SYSTEMATICS AND PHYLOGENY

Phylogenetic classification of *Trametes* (Basidiomycota, Polyporales) based on a five-marker dataset

Alfredo Justo & David S. Hibbett

Clark University, Biology Department, 950 Main St., Worcester, Massachusetts 01610, U.S.A.
Author for correspondence: *Alfredo Justo, ajusto@clarku.edu*

Abstract: The phylogeny of *Trametes* and related genera was studied using molecular data from ribosomal markers (nLSU, ITS) and protein-coding genes (RPB1, RPB2, TEF1-alpha) and consequences for the taxonomy and nomenclature of this group were considered. Separate datasets with rDNA data only, single datasets for each of the protein-coding genes, and a combined five-marker dataset were analyzed. Molecular analyses recover a strongly supported trametoid clade that includes most of *Trametes* species (including the type *T. suaveolens*, the *T. versicolor* group, and mainly tropical species such as *T. maxima* and *T. cubensis*) together with species of *Lenzites* and *Pycnoporus* and *Coriolopsis polyzona*. Our data confirm the positions of *Trametes cervina* (= *Trametopsis cervina*) in the phlebioid clade and of *Trametes trogii* (= *Coriolopsis trogii*) outside the trametoid clade, closely related to *Coriolopsis gallica*. The genus *Coriolopsis*, as currently defined, is polyphyletic, with the type species as part of the trametoid clade and at least two additional lineages occurring in the core polyporoid clade. In view of these results the use of a single generic name (*Trametes*) for the trametoid clade is considered to be the best taxonomic and nomenclatural option as the morphological concept of *Trametes* would remain almost unchanged, few new nomenclatural combinations would be necessary, and the classification of additional species (i.e., not yet described and/or sampled for molecular data) in *Trametes* based on morphological characters alone will still be possible. Alternative scenarios to divide the trametoid clade in five or ten genera were considered but if any of these options were to be adopted morphological distinction of the segregated genera and the ascription of additional species to any of these genera would be very difficult and in some cases impossible. The genera *Artolenzites*, *Coriolopsis* (as currently typified), *Coriolus*, *Cubamyces*, *Cyclomycetella*, *Lenzites*, *Poronidulus*, *Pseudotrametes* and *Pycnoporus* are considered synonyms of *Trametes*.

Keywords generic concepts; large-scale phylogeny; multi-marker analysis; nomenclature; Polyporaceae; Polyporales; taxonomy; *Trametes*

Supplementary Material Figures S1–S5 are available in the free Electronic Supplement to the online version (Supplementary Data section) of this article (http://ingentaconnect.com/content/iapt/tax).

■ INTRODUCTION

The genus *Trametes* Fr. (Polyporales, Basidiomycota) is characterized by the combination of pileate basidiocarps, poroid hymenophore, trimitic hyphal system, thin-walled smooth basidiospores not reacting in presence of Melzer's reagent and production of a white-rot type of wood decay (Gilbertson & Ryvarden, 1987). It is a cosmopolitan genus present in virtually any type of forest ecosystem in temperate, boreal, and tropical areas (Gilbertson & Ryvarden, 1987). *Trametes versicolor* ("turkey tails") is among the most common and widespread species of mushroom-forming fungi (Fig. 1) and its whole genome is currently being sequenced (http://www.jgi.doe.gov/). To give an idea of how widespread and ecologically important *Trametes* species are the USDA databases (http://nt.ars-grin.gov/fungaldatabases/fungushost/FungusHost.cfm) currently register 295 plant species in which *Trametes versicolor* has been recorded, including angiosperms (e.g., *Acer*, *Betula*, *Eucalyptus*, *Malus*, *Populus*, *Quercus*) and conifers (e.g., *Abies*, *Cupressus*, *Larix*, *Pinus*). While the concept of *Trametes* just outlined is widely accepted (e.g., Ryvarden, 1991; Ryvarden & Gilbertson, 1994; Bernicchia, 2005) it is not the only one that has been proposed. Corner (1989) had a much wider generic concept that synonymized under *Trametes* 15 other genera of Polyporales with trimitic hyphal systems (Table 1), including taxa with stipitate basidiocarps (e.g., *Microporus*) and genera causing a brown-rot type of decay (*Daedalea*, *Fomitopsis*). Though he used the name *Trametes* for this genus the oldest generic name for *Trametes* sensu Corner would be *Daedalea*. Ryvarden (1991) defined the *Trametes*-group of the family Polyporaceae Corda by the combination of trimitic hyphal system and white-rot type of decay and there he included all the genera synonymized by Corner (1989) with the exception of the brown-rot *Daedalea* and *Fomitopsis* and the stipitate *Lignosus*. Ryvarden (1991) also included some genera not considered by Corner (1989) like *Cryptoporus*, *Elmerina* and *Fomitella* in the *Trametes*-group of the Polyporaceae (Table 1).

The conflicting concepts about the generic limits of *Trametes* and the lack of diagnostic morphological features in the group of trimitic Polyporales have resulted in a large number of nomenclatural combinations in the genus. The MycoBank database (Crous & al., 2004, http://www.MycoBank.org) registers

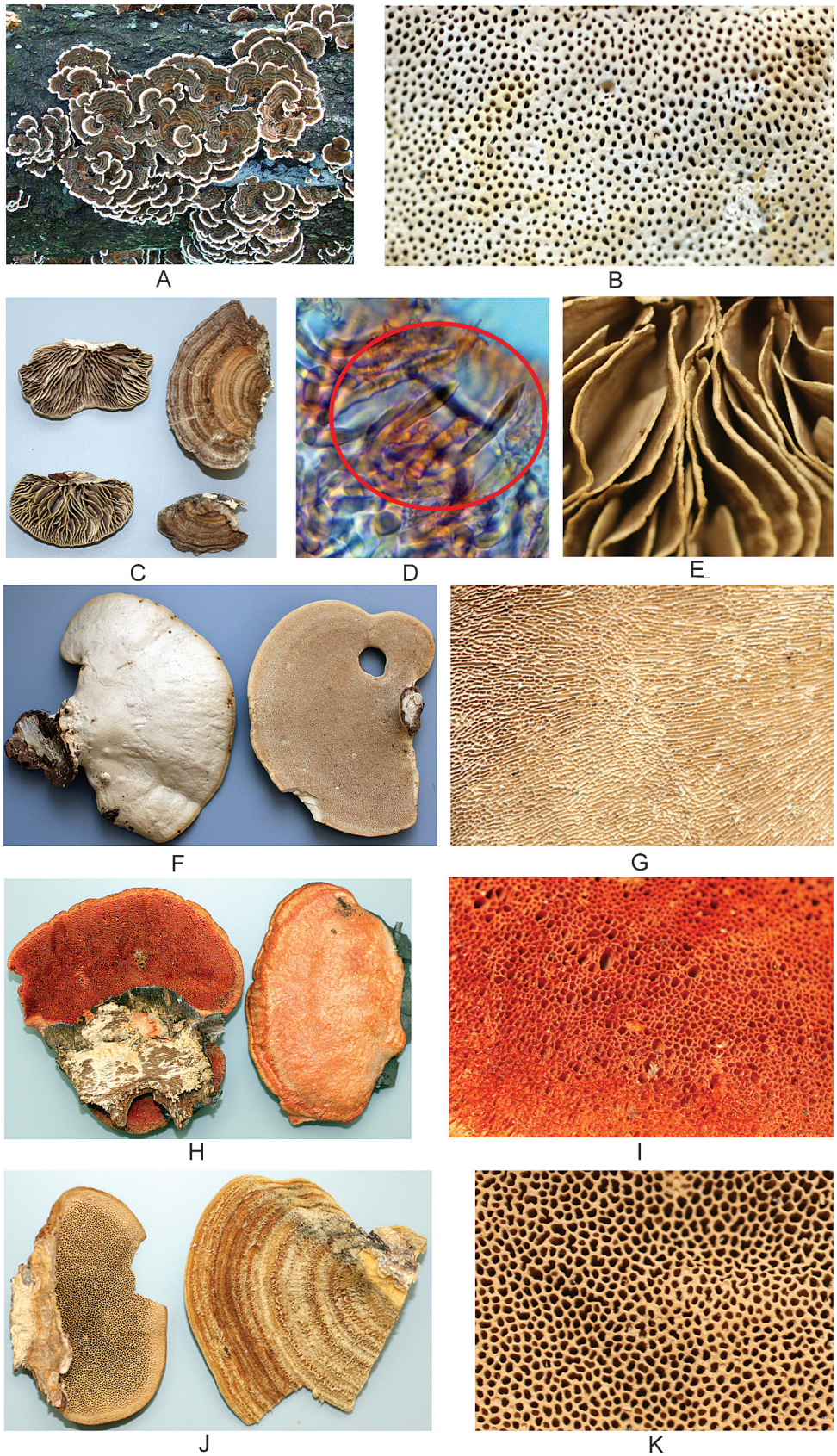

Fig. 1. Morphological overview of the trametoid clade. **A,** *Trametes versicolor*; **B,** hymenophore of *Trametes suaveolens*; **C,** *Lenzites betulinus*; **D,** sword-like hyphae of *L. betulinus*; **E,** hymenophore of *L. betulinus*; **F,** *Trametes elegans*; **G,** hymenophore of *T. elegans*; **H,** *Pycnoporus cinnabarinus*; **I,** hymenophore of *P. cinnabarinus*; **J,** *Coriolopsis polyzona*; **K,** hymenophore of *C. polyzona*.

Table 1. Overview of the genera of *Trametes* sensu Corner (1989) and the *Trametes*-group sensu Ryvarden (1991).

Genus (year of publication)	*Trametes* sensu Corner (1989)	*Trametes* group sensu Ryvarden (1991)	Phylogenetic placement
Cerrena Gray (1821)	Yes	Yes	Polyporales /phlebioid clade (Ko & Jung, 1999a; Lee & Lim, 2010; present study)
Coriolopsis Murrill (1905)	Yes	Yes	Polyporales /core polyporoid clade/ Type species (*C. polyzona*) in the /trametoid clade. At least two other independent lineages in the /polyporus clade (present study)
Cryptoporus (Peck) Shear (1902)	No	Yes	Polyporales /core polyporoid clade /polyporus clade (Ko & Jung, 1999b; Binder & al., 2005; present study)
Daedalea Pers. (1801)	Yes	No	Polyporales /antrodia clade (Ko & Jung 1999b; Binder & al., 2005; present study)
Daedaleopsis J. Schröt. (1888)	Yes	Yes	Polyporales /core polyporoid clade /polyporus clade (Ko & Jung, 1999b; Binder & al., 2005; present study)
Datronia Donk (1966)	Yes	Yes	Polyporales /core polyporoid clade /polyporus clade (Ko & Jung, 1999b; Hibbett & Donoghue, 2001; Binder & al., 2005; present study)
Earliella Murrill (1905)	Yes	Yes	Polyporales /core polyporoid clade /polyporus clade (present study)
Elmerina Bres. (1912)	No	Yes	Tremellales (Larsson & al., 2004)
Fomitella Murrill (1905)	No	Yes	Unknown; no molecular data are available for the type species (*Fomitella supina*)
Fomitopsis P. Karst. (1881)	Yes	No	Polyporales /antrodia clade (Ko & Jung, 1999b; Hibbett & Donoghue, 2001; Binder & al., 2005; present study)
Hexagonia Fr. (1838)	Yes	Yes	Polyporales /core polyporoid clade /polyporus clade (Ko & Jung 1999b; present study)
Lenzites Fr. (1836)	Yes	Yes	Polyporales /core polyporoid clade /trametoid clade (Ko & Jung, 1999b; Binder & al., 2005; Tomsovský & al., 2006; present study)
Lignosus Lloyd ex Torrend (1920)	Yes	No	Polyporales /core polyporoid clade /polyporus clade (Sotome & al., 2008; present study)
Megasporoporia Ryvarden & J.E. Wright (1982)	Yes	Yes	Polyporales /core polyporoid clade /polyporus clade (Ko & Jung, 1999b; present study)
Microporus P. Beauv. (1805)	Yes	Yes	Polyporales /core polyporoid clade /polyporus clade (Sotome & al., 2008; present study)
Mollicarpus Ginns (1984)	Yes	Yes	Unknown; no molecular data are available for the type species (*Mollicarpus cognatus*)
Pycnoporus P. Karst. (1881)	Yes	Yes	Polyporales /core polyporoid clade /trametoid clade (Tomsovský & al., 2006; present study)
Trichaptum Murill (1904)	Yes	Yes	Hymenochaetales (Hibbett & Donoghue, 1995; Binder & al., 2005; Larsson & al., 2006)

750 specific and infraspecific names in *Trametes* and Index Fungorum (http://www.indexfungorum.org) registers 818, but the actual number of species that belong in *Trametes* sensu Ryvarden (1991) is much lower, with 18 species reported from North America, 9 from Europe, and ca. 20 species in the Neotropics (Gilbertson & Ryvarden, 1987; Ryvarden & Gilbertson, 1994; Quanten, 1997; Ryvarden, 2000). Kirk & al. (2008) estimate the global diversity of the genus is ca. 50 species.

The most inclusive phylogenetic analysis of the order Polyporales (Binder & al., 2005) used four ribosomal DNA (rDNA) markers (nuclear ribosomal large subunit [nLSU], mitochondrial large subunit [mtLSU], nuclear ribosomal small subunit [nSSU], mitochondrial small subunit [mtSSU]) in approx. 124 species of Polyporales. According to their results, the order Polyporales was divided into four informally named clades, viz. antrodia clade, core polyporoid clade, phlebioid clade, and residual polyporoid clade (throughout the paper clade names are written with no capitals and not italicized to avoid confusion with formal taxonomic names). The type species of *Trametes* (*T. suaveolens*) was placed in the core polyporoid clade together with many of the genera traditionally classified in the families Polyporaceae and Ganodermataceae (Donk) Donk (Ryvarden, 1991).

Recent molecular studies have helped to clarify the higher-level and generic relationships of polyporoid fungi, and some of the genera considered as part of the *Trametes*-group have been placed outside Polyporales: *Trichaptum* in Hymenochaetales (Hibbett & Donoghue, 1995; Binder & al., 2005; Larsson & al., 2006), and *Elmerina* in Tremellales (Larsson & al., 2004). Other genera in the *Trametes*-group or *Trametes* sensu Corner (1989) belong in Polyporales but are not closely related to *Trametes*: *Cerrena* belongs in the phlebioid clade (Ko & Jung, 1999a; Lee & Lim, 2010) and the brown-rot genera *Daedalea* and *Fomitopsis* are placed in the antrodia clade (Ko & Jung, 1999b; Hibbett & Donoghue, 2001; Binder & al., 2005). Based on the studies just mentioned, the articles by Tomšovský & al. (2006) and Sotome & al. (2008), and the results presented here the remaining genera of the *Trametes*-group belong in the core polyporoid clade (Table 1; Fig. 1).

The most inclusive phylogenetic studies with a focus on *Trametes* are those of Tomšovský & al. (2006), who studied ITS (internal transcribed spacers 1 and 2 including 5.8S nuclear rDNA) and nLSU sequences in 11 isolates representing seven European species, and Ko & Jung (1999b), who studied mtSSU sequences in seven isolates of *Trametes*. Collectively, these studies support the placement of most *Trametes* species in the core polyporoid clade, but also suggested that *Trametes* is paraphyletic or polyphyletic, with *Lenzites* and *Pycnoporus* species intermixed with *Trametes* species.

Molecular data also showed that some species classified in *Trametes* by Corner (1989), Gilbertson & Ryvarden (1987), and Ryvarden & Gilbertson (1994) do not belong in the genus: (i) *Trametes trogii* is more closely related to *Coriolopsis gallica* than to the other species of *Trametes* (Ko & Jung, 1999b; Tomšovský & al., 2006); (ii) *Trametes consors* belongs in the genus *Cerrena* (Ko & Jung, 1999a); (iii) Tomšovský (2008) showed that *Trametes cervina* is probably related to *Ceriporiopsis* and has been transferred to the new genus *Trametopsis* (Tomšovský, 2008).

All the phylogenetic studies mentioned so far, with the exception of Sotome & al. (2008) and Lee & Lim (2010), rely exclusively on rDNA data. Protein-coding genes such as the RNA polymerase II largest subunit (RPB1), RNA polymerase II second-largest subunit (RPB2), and translation elongation factor 1-alpha (TEF1) have proven to be useful for phylogenetic reconstruction at different taxonomic levels in Agaricomycetes (e.g., Matheny & al., 2002, 2007; Frøslev & al., 2005) but data from these genes are lacking for many species of *Trametes* and putatively related taxa. The purpose of the present study is to perform a phylogenetic study focused on *Trametes* and related genera using data from ribosomal markers (nLSU, ITS) and protein-coding genes (RPB1, RPB2, TEF1), examine and discuss the taxonomic and nomenclatural implications of the results and finally propose a formal taxonomic arrangement for the trametoid polypores at the generic level.

■ MATERIALS AND METHODS

Fungal isolates and DNA extraction. — Specimens and culture collections were retrieved from the Forest Products Laboratory (USDA Forest Service, Madison, Wisconsin, U.S.A.) supplemented with new collections made in the northeastern and southeastern United States, with a total of 117 isolates (Appendix). Sampling focused on species of *Trametes* sensu Gilbertson & Ryvarden (1987), with special attention to type species of genera currently believed to be synonymous with *Trametes*, and genera considered as part of the *Trametes*-group by Ryvarden (1991).

Cultures were grown for 2–3 weeks at 25°C–30°C on solid media (MEA: 20 g malt extract, 0.5 g yeast extract, 20 g agar in 1 l of water). When the plate was totally covered with new mycelium the tissue was scrapped with sterile scalpels and transferred to a 1.5 ml microtube and ground with a sterile plastic pestle. In the case of specimens a small portion of the fruiting body was ground with liquid nitrogen. Cell lysis proceeded 1 h at 65°C with the addition of 600 ml extraction buffer (50 mM EDTA, 50 mM Tris-HCl, 3% SDS, pH 8). Cell debris, polysaccharides, and proteins were separated from aqueous DNA portions through two purification steps with equal volumes of phenol : chloroform (1 : 1) and chloroform : isoamylalcohol (24 : 1). Total DNA was precipitated with the addition of 3 M sodium acetate (0.1 Vol.%) and isopropanol (0.54 Vol.%) and incubation for 30 to 60 min at −20°C. The DNA pellets were washed in 1 ml 70% EtOH, dried at 65°C for 5 to 15 minutes and resuspended in 100 mL sterile H_2O. Dilutions of the original DNA extraction, usually ranging from 1 : 10 to 1 : 500, were used in the PCR experiments.

PCR amplification and sequencing. — The ITS region (approx. 600–700 bp) was amplified for all 117 samples studied here using the primer pair ITS-1F/ITS4 (White & al., 1990; Gardes & Bruns, 1993). Sequence data of nLSU, RPB1, RPB2, and TEF1 were obtained for a subset of 28 taxa. We successfully amplified these four genes for all selected taxa, except for

the TEF1 sequence of *Coriolopsis gallica*. An RPB1 sequence was also generated for the AFTOL (http://aftol.org/) isolate of *Pycnoporus cinnabarinus*, for which data of all other markers studied here have been already generated (Matheny & al., 2007). For nLSU (approx. 1300 bp) the primer pair LR0R/LR7 (Vilgalys Lab, http://www.biology.duke.edu/fungi/mycolab/primers) was used. For rDNA markers the following PCR protocol was used: (1) initial denaturation at 95°C for 2 min, (2) denaturation at 94°C for 45 s, (3) annealing at 50°C for 1 min 10 s, (4) extension at 72°C for 2 min, (5) repeat for 34 cycles starting at step 2, (6) leave at 72°C for 10 min (Binder & al., 2010). Sequencing primers for ITS and nLSU were the same used for PCR and in the case of nLSU with two additional internal primers: LR3R and LR5 (Vilgalys Lab).

RPB1, RPB2, and TEF1 were amplified with the following specifications. The area between conserved domains A and C of RPB1 (approx. 1400 bp) was amplified using the primer pair RPB1-Af and RPB1-Cr (Stiller & Hall, 1997; Matheny & al., 2002). In some cases the primer RPB1-2.2f (Binder & al., 2010) was used as an alternative to RPB1-Af, giving a slightly shorter product (approx. 1000 bp). Additional sequencing primers were: RPB1-2f, RPB1-2.1f, RPB1-2.2f, and RPB1-2.1r (Frøslev & al., 2005). The area between conserved domains 5 and 11 of RPB2 (approx. 2100 bp) was amplified in two separate reactions using the primer pairs RPB2-f5F/RPB2-7.1R (Liu & al., 1999; Matheny, 2005) and RPB2-6.9F/RPB2-b11R1 (Matheny & al., 2007). Additional sequencing primers were RPB2-b6F/RPBb6R2 (Matheny, 2005; Matheny & al., 2007) for the first PCR and RPB2-f7cF/RPB2-b8.2R (Liu & al., 1999; Matheny & al., 2007) for the second PCR. Approximately 900–1200 bp of TEF1 was amplified using the primer pair EF1-983F/EF1-2212R (Rehner & Buckley, 2005). Additional sequencing primers were EF1-1577F and EF1-1567R (Rehner & Buckley, 2005).

For all protein-coding genes the following "touchdown" PCR protocol was used: (1) initial denaturation at 94°C for 2 min, (2) denaturation at 94°C for 40 s, (3) annealing at 60°C for 40s (minus 1 C per cycle), (4) extension at 72°C for 2 min, (5) repeat for 9 cycles starting at step 2, (6) denaturation at 94°C for 45 s, (7) annealing at 53°C for 1 min 30 s, (8) extension at 72°C for 2 min, (9) repeat for 36 cycles starting at step 6, (10) leave at 72°C for 10 min.

The amplification products for all markers were sequenced using BigDye 3.1 terminator sequencing chemistry (Applied Biosystems, Foster City, California, U.S.A.) and run on an Applied Biosystems 3130 Genetic Analyzer. Raw data were processed using Sequencher v.4.7 (GeneCodes, Ann Arbor, Michigan, U.S.A.). Expected fragment lengths and degree of primer overlap for each one of the protein-genes, as well as possible alternatives to the primers used here, is posted at http://wordpress.clarku.edu/polypeet/datasets/primer-information/.

Sequence alignment and phylogenetic analyses. — In addition to the sequences generated here an additional 111 sequences were retrieved from GenBank (Benson & al., 2011) and come mainly from the molecular studies mentioned in the introduction. Accession numbers of ITS sequences used in the analysis of the trametoid clade are given in Fig. 3 and all other accesion numbers are listed in the Appendix. The sequences were aligned using MAFFT v.6 (Katoh & Toh, 2008; http://mafft.cbrc.jp/alignment/server/). The strategy G-INS-i was selected for all genes except for the alignment of ITS sequences across the Polyporales where the strategy Q-INS-i was used. The alignments were manually corrected using MacClade v.4.08 (Maddison & Maddison, 2002; http://macclade.org/). For the combined datasets each marker was aligned separately and then concatenated in MacClade. Six different datasets were assembled for the phylogenetic analyses (Table 2).

Three different phylogenetic analyses were performed in all the datasets: (i) Maximum likelihood analyses (ML) were run in the RAxML servers, v.7.2.8 (http://phylobench.vitaleit.ch/raxmlebb/index.php; Stamatakis & al., 2008), under a GTR model with one hundred rapid bootstrap replicates. (ii) Equally weighted parsimony analyses were performed using PAUP*

Table 2. Description and comparison of the datasets used for the phylogenetic analysis. The *Trametes*-group is considered in the sense of Ryvarden (1991).

Dataset	Ingroup sequences	Outgroup	Total characters (gaps included)	Parsimony-informative characters	Consistency index/retention index	Well-supported nodes
nLSU+ITS	41 *Trametes*-group taxa and 24 other Polyporales	*Boletopsis leucomelaena* and *Hydnellum geogenium* (Thelephorales)	1825	345 (19%)	0.38/0.62	28 out of 52 (54%)
ITS	155 trametoid clade sequences	*Dentocorticium sulphurellum* and *Lopharia cinerascens* (Polyporales)	565	157 (28%)	0.51/0.91	22 out of 71 (31%)
RPB1	28 *Trametes*-group taxa and 8 other Polyporales	*Camarophyllus basidiosus* and *Cantharelulla umbonata* (Agaricales)	1178	561 (48%)	0.32/0.43	21 out of 33 (64%)
RPB2	28 *Trametes*-group taxa and 19 other Polyporales	*Boletopsis leucomelaena* and *Hydnellum geogenium* (Thelephorales)	2096	814 (39%)	0.25/0.36	24 out of 46 (52%)
TEF1	25 *Trametes*-group taxa and 11 other Polyporales	*Boletopsis leucomelaena* and *Hydnellum geogenium* (Thelephorales)	1012	321 (31%)	0.35/0.37	10 out of 25 (40%)
nLSU+ITS+RPB1+RPB2+TEF1	28 *Trametes*-group taxa and 21 other Polyporales	*Boletopsis leucomelaena* and *Hydnellum geogenium* (Thelephorales)	6022	1981 (33%)	0.30/0.40	41 out of 47 (87%)

v.4.0.b10 (Swofford, 2002). One thousand heuristic search replicates were performed with starting trees generated by stepwise addition with random addition sequences followed by tree bisection reconnection branch swapping. Up to two trees were kept in each replicate. Parsimony bootstrap analysis was performed with 1000 replicates, each with 10 random taxon addition sequences and branch swapping set to subtree pruning and regrafting. (iii) Bayesian analyses (BY) were run using MrBayes v.3.1 (Ronquist & Huelsenbeck, 2003) at the Cipres Science Gateway (Miller & al., 2010; http://www.phylo.org/) for 10 million generations, under a GTR model, with four chains, and trees sampled every 100 generations. The initial burn-in phase was set to 2.5 million generations and after examining the graphic representation of the likelihood scores of the sampled trees that was confirmed to be an adequate value for all datasets. A fifty percent majority-rule consensus tree was computed using the remaining trees. A node is considered to be well supported if it is supported in at least two of the three analyses by a bootstrap (BS) value equal or greater than 75% and/or a posterior probability (PP) equal or greater than 0.95.

For RPB1, RPB2, and TEF1 two alternative datasets were analyzed using ML, one excluding 3rd codon positions in coding regions, which are prone to saturation, and another using amino acid instead of nucleotide data. For all three genes the phylogenetic resolution of the resulting trees and their support values decreased with the exclusion of 3rd codon positions or the use of amino acid data (data not shown), therefore nucleotide data including 3rd codon positions were used for these genes.

A search for potential conflicts between the rDNA (nLSU+ITS) dataset and each of the protein-coding genes was performed by comparing the resulting trees for each dataset and looking for strongly supported positive conflict. No conflicts were detected between the datasets analyzed in the present study.

■ RESULTS

New sequences and alignments. — A total of 230 new sequences were generated for this study: 117 ITS, 28 nLSU, 29 RPB1, 29 RPB2, and 27 TEF1. A comparative overview of the different datasets used for the phylogenetic analyses is given in Table 2. The alignments have been deposited in TreeBASE (http://purl.org/phylo/treebase/phylows/study/TB2:S11678).

nLSU+ITS dataset of Polyporales (Fig. 2). — Three major lineages, the core polyporoid, phlebioid and antrodia clades, appear as well supported (Fig. 2). The genus *Grifola* Gray, which in some analyses (Binder & al., 2005; García-Sandoval & al., 2011) appears as a member of the antrodia clade, appears in our analyses as sister to the core polyporoid clade. The latter can be divided in three well-supported subclades, here named as trametoid clade, polyporus clade, and dentocorticium clade.

The trametoid clade includes all sampled species of *Trametes* as defined by Gilbertson & Ryvarden (1987) and Ryvarden & Gilbertson (1994) with the exception of *Trametes cervina* (= *Trametopsis cervina*), placed in the phlebioid clade and *Trametes trogii* (= *Coriolopsis trogii*) placed in the polyporus clade. It also includes *Lenzites betulinus*, *Coriolopsis polyzona*, and the genus *Pycnoporus*. Some groups in this clade are well supported: (i) The type of the generic name (*T. suaveolens*) is grouped with the *T. versicolor* group; (ii) *L. betulinus* is grouped with *T. gibbosa*, *T. membranacea*, *T. pavonia*, and *T. pocas*; (iii) the three *Pycnoporus* species also are grouped together. However, relationships between these groups and the placement of other species of *Trametes* are unresolved in the analyses. Our results from the nLSU+ITS dataset are in general agreement with the data presented by Ko & Jung (1999b) and Tomšovský & al. (2006).

The polyporus clade includes the type genus of the family (*Polyporus*), which in its current taxonomic concept (e.g., Bernichia, 2005) is clearly polyphyletic. Six genera of the *Trametes*-group (Ryvarden, 1991) are placed in this clade: *Cryptoporus*, *Daedaleopsis*, *Datronia*, *Earliella*, *Megasporoporia*, and *Microporus*. *Coriolopsis* species appear in two separate groups, and also separate from the type of the genus (*C. polyzona*) that is placed in the trametoid clade. In general the internal relationships of this clade receive low support.

The dentocorticium clade includes *Dentocorticum sulphurellum* and *Lopharia cinerascens*. It is placed, with no significant support, as sister to the trametoid clade.

The remaining member of the *Trametes*-group sampled here, the genus *Cerrena*, is placed in the phlebioid clade.

ITS dataset of the trametoid clade (Fig. 3). —All members of the trametoid clade present in the nLSU+ITS dataset, except *T. pocas* for which no ITS is available, are represented here, together with two additional taxa that were not included in the nLSU+ITS dataset as no nLSU data is available: *Trametes* sp. (collection AJ354) and *Lenzites warnieri*.

Eighteen major lineages, representing morphological species or monophyletic species-complexes (e.g., *T. versicolor* group), are recovered in the analyses. The sequences of *T. junipericola* and *Trametes* sp. appear in an unresolved position together with *T. conchifer* and the *T. versicolor* group. With the exception of *Pycnoporus sanguineus* (including *P. coccineus*) and *T. hirsuta* each one of these 18 major lineages is well supported. However, only the sister-taxa relationship between *L. betulinus* and *T. gibbosa* and the grouping of the *T. versicolor* group and related species receive significant statistical support.

RPB1, RPB2, and TEF1 datasets of the Polyporales (Figs. S1–S3). —With the exception of the 5′ end of intron 2 of RPB1 (approx. 470 bp) all intron regions for the three protein-genes had to be excluded almost entirely because of ambiguous alignment. The original alignments including all introns are available at http://wordpress.clarku.edu/polypeet/datasets/.

The general topology of the RPB1 (Fig. S1) and RPB2 (Fig. S2) trees is similar to the nLSU+ITS trees (Fig. 2). Support values and the overall resolution are generally better in the RPB1 trees than in the nLSU+ITS or the RPB2 trees (Table 2). The dentocorticium clade appears as sister to the clade including the polyporus and trametoid clades, with good statistical support, in the RPB1 trees. It appears as sister to the polyporus clade, with no statistical support, in the RPB2 tree. The TEF1 trees (Fig. S3) are very poorly resolved. Because of this lack of resolution a four-marker dataset (nLSU+ITS+RPB1+RPB2) was

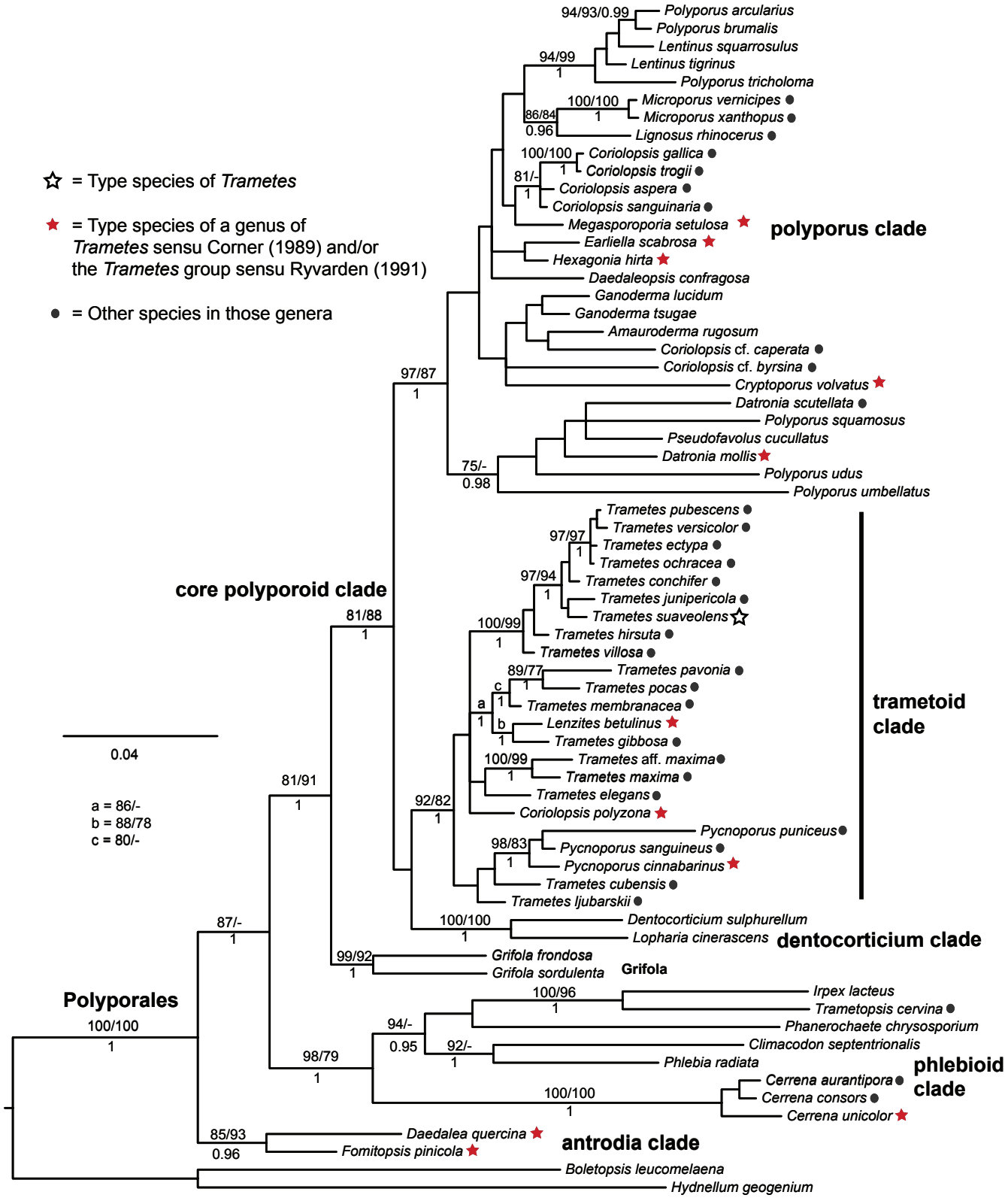

Fig. 2. Fifty percent majority-rule consensus tree from the BY analysis of the nLSU+ ITS dataset of the Polyporales. BS values from the ML and MP analyses ≥75 (ML/MP) and PP ≥ 0.95 from the BY analysis for nodes supported in at least two of the analyses are given on or below the branches.

analyzed and the resulting trees (results not shown) compared to the same dataset with TEF1 data. Inclusion or exclusion of TEF1 does not significantly change the topology or support values in the resulting trees, therefore TEF1 sequences were used in the combined five-marker dataset though it appears that this gene contributes very little to resolving the higher-level phylogeny of Polyporales.

Combined (nLSU+ITS+RPB1+RPB2+TEF1) dataset of the Polyporales (Fig. 4). —*Fomitopsis* (antrodia clade) appears as sister to the remaining Polyporales, followed by the split between the phlebioid clade and the remaining taxa. *Grifola* appears as sister to the core polyporoid clade, which again can be subdivided in three subclades: trametoid clade and polyporus clade as sister taxa and the dentocorticium clