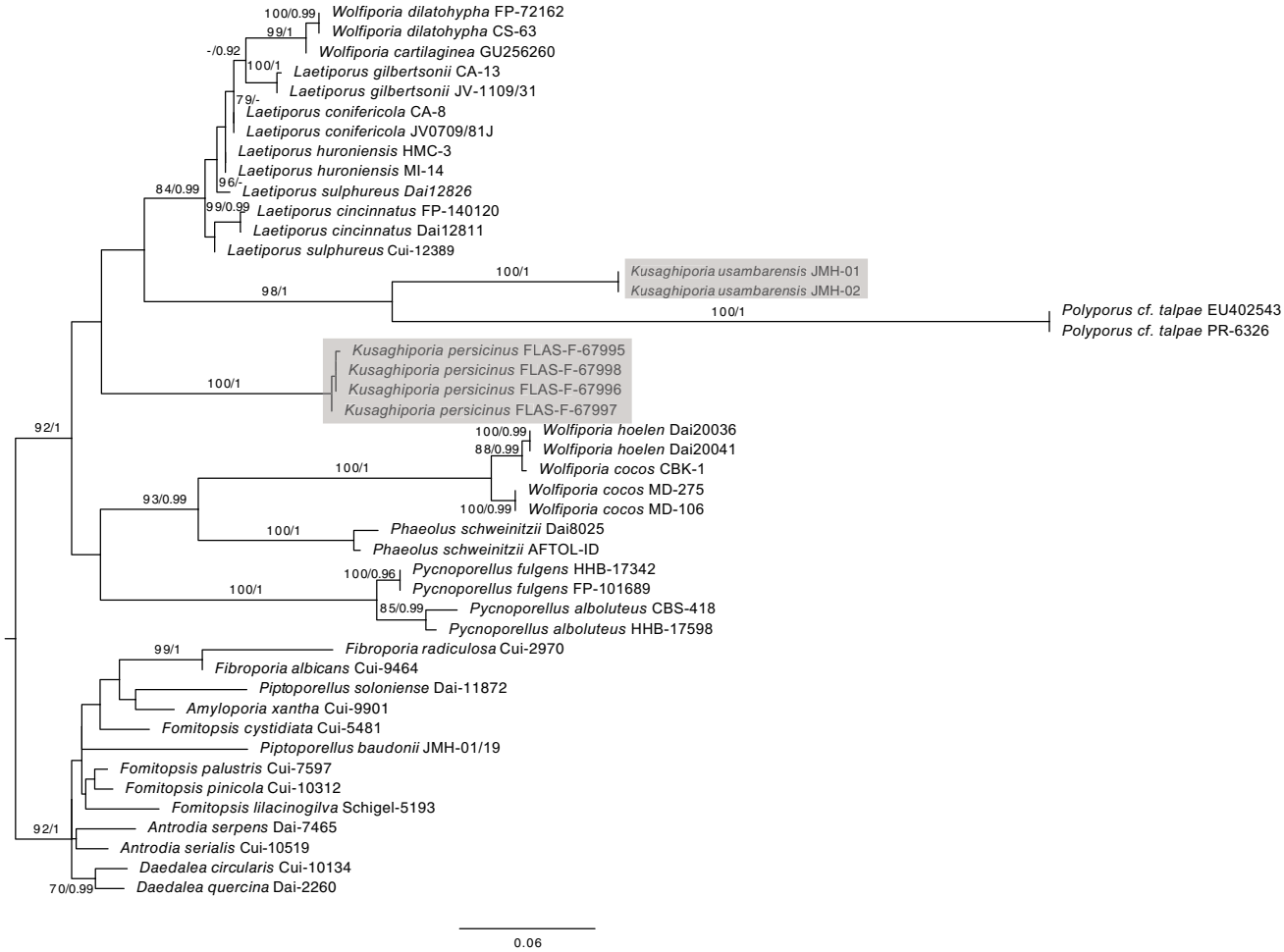

Figure 2. Phylogenetic tree of *Kusaghiporia persicinus* and related fungi based on maximum likelihood (ML) analysis of 28S rDNA. Numbers next to nodes represent ML bootstrap support values. Bootstrap values ≥70% and posterior probability ≥0.95 are shown here.

tight clustering of *L. persicinus* specimens from across the southeastern United States and because it also shows that *L. persicinus* is only distantly related with species of *Laetiporus* sensu stricto.

