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Relationships among North American and Japanese *Laetiporus* isolates inferred from molecular phylogenetics and single-spore incompatibility reactions

Mark T. Banik[1]
Daniel L. Lindner

US Forest Service, Northern Research Station, Center for Forest Mycology Research, One Gifford Pinchot Drive, Madison, Wisconsin 53726

Yuko Ota

Forestry and Forest Products Research Institute, 1 Matsunosato, Tsukuba, Ibaraki 305-8687, Japan

Tsutomu Hattori

Kansai Research Center, Forestry and Forest Products Research Institute, Kyoto, Kyoto 612-0855, Japan

Abstract: Relationships were investigated among North American and Japanese isolates of *Laetiporus* using phylogenetic analysis of ITS sequences and single-spore isolate incompatibility. Single-spore isolate pairings revealed no significant compatibility between North American and Japanese isolates. ITS analysis revealed 12 clades within the core *Laetiporus* clade, seven of which are known to occur in North America (including Hawaii and the Caribbean), three in Japan, two in South America, three in Europe and one in South Africa. The identity of *L. sulphureus* s.s. has yet to be determined and could be either *L.* ''*sulphureus*'' (clade C), which appears to be restricted to Europe and occurs on angiosperms and gymnospersm, or *L.* ''*sulphureus*'' (clade E), which is found in Europe, North America and South America exclusively on angiosperms. Three clades, one from the Caribbean, one from Hawaii and one from South Africa, have yet to be named formally. Of the three *Laetiporus* species found in Japan two have been named recently (*L. cremeiporus* and *L. montanus*) and one has been epitypified (*L. versisporus*). The single-spore incompatibility and ITS data support recognition of the three Japanese taxa as distinct biological and evolutionary species.

Key words: evolution, Fungi, Polyporaceae, Polyporales, root rot, sulfur shelf

INTRODUCTION

Laetiporus Murrill is an important polypore genus with worldwide distribution. Members of this genus have long been recognized as important forest pathogens, causing a cubical brown rot in living and dead wood of both conifers and angiosperms. *Laetiporus* is one of the few polypore genera that produce conspicuous, edible fruiting bodies. *Laetiporus* fruiting bodies, in addition to being harvested for consumption, also have been investigated for medicinal and antimicrobial purposes (Turkoglu et al. 2007).

Laetiporus sulphureus (Bull.:Fr) Murill is the type of the genus and, along with most members of the genus, is easily recognized by its bright orange, multilobed fruiting bodies. Members of the genus produce fruiting bodies with dimitic-binding hyphal systems, simple septa and hyaline spores. *Laetiporus persicinus* (Berk & M.A. Curtis) Gilbertson is similar in micromorphology to *L. sulphureus* but has brown to tan fruiting bodies that occur as rosettes arising from the soil. *Laetiporus sulphureus* and *L. persicinus* along with *L. sulphureus* var. *semialbinus* Peck were until recently the only widely recognized members of the genus in North America (Peck 1906, Gilbertson and Ryvarden 1986).

Banik and Burdsall (1999) developed a technique based on changes in culture morphology to assess incompatibility among *Laetiporus* single-spore isolates (SSI). Four reaction types were observed, and the nuclear condition of the mycelium in each type was established with allozyme analysis. The results of sibling SSI pairings indicated the presence of a unifactorial mating system in *Laetiporus*. SSI pairings, RFLP typing, morphological, ecological and geographic differences were used to elucidate the presence of previously unrecognized species within the *L. sulphureus* complex (Banik and Burdsall 2000, Banik et al. 1998). Based on these findings Burdsall and Banik (2001) recognized these species within the genus in North America: *L. cincinnatus* (Morgan) Burds, Banik & Volk, *L. conifericola* Burds & Banik, *L. gilbertsonii* Burds var. *gilbertsonii*, *L. gilbertsonii* var. *pallidus*, *L. huroneinsis* Burds & Banik, *L. persicinus* and *L. sulphureus*.

Lindner and Banik (2008) used ITS and nLSU DNA sequence analysis to investigate relationships among North American species of *Laetiporus* and among other genera of brown-rot polypores in North American, including *Leptoporus*, *Phaeolus*, *Pycnoporellus* and *Wolfiporia*. LSU sequence analysis placed *Laetiporus* firmly in the ''Antrodia clade'' of the polyporoid clade and also identified *L. persicinus* as

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[1] Corresponding author. E-mail: mbanik@fs.fed.us

not closely related to core *Laetiporus* species. *Wolfiporia dilatohypha* was found to be a closely related sister group of core *Laetiporus* species, possessing an ITS region that could be easily aligned with other *Laetiporus* species. None of the other brown-rot polypore species tested were closely related to *Laetiporus*. Subsequent sequence analysis of another *Wolfiporia* species, *W. cartilaginea*, demonstrated that its LSU sequence differed from that of *W. dilatohypha* by just a few base pairs (author unpubl). Together these two species form a clade that is closely related to, but distinct from, the core *Laetiporus* clade, thus serving as an excellent outgroup for *Laetiporus* sequence analysis.

Lindner and Banik (2008) found the variability in the *Laetiporus* ITS region to be suitable for differentiating North American biological species, thus supporting the species designations established by Burdsall and Banik (2001). Five clades were recognized within *Laetiporus*, with each clade corresponding to one of the described species. The ''*L. sulphureus* s.s.'' clade of Lindner and Banik (2008) included several sequences of European origin, thus seeming to promote the conspecificty of North American and European *L. sulphureus*. However an analysis by Vasaitis et al. (2009) found two clades (C and E) that contain European *Laetiporus* isolates from angiosperms. This indicates that the name ''*L. sulphureus* s.s.'' could be applied to two distinct clades, one from Europe, North America and South America exclusively associated with angiosperms (E) and one from Europe associated with gymnosperms and angiosperms (C). Further work is needed to establish conclusively the identity of *L. sulphureus* s.s.

Many species of *Laetiporus* from various areas of the world have yet to be fully characterized. The analysis of Lindner and Banik (2008) identified two potentially undescribed *Laetiporus* species, one from the Caribbean and one from Hawaii, while Vasaitis et al. (2009) identified multiple potentially undescribed species from Asia and one from South Africa. In eastern Asia several species of *Laetiporus* have been described, including *L. sulphureus* var. *miniatus*, *L. sulphureus* var. *sulphureus* and *L. versisporus* (Imazeki and Hongo 1989, Núñez and Ryvarden 2001). Relationships among *Laetiporus* taxa occurring in Japan were assessed by Ota and Hattori (2008) with phylogenetic analysis of the ITS, β-tubulin and EF1α genes as well as incompatibility tests. Ota and Hattori (2008) identified three major taxa: *L. sulphureus/versisporus* group, *L. sulphureus* var. *miniatus* white pore form and *L. sulphureus* var. *miniatus* yellow pore form. Their results demonstrated conclusively that *Laetiporus versisporus* is an anamorphic form of ''*L. sulphureus* var. *sulphureus*'' as found in Japan. *L. sulphureus/versisporus* sequences exhibited intragroup variation, falling into two distinct clades for all three of the genes analyzed. Some isolates in this group possessed sequence polymorphisms attributed to both clades. Ota and Hattori (2008) suggested speciation via hybridization might be ongoing in the *L. sulpureus/versisporus* group.

For the purposes of this paper these names will be applied to taxa recognized by Ota and Hattori (2008): ''*L. sulphureus* var. *miniatus* white pore form'' will be referred to as *L. cremeiporus* Y. Ota & T. Hatt., ''*L. sulphureus* var. *miniatus* yellow pore form'' will be *L. montanus* Cerny ex Tomsovsky & Jankovsky and ''*L. sulpureus/versisporus* group'' will be *L. versisporus* (Lloyd) Imazeki. *L. cremeiporus* and *L. versisporus* are names based on current nomenclatural work being conducted in Japan (Ota et al. 2009), while *L. montanus* is a name based on the species description by Tomsovsky and Jankovsky (2008).

The goal of our current work is to examine relationships among the *Laetiporus* taxa established by Ota and Hattori (2008) and Lindner and Banik (2008) from Japan and North America. Further work and a broader sampling effort will be needed to fully characterize worldwide *Laetiporus* species, many of which undoubtedly remain undescribed.

MATERIALS AND METHODS

Pairing tests.—Single-spore isolates (SSI) were obtained from *Laetiporus* fruiting bodies in Japan and the United States with the techniques of Banik and Burdsall (1999). Five SSI from different fruiting bodies were selected for these North American species: *L. cincinnatus*, *L. conifericola*, *L. gilbertsonii* (two from *L. gilbertsonii* var. *pallidus* and three from *L. gilbertsonii* var. *gilbertsonii*) and *L. "sulphureus"* (clade E) (see TABLE I). Isolates chosen were those used in Banik et al. (1998) and Banik and Burdsall (1999) or were identified to species based on pairings with known tester isolates. Collection information for the isolates is presented in Banik and Burdsall (2000) and Lindner and Banik (2008) except for *L. sulphureus*, TJV-95-56, Baraga County, Michigan; *L. cincinnatus*, DA-35, Dane County, Wisconsin; *L. cincinnatus*, HHB-15746, Iowa County, Wisconsin. *Laetiporus huroniensis* was not included in the pairing study because studies with SSI of this species indicated it produces pairing reactions that are not interpretable, possibly because it is homothallic (Banik and Burdsall 2000).

Japanese SSI were chosen from one of three *Laetiporus* incompatibility groups established by Ota and Hattori (2008): the ''*L. sulphureus* var. *miniatus* white pore'' group, hereafter referred to as *L. cremeiporus* (clade D); ''*L. sulphureus* var. *miniatus* yellow pore'' group, hereafter referred to as *L. montanus* (clade A2); and ''*L. sulphureus/versisporus*'' group, hereafter referred to as *L. versisporus* (clade G) (TABLE II). We documented relationships be-

TABLE I. Clades identified within genus *Laetiporus* using the ITS region

Names applied to *Laetiporus* clades by various authors							
Current paper[a]	Vasaitis et al. (2009)	Ota & Hattori (2008)	Lindner & Banik (2008)	Tomsovsky & Jankovsky (2008)	Pore color	Host	Distribution
Laetiporus huroniensis (clade A1)	clade A	—	*Laetiporus huroniensis*	—	yellow	conifer	North America
Laetiporus montanus (clade A2)	clade A	*L. sulphureus* var. *miniatus* yellow pore	—	*Laetiporus montanus*	yellow	conifer	Europe, Japan
Laetiporus conifericola (clade B)	clade B	—	*Laetiporus conifericola*	—	yellow	conifer	North America
Laetiporus "sulphureus" (clade C)	clade C	—	Unknown *Laetiporus* sp. (GenBank)	—	yellow	angiosperm/ conifer	Europe
Laetiporus cremeiporus (clade D)	clade D	*L. sulphureus* var. *miniatus* white pore	—	—	white	angiosperm/ conifer (?)	Japan, Korea
Laetiporus "sulphureus" (clade E)	clade E	—	*Laetiporus sulphureus* s.s.	—	white/yellow	angiosperm	North America, South America & Europe
Laetiporus gilbertsonii (clade F)	clade F	—	*Laetiporus gilbertsonii*	—	white/yellow	angiosperm	North America & South America
Laetiporus versisporus (clade G)	clade G	*L. sulphureus/ versisporus* clade I & II	—	—	white/yellow	angiosperm	Japan, Korea
Laetiporus sp (clade H)	clade H	—	—	—	—	—	South Africa
Laetiporus sp. (clade I)	clade I	—	Unknown *Laetiporus* sp. (Hawai'i)	—	yellow	angiosperm	Hawai'i
Laetiporus sp. (clade J)	clade J	—	Unknown *Laetiporus* sp. (Caribbean)	—	yellow	angiosperm	Caribbean
Laetiporus cincinnatus (clade K)	clade K	—	*Laetiporus cincinnatus*	—	white	angiosperm	North America

[a] Clade designations in the current paper follow FIG. 1.

TABLE II. Results of 280 pairings between *Laetiporus* single-spore isolates from North America and Japan

Taxa paired[b]	Number of pairings	Ratings of pairings by test location[a]		
		positive	not interpretable	negative
L. cremeiporus (clade D) × *L. "sulphureus"* (clade E)	25	0 / 1	0 / 1	25 / 23
L. cremeiporus (clade D) × *L. cincinnatus* (clade K)	25	0 / 0	0 / 0	25 / 25
L. cremeiporus (clade D) × *L. gilbertsonii* (clade F)	25	0 / 0	0 / 0	25 / 25
L. cremeiporus (clade D) × *L. conifericola* (clade B)	25	0 / 0	0 / 0	25 / 25
L. montanus (clade A2) × *L. "sulphureus"* (clade E)	20	0 / 0	0 / 0	20 / 20
L. montanus (clade A2) × *L. cincinnatus* (clade K)	20	0 / 0	0 / 0	20 / 20
L. montanus (clade A2) × *L. gilbertsonii* (clade F)	20	0 / 0	0 / 0	20 / 20
L. montanus (clade A2) × *L. conifericola* (clade B)	20	0 / 0	0 / 0	20 / 20
L. versisporus (clade G) × *L. "sulphureus"* (clade E)	25	0 / 0	1 / 2	24 / 23
L. versisporus (clade G) × *L. cincinnatus* (clade K)	25	0 / 4	4 / 3	21 / 18
L. versisporus (clade G) × *L. gilbertsonii* (clade F)	25	0 / 2	9 / 0	16 / 23
L. versisporus (clade G) × *L. conifericola* (clade B)	25	0 / 6	5 / 1	20 / 18

[a] Numerals to the left of slash represent the number of pairings for each category recorded at Tsukuba, Japan, while those to the right represent pairing recorded at Madison, Wisconsin.

[b] Taxonomic names and clade designations follow TABLE I.

tween the taxonomic names used in the current paper and previous papers (TABLE I); to promote uniformity across publications all clade designations in the current paper follow those of Vasaitis et al. (2009). Five isolates from each incompatibility group were selected except for *L. montanus* for which only four were available. The five *L. cremeiporus* SSI all came from different fruiting bodies; four *L. montanus* SSI came from two different fruiting bodies (two isolates from two separate fruiting bodies), and five *L. versisporus* SSI came from four fruiting bodies (one SSI from three separate fruiting bodies and two SSI from a fourth fruiting body). Collection information for all Japanese SSI is presented in Ota and Hattori (2008).

Single-spore isolates selected were given a random number, and pairings between SSI were numbered sequentially to mask the identity of the isolates paired. A complete set of pairings consisted of pairing each SSI from Japan with each SSI from North America for a total of 280 pairings. The complete set was replicated twice, once in Madison, Wisconsin, and once in Tsukuba, Ibaraki, Japan, (TABLE II) following the paring protocol of Banik and Burdsall (1999). Pairings were read after approximately 1 and 2 wk and assigned this rating: positive (+) exhibiting an increase in density and pigmentation (IDAP) indicative of sustained nuclear cohabitation; negative (−) characterized by the formation of a dark line (DL), separation of the SSI without the formation of a line (SWAL) or fusion reactions indicative of no sustained nuclear migration; or as not interpretable (TABLE II).

Phylogenetic analyses.—All DNA amplification, sequencing and alignment protocols followed Lindner and Banik (2008). New sequence data were deposited in GenBank and alignments deposited in TreeBase. Maximum parsimony and Bayesian analyses were run on ITS sequences with methods described in Lindner and Banik (2008) with the exception that for Bayesian inference 6 000 000 generations were performed with samples taken in increments of 100. The first 15 000 trees (25%) were considered burn-in and were excluded from construction of the consensus tree. After running the analysis the standard deviation of the split frequencies was examined to confirm it was approximately 0.01 and the plot of the generations versus the log probability of the data (the log likelihood values) was examined to confirm it had reached the stationary phase. Two independent Bayesian runs were performed and posterior probabilities were averaged across runs.

The ITS regions for all isolates used in pairings were sequenced in Madison, Wisconsin. All ITS regions matched those deposited in GenBank by Ota and Hattori (2008) and Lindner and Banik (2008). The ITS regions of the isolates used in the pairing were aligned with a selection of other Japanese isolates (Ota and Hattori 2008) and North American isolates (Lindner and Banik 2008). A broader selection of ITS sequences from GenBank also was included to ensure sampling covered all available geographic regions of the world. This selection included representatives from all clades identified by Vasaitis et al. (2009) (FIG. 1). The ITS region from *Wolfiporia cartilaginea* (voucher 13121) from Japan also was sequenced for this study.

RESULTS

Pairing tests.—All 100 pairing reactions among *L. cremeiporus* SSI and the four North American *Laetiporus* SSI were rated as incompatible (DL) in Tsukuba. Reaction ratings were similar in Madison except for one questionable and one positive reaction with two *L.* "*sulphureus*" (clade E) SSI (TABLE II). All 80 reactions between *L. montanus* SSI and North American SSI were rated as incompatible (DL) at both locations (TABLE II).

Interactions between *L. versisporus* SSI and North

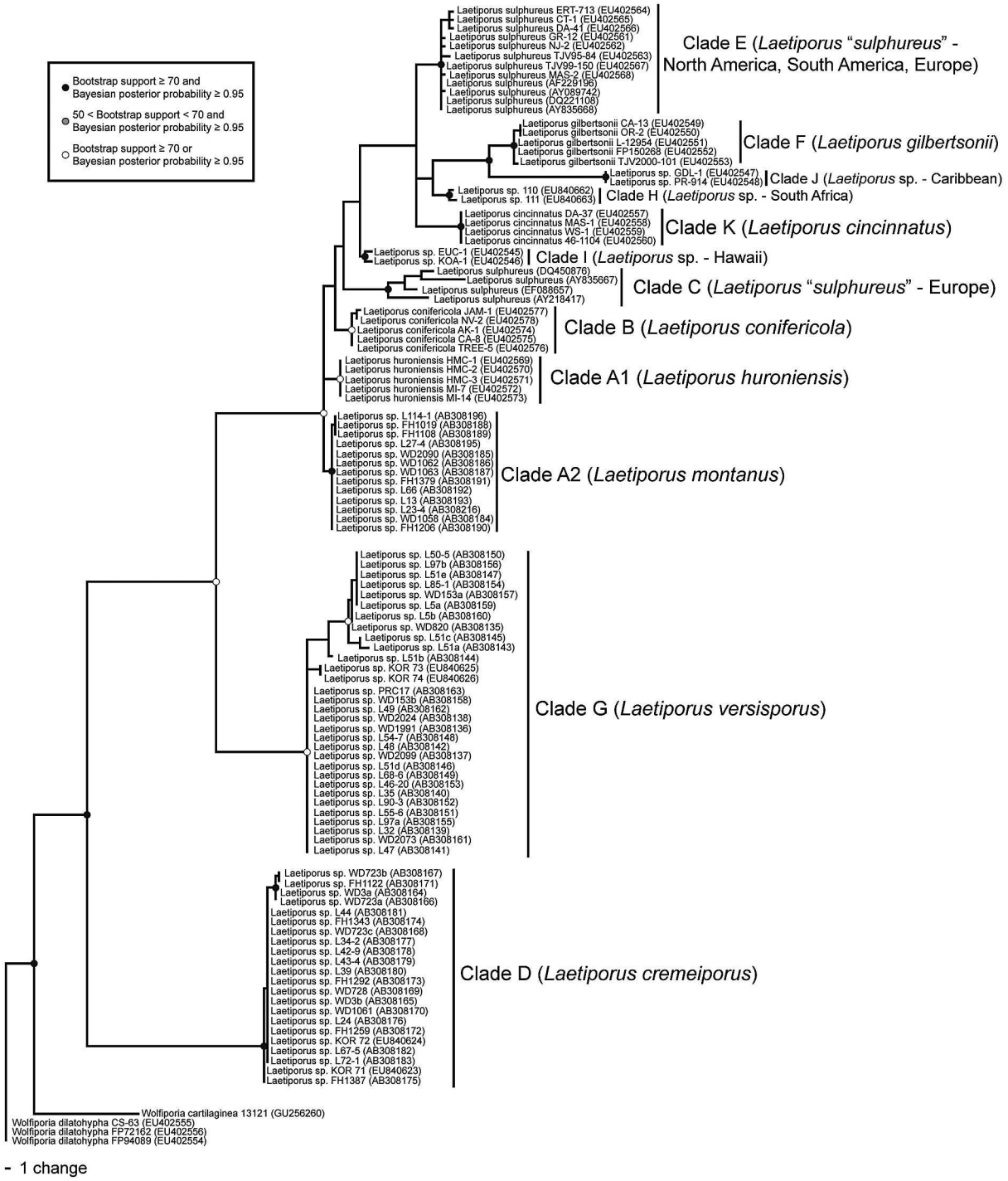

FIG. 1. Phylogenetic relationships among *Laetiporus* isolates based on analyses of ITS sequences. The tree was generated with MrBayes. All isolates are labeled with collection numbers when available and GenBank accession numbers are in parentheses.

American SSI exhibited a greater degree of variation than those involving the other two Japanese incompatibility groups. Consequently more inconsistencies in pairing results were observed between the two study locations. Overall none of the pairings performed at Tsukuba were rated as compatible. Madison ratings demonstrated a low level of compatibility between several taxa. *Laetiporus cremeiporus* was 4% compatible with *L.* ''*sulphureus*'' (clade E), while *L. versisporus* was 16%, 8% and 24% compatible respec-

tively with *L. cincinnatus*, *L. gilbertsonii* and *L. conifericola*.

Phylogenetic analyses.—The maximum parsimony and Bayesian analyses produced similar overall trees, with the exception that Bayesian analysis showed statistical support (posterior probability ≥ 95%) for a single clade (G) containing all *L. versisporus* isolates. A total of 12 clades were identified (TABLE I, FIG. 1) with moderate to strong statistical support (bootstrap ≥ 70% or posterior probability ≥ 95%). The 12 clades represent eight clades reported by Lindner and Banik (2008) from North America and Europe, plus three clades reported from Japan by Ota and Hattori (2008), plus one clade reported from South Africa by Vasaitis et al. (2009).

DISCUSSION

Based on data from pairings conducted at both Madison and Tsukuba, *Laetiporus cremeiporus* and *L. montanus* are distinct incompatible groups from the four North American taxa in this study: *L. ''sulphureus''* (clade E), *L. cincinnatus*, *L. gilbertsonii* and *L. conifericola*. Phylogenetic analysis of the ITS region revealed *Laetiporus cremeiporus* to be one of the most distinctive *Laetiporus* clades examined so far, despite having been recognized as a variety of *L. sulphureus* s.l. (Ota and Hattori 2008). *Laetiporus montanus* in contrast is closely related to previously recognized taxa and falls in the ''Conifericola Clade'' identified by Lindner and Banik (2008). In the absence of pairing data it would be reasonable to conclude that *Laetiporus montanus* and *L. conifericola* are conspecific because the two clades differ by a small number of base pairs and both taxa occur on conifers. However the lack of compatible pairings indicates that if indeed these two taxa were at one time conspecific they have lost the ability to interbreed. Based on this observation it seems reasonable at this time to consider them distinct taxa. Mating compatibility information for *L. huroniensis* and *L. montanus* would be desirable, but SSI of *L. huroniensis* unfortunately do not appear to form compatible reactions, even within a single fruiting body.

Paring data for *L. versisporus* were not as clear as for the other two Japanese taxa; however the data support recognition of this group as distinct from other taxa investigated. At both test sites a majority of the pairings was rated incompatible but a significant number of pairings could not be unambiguously rated. At Madison a number of pairings were rated as compatible, especially among SSI of *L. versisporus* and *L. cincinnatus* and *L. conifericola*. Allozyme analysis (unpubl) confirmed that in many of these compatible reactions stable nuclear exchange did occur. Despite indications of low levels of compatibility, phylogentic analyses did not reveal a close relationship between *L. versisporus* and any of the North American clades. Although parsimony analyses consistently split *L. versisporus* into two or three clades, the mating reactions of this group (Ota and Hattori 2008) and Baysian analyses support the coherence of this group. *Laetiporus versisporus* is unusual in that it produces a conspicuous anamorph. The common production of an anamorphic state might have implications for its nuclear condition, which could affect its pairing behavior, perhaps resulting in pairings that are not easily interpreted. In this respect it might be similar to *L. huroniensis*, which exhibits unusual pairing reactions, possibly indicative of homothallism or amphithallism (Banik and Burdsall 2000). In *L. huroniensis* only the teleomorph has been documented in nature.

Overall phylogenetic analysis and pairing data both support recognition of the three Japanese taxa as distinct from the *Laetiporus* species known from North America and the rest of the world. Of the three *Laetiporus* taxa found in Japan two (*L. montanus* and *L. cremeiporus*) were named and one (*L. versisporus*) was epitypified (Tomsovsky and Jankovsky 2008, Ota et al. 2009). The name *Laetiporus sulphureus* is typified based on European material, and it appears this name should not be applied to any taxa currently known from Japan. Based on the analyses of Vasaitis et al. (2009), the name *L. sulphureus* could be applied to either *L. ''sulphureus''* '' (clade C), which appears to be restricted to Europe and occurs on angiosperms and gymnosperms, or *L. ''sulphureus''* (clade E), which is found in Europe, North America and South America exclusively on angiosperms. Further collecting in Europe will be needed to resolve this problem.

Data from North America, Japan and now between North American and Japanese isolates indicate that within *Laetiporus* ITS-based phylogenetic analyses and pairings between SSI are both excellent tools for delimiting taxa. However ITS-based data have several advantages over SSI pairings, which might make ITS the more widely applicable tool for species identification and delimitation. Advantages of ITS include the ability to test nonviable and historic material, as well as the ease with which samples can be assigned to known groups. Now that baseline congruence has been established between pairing and ITS data, it might be possible in future studies to rely solely on DNA-based data to determine taxon status in genus *Laetiporus*.

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