TAXONOMY

Kusaghiporia persicinus (Gilb.) C.A. Paez, Kraisit. & M. E. Sm., comb. nov.

MycoBank MB838900

Obligate synonyms

≡ *Polyporus persicinus* Berk. & M.A. Curtis, Annals and Magazine of Natural History 12:430. 1853 (Basionym).

≡ *Scutiger persicinus* (Berk. & M.A. Curtis) Murrill, Bull Torrey Bot Club 30(8):431. 1903 (Synonym).

≡ *Meripilus persicinus* (Berkeley & M.A. Curtis) Ryvarden, Norwegian Journal of Botany 19:232. 1972.

≡ *Buglossoporus persicinus* (Berkeley & M.A. Curtis) Corner, Beihefte zur Nova Hedwigia 78:174. 1984.

≡ *Cladoporus persicinus* (Berkeley & M.A. Curtis) Teixeira, Revista de Botanica 15(2):125. 1992.

≡ *Laetiporus persicinus* (Berkeley & M.A. Curtis) Gilb., Mycotaxon 12(2):385. 1981.

Taxonomic synonyms

= *Polyporus talpae* Cooke, Grevillea 16(77):15. 1887.

= Amauroderma brittonii Murrill, Mycologia 2:193. 1910.

= *Polyporus mesotalpae* Lloyd, Mycological Writings 4(41):564. 1916.

= *Polyporus beardsleei* Lloyd, Mycological Writings 7 (Letter 73):1330. 1924.

= *Polyporus subcolossus* Beeli, Bulletin du Jardin Botanique de l'État à Bruxelles 8 (3):252. 1930.

= *Dendrochaete vallata* G. Cunn., Bulletin of the New Zealand Department of Scientific and Industrial Research 164:261. 1965.

Basidiocarp annual, centrally stipitate, single circular pileus or in rosette with multiple pilei, up to 30 cm diam. Basidiocarp dense and heavy when wet but very

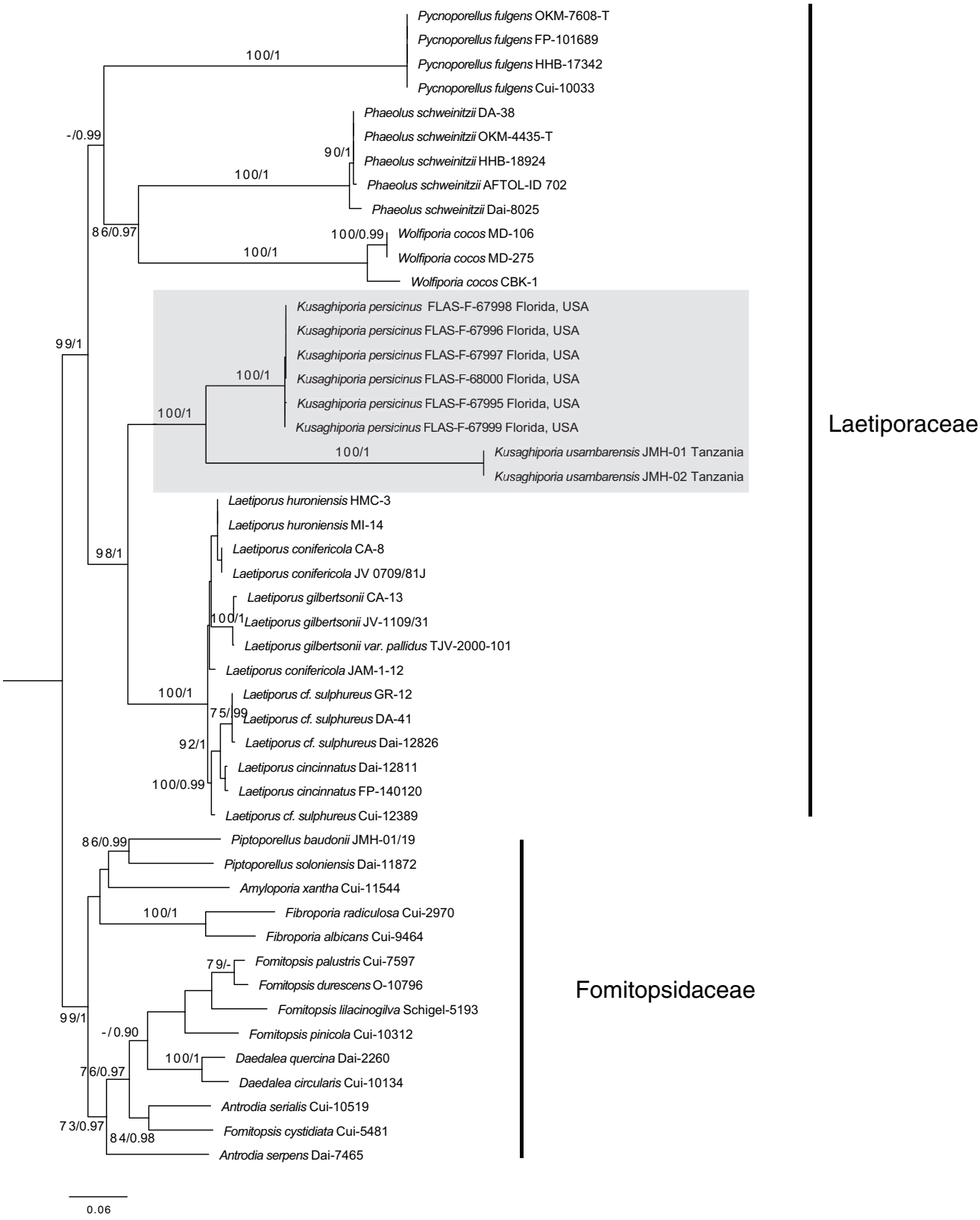

Figure 3. Phylogenetic tree of *Kusaghiporia persicinus* and related fungi based on maximum likelihood (ML) analysis of four concatenated genes (18S, 28S, *rpb2*, and *tef1*). Numbers next to nodes represent Bayesian posterior probabilities followed by ML bootstrap support values. Bootstrap values ≥70% and posterior probability ≥0.95 are shown here.

light when dried. Upper surface of pileus color ranges from pinkish to brown when young (FIG. 4A), dark brown when older, texture of the entire basidiocarp soft when young, becoming hard with age, with wavy to lobed margin, pileus surface azonate to faintly zonate and up to 2 cm thick and the context tissue is pinkish to tan with concentric faint to dark zones (Gilbertson and Ryvarden 1986). Basidiocarp tissue rapidly turning burgundy red with addition of 3% KOH (carmine to deep carmine; Stanley 1974). Stipe up to 10 cm long, simple at the base. Plant debris often attached to the base of the stipe and occasionally also incorporated into the pileus. Pores circular (3–4 per mm), cream to pinkish cream, becoming pale brown at maturity, rapidly staining reddish brown when bruised (FIG. 4B). Odor resembling ham or bacon when fresh (Bessette et al. 2019; Gilbertson and Ryvarden 1986), edible, taste described as sour or like fermented ham (Bessette et al. 2019). Basidiospores ovoid to ellipsoid, 5–9 × 4–7 µm (mean ± SD = 6.9 × 5.5 ± 1.04 × 0.82 µm), hyaline, with a refractive oil drop in 3% KOH, smooth and nonamyloid. Basidia clavate 25–30 × 8–10 µm with 4 sterigmata, simple septate at the base (Gilbertson and Ryvarden 1986). Hyphal system dimitic with binding and generative hyphae; generative hyphae 7–18 µm diam, thin-walled, hyaline with simple septa. Binding hyphae 5–10 µm, thick-walled 1–3 µm, hyaline and occasionally septate (Gilbertson and Ryvarden 1986). Terminal, pyriform to globose chlamydospores present (A. Loyd, personal observation) and clamp connections absent from both generative and binding hyphae.

Habitat: Fruiting on the ground, usually close to the base of hardwood trees and most commonly with oaks (*Quercus*), presumably attached to dead roots, found in both urban and forested areas.

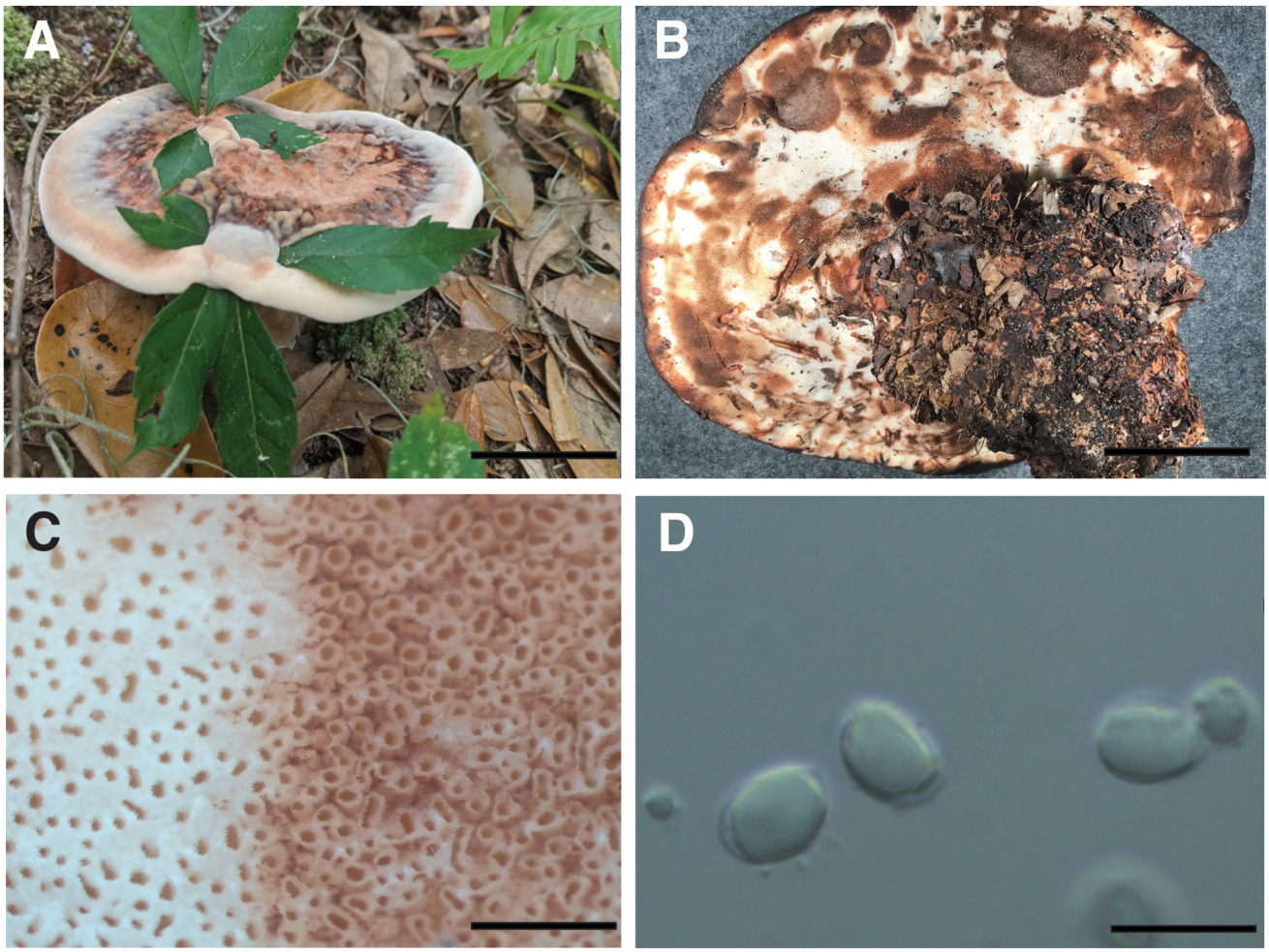

Figure 4. A. Basidiomata of *Kusaghiporia persicinus* in situ (photo Curtis Peyer). B. Underside of fresh basidiomata showing the prominent central stipe and the brown bruising reaction on the white pore surface. C. Pores of fresh basidiomata. D. Hyaline basidiospores with a prominent refractive oil droplet. Bars: A = 8 cm; B = 4 cm; C = 6 mm; D = 15 µm.

Distribution: Eastern United States, including the Gulf Coast and Mid-Atlantic regions, with verified specimens (based on molecular data) from Florida, Louisiana, North Carolina, South Carolina, Maryland, and Tennessee and morphologically identified specimens or high-quality photos from Alabama, Mississippi, Texas, Georgia, Virginia, Pennsylvania, Arkansas, and New Jersey (FIG. 1)
Specimens examined: USA. FLORIDA: Escambia County, Pensacola, on soil close to *Quercus virginiana*, 30 Jun 2019, *William Lingo* (FLAS-F-67995, FLAS-F-67996 and FLAS-F-67998); Alachua County, Gainesville, on ground close to *Quercus virginiana*, 25 Jul 2017, *Eric Linder* (FLAS-F-67999); Micanopy, on ground close to *Quercus* trees, 10 Jul 2019, *Jason A. Smith* (FLAS-F-67997); Putnam County, Hawthorne, on Ordway-Swisher Biological Station, close to hardwood forest, 23 Oct 2016, *Nicole Reynolds NKR-40* (FLAS-F-60416); 20 Jun 2017, *Matthew E. Smith, Laurel Kaminsky, David Borland* (FLAS-F-61002); Sarasota County, Sarasota, on ground close to *Quercus virginiana*, 16 Oct 2017, *Tammy Kovar* (FLAS-F-68000); NORTH CAROLINA: Wake County, Raleigh, growing on mulch close to *Quercus alba*, 16 Jul 2011, *Charles Hodges* (NCSLG-18429); SOUTH CAROLINA: Pickens County, Clemson University, growing on *Quercus alba*, 11 Aug 2020, *Bruce Fraedrich AL1031* (FLAS-F-68088); substrate undetermined, 1872, *Henry W. Ravenel* (BPI 216927, isotype); MARYLAND: Anne Arundel County, Linthicum, 6006 Medora Road, growing on *Quercus alba*, 18 Aug 2020, *Geoffrey Thill AL1033* (FLAS-F-68089).

DISCUSSION

The generic placement of *Kusaghiporia persicinus* has been historically controversial, as discussed previously by Burdsall and Banik (2001). For more than 40 years, *K. persicinus* was placed in the genus *Laetiporus* (Gilbertson 1981). *Kusaghiporia persicinus* was first described as *Polyporus persicinus* by Berkeley and Curtis (1853), but Murrill (1903) later transferred the species to the genus *Scutiger* based on the morphology (central stipe, fleshy-tough fruiting body, and spores that are smooth and hyaline). However, the type species of the genus *Scutiger, S. tuberosus*, belongs to the order Russulales (http://www.indexfungorum.org/). Ryvarden (1972) transferred *K. persicinus* again to the genus *Meripilus* based on the central stipe that is connected to decaying roots, the concentric zones on the cap, and the flesh that bruises when damaged (Ryvarden and Johansen 1980). However, *Meripilus* has a monomitic hyphal system and is a white-rot fungus, whereas *K. persicinus* has a dimitic hyphal system and is a brown-rot fungus (Fidalgo and Mepk 1967; Larsen and Lombard 1988). Furthermore, the genus *Meripilus* and members of the Meripilaceae are phylogenetically distant from the Laetiporaceae (Justo et al. 2017; Larsen and Lombard 1988). Gilbertson (1981) transferred the species yet again, this time to *Laetiporus*, based on its brown-rot ecology, hyphal system, and spore characteristics. Nonetheless, Corner (1984) ignored this placement and transferred *L. persicinus* to *Buglossoporus* based on similarities with the type *Buglossoporus quercinus*. However, Corner's (1984) analysis of *K. persicinus* was based primarily on specimens from gardens and secondary forests in the Malay Peninsula, and he also mentions that *K. persicinus* can be found in Brazil and Africa. We therefore conclude that Corner's (1984) concept of *K. persicinus* included a wide range of taxa with similar characteristics. It is unclear whether Corner studied the type of *K. persicinus* from South Carolina (USA) or not. Although *K. persicinus* is morphologically similar to *Buglossoporus quercinus* in the dimitic hyphae, brown rot, hyaline nonamyloid spores, lack of cystidia, and brown bruising, *B. quercinus* is a temperate European taxon that is not centrally stipitate and is associated almost exclusively with old growth oak forests (Szczepkowski et al. 2019). Furthermore, a recent phylogenetic study by Han et al. (2016) found that *B. quercinus* is related to *Neolentiporus* and only distantly related to *Laetiporus* and other Laetiporaceae (Han et al. 2016). Although *K. persicinus* was generally accepted within the genus *Laetiporus* during the 1980s and 1990s, Teixeira (1992) nonetheless transferred *K. persicinus* to *Cladoporus* as *C. persicinus* (Teixeira 1992). However, *Cladoporus* has been considered a synonym of *Laetiporus* (Ryvarden 1987). Ryvarden (1987) proposed the conservation of the genus *Laetiporus* because it is broadly accepted in mycological, arboriculture, and forest pathology literature (Ryvarden 1987).

In addition to the many obligate synonyms for *K. persicinus*, there are also a number of heterotypic synonyms that have been applied to this species, all of which were described after the publication of the basionym *Polyporus persicinus* (Berkeley and Curtis 1853). These descriptions of potential synonyms include taxa from a wide array of countries, including Brazil, Jamaica, Sri Lanka, Congo, and Australia (https://www.mycobank.org/). Some of the species that are suggested as synonyms of *L. persicinus* include *Polyporus talpae* (Brazil), *Amauroderma brittonii* (Jamaica), *P. mesotalpae* (Sri Lanka), *P. beardsleei* (Florida), *P. subcolossus* (Congo), and *Dendrochaete vallata* (Australia).

Lindner and Banik (2008) suggested that *K. persicinus* was not a synonym of *P. talpae* Cooke based on the morphological characteristics and 28S rDNA sequences of specimens from Puerto Rico (PR-2 and PR-6326, which they referred to as *Polyporus cf. talpae*). Fidalgo and Mepk (1967) also suggest that *P. talpae* is monomitic, whereas *K. persicinus* is well documented as dimitic (Gilbertson 1981), another reason to suggest that *P. talpae* is not a synonym of *K. persicinus*. Our analysis of the 28S rDNA (FIG. 2) suggests that *P. cf. talpae* may represent a third species of *Kusaghiporia*. However, we refrain from transferring this species to the genus *Kusaghiporia* until the type specimen of *P. talpae* can be reevaluated and new collections from the type locality (in Brazil) can be used to clarify the identity of *P. talpae* using molecular data.

Murrill (1910) described the stipitate polypore *Amauroderma brittonii* from Jamaica and mentioned the dark, ornamented spores. However, Fidalgo and Mepk (1967) later examined the holotype of *A. brittonii* revealing only smooth and subglobose to ovate spores. They concluded that the spores described by Murrill (1910) were probably the result of contamination (Fidalgo and Mepk 1967). *Amauroderma brittonii* has also been treated as synonym of *P. talpae* based on fruiting body morphology, hyphal system (monomitic and absence of clamp connections), and smooth spores (Fidalgo and Mepk 1967). However, more work is needed to determine whether *A. brittonii* is a synonym of *P. talpae* or is a separate and unique species.

Lloyd (1916) described *P. mesotalpae* from Sri Lanka, but Fidalgo and Mepk (1967) suggested that *P. mesotalpae* was a synonym of *P. talpae* (and therefore a synonym of *K. persicinus*). Given the geographic separation between Sri Lanka and the type localities of the other species in the Americas, we think it is unlikely that *P. mesotalpae* is a synonym of either taxon. Lloyd (1924) later also described *P. beardsleei* from Florida. Given the morphological description and the location, we think it is unlikely that *P. beardsleei* is a later synonym of *K. persicinus*, since the description of the context tissue of the pileus (white) does not match the description by Gilbertson and Ryvarden (1986) or our observations that the context tissue is pinkish to tan with concentric faint to dark zones in *K. persicinus*. Beeli (1930) described *P. subcolossus* from the Congo, and some previous authors have considered this species to be a later synonym of *K. persicinus*. Based on the morphological characteristics and location of the description, it is possible that this species is actually an older name for *Kusaghiporia usambarensis*. However, no spores were mentioned in the original description, so more work is needed to evaluate this possibility (Beeli 1930). Cunningham (1965) named *Dendrochaete vallata* based on collections of a wood-decay polypore from buried wood at the base of dead trees in Queensland, Australia. Although it is possible that *Dendrochaete* could be appropriate as a generic name for this group, this synonym is not supported by either morphology or geography. Cunningham (1965) clearly states that all of the species he placed in the genus *Dendrochaete* are characterized by peculiar setae on their caps, and he also notes that *D. vallata* is monomitic and does not bruise when handled. Based on these morphological differences and on the known distribution of *D. vallata*, we can safely rule out *D. vallata* as a synonym of *K. persicinus* (and as a potential alternative genus name for *Kusaghiporia*). Furthermore, *Dendrochaete* is currently considered a synonym of *Echinochaete* (Polyporaceae) and is therefore phylogenetically distant from Laetiporaceae (Justo et al. 2017; Ota et al. 2009).

Burdsall and Banik (2001) suggested that *K. persicinus* (then *L. persicinus*) needed a new generic placement because of its molecular and morphological differences from the core *Laetiporus* species. However, at the time, there was little information regarding the relationships among *L. persicinus* and other brown-rot taxa. The publication of the new genus *Kusaghiporia*, with a description and phylogenetic placement of the type, *K. usambarensis* J. Hussein, S. Tibell & Tibuhwa (Hussein et al. 2018, http://www.indexfungorum.org/ 2021) from Tanzania, provided an opportunity to clarify the identity of *K. persicinus*. Although Hussein et al. (2018) did not include a comprehensive comparison with *K. persicinus* in their study, our molecular and morphological data presented here support the close relationship to *K. usambarensis*.

Our multilocus phylogeny (FIG. 3) based on four loci (18S, 28S, *rpb2*, and *tef1*) provides strong support for the placement of *K. persicinus* within the genus *Kusaghiporia* and also suggests that *Kusaghiporia* is likely the sister group of *Laetiporus* sensu stricto. This relationship was supported by both maximum likelihood and Bayesian analyses. A similar topology that shows a sister relationship between *K. persicinus* and *K. usambarensis* was also recovered in the 18S, *rpb2*, and *tef1* phylogenies (SUPPLEMENTARY FIGS. 2, 3, and 4) but was not resolved in the ITS or 28S phylogenies (FIG. 2; SUPPLEMENTARY FIG. 1). We could not evaluate the relationship of *K. persicinus* and *K. usambarensis* based on ITS because there is no ITS sequence available for *K. usambarensis*. In our individual analysis of the 28S, the results were slightly different; *K. persicinus* is resolved as the sister group of a larger group of fungi that includes *K. usambarensis, Polyporus* cf. *talpae*, and *Laetiporus* sensu

stricto including two *Wolfiporia* species, *W. dilatohypha* and *W. cartilaginea*, that are apparently distantly related to the type species *W. cocos* (FIG. 2). *Polyporus* cf. *talpae* and *K. usambarensis* are part of a supported monophyletic group, but both species are on long branches. It is also notable that many of the basal nodes in this 28S phylogeny had low bootstrap support values.

Although the ITS region was not as phylogenetically informative as other regions, it was useful as a DNA barcode to evaluate the genetic similarity among isolates examined in our study and to examine the similarity in this region to other related taxa in Laetiporaceae. In our phylogenetic analyses of ITS rDNA, we compared *K. persicinus* specimens from different locations (North Carolina, South Carolina, Louisiana, Tennessee, Maryland, and Florida) to corroborate their similarity. All isolates of *K. persicinus* had almost identical ITS rDNA sequences (99.5% similarity) and were resolved as a well-supported monophyletic group. The ITS phylogeny also confirms a pattern that we observed in all of the various loci that we analyzed; *K. persicinus* is only distantly related to species within *Laetiporus* sensu stricto.

We also examined the morphology of the available specimens and compared them with the isotype specimen from the U.S. National Fungus Collection (BPI 216927) to confirm that all of these collections represent *K. persicinus*. Morphologically, *K. persicinus* is similar to *K. usambarensis* in that both have annual and centrally stipitate basidiomata that are spongy when young (Hussein et al. 2018). The two species also share similarities in the coloration of the upper pileus and in the hyphal system (Hussein et al. 2018). Both species have creamy whitish pores that stain reddish brown when bruised. Both also produce a white spore print. However, *K. persicinus* is morphologically different from *K. usambarensis* in the basidiospore size and shape. Basidiospores of *Kusaghiporia usambarensis* are globose to subglobose and 5.9 × 5.7 µm (Hussein et al. 2018), whereas those of *K. persicinus* are ovoid to ellipsoid and 6.9 × 5.5 µm (FIG. 4D). The morphological features are consistent with the phylogenetic evidence that *K. persicinus* fits better in *Kusaghiporia* than in *Laetiporus*.

Our analysis suggests that *K. persicinus* is limited to the southeast and southern Mid-Atlantic regions of the United States (FIG. 1), but this species could be distributed in other geographic regions in the United States that were not sampled. It is also possible that *K. persicinus* and/or relatives are also found in other tropical to subtropical areas of the world but have yet to be discovered. A species similar to *K. usambarensis* and *K. persicinus* was recently reported from Brazil (Oliveira et al. 2019, unpublished manuscript), and it was suggested that the new specimens are morphologically similar to *Polyporus talpae*. They also noted that the Brazilian collections are superficially similar to *K. usambarensis* from Tanzania, including the dimitic hyphal system (with both generative and skeletal hyphae), the white pore surfaces that bruise when handled, the large and centrally stipitate basidiomata, and the globose to subglobose smooth and hyaline basidiospores. Although it seems likely that the Brazilian collections of *Polyporus talpae* may represent a third species of *Kusaghiporia*, additional morphological comparisons and phylogenetic analyses will be needed to confirm this hypothesis.

There are several polypore fungi in the Gulf Coast and Mid-Atlantic regions that could potentially be confused with *K. persicinus* based on morphological features. *Phaeolus schweinitzii* (Fr.) Pat, *Onnia tomentosa* (Fr.) P. Karst, *Ischnoderma resinosum* (Schrad.) P. Karst., and *Microporellus dealbatus* (Berk. & M.A. Curtis) Murril are all occasionally misidentified as *K. persicinus*. These taxa all have a similar pileal surface (brownish to rusty brown) and have a central stipe, with the exception of the sessile species *Ischnoderma resinosum*. However, *P. schweinitzii* and *O. tomentosa* can be separated from *K. persicinus* because they occur strictly on conifers and have a darker pore surface and context tissue than *K. persicinus* (Bessette et al. 2019; Sinclair and Lyon 2005). Although both *I. resinosum* and *M. dealbatus* occur on hardwood hosts just like *K. persicinus*, both of these species produce clamp connections whereas *K. persicinus* does not (Bessette et al. 2019). In addition, *P. schweinitzii* has a velvety-like cap and when young is yellow or orange and *I. resinosum* has a bracket-shaped or nearly semicircular velvety cap; therefore, it is easy to distinguish them from *K. persicinus* when they are fresh (Bessette et al. 2019; Gilbertson 1981; Lindner and Banik 2008; Sinclair and Lyon 2005).

Lastly, we note that it would have been possible to propose a taxonomic scheme that recognizes *K. persicinus* in the genus *Laetiporus* by recognizing a broader concept of the genus. However, in this case, we chose to recognize the two well-known taxa within *Kusaghiporia* (*K. persicinus* and *K. usambarensis*) as a separate genus because both species share the unifying features of large, brown, centrally stipitate basidiomata that bruise rapidly when handled and typically fruiting from decayed roots that are away from the base of the tree hosts (Gilbertson 1981; Hussein et al. 2018; Murrill 1904). In contrast, most of the taxa in the core *Laetiporus* clade produce bright orange to yellow, laterally stipitate basidiomata and fruit on trunks of trees (Bessette et al. 2019; Gilbertson 1981). We also hold off on making additional taxonomic changes for now because we note

that *Wolfiporia dilatohypha* and *W. cartilaginea* are only included in our analyses of ITS and 28S due to the lack of sequences of other regions (FIG. 2; SUPPLEMENTARY FIG. 1). However, they are resolved in the core *Laetiporus* clade (unsupported in the ITS phylogeny), distant from *W. cocos* (the type species of *Wolfiporia)* and *W. hoelen*. A similar result was found by Lindner and Banik (2008). Species in the genus *Wolfiporia* generally produce white resupinate fruiting bodies (Ryvarden and Gilbertson 1984) and are quite different from the other taxa treated here. This also suggests that as additional taxa within Laetiporaceae continue to be sampled and more DNA sequences become available, the phylogenetic resolution and our understanding of these fungi may necessitate future changes.

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DISCLOSURE STATEMENT

No potential conflict of interest was reported by the author(s).

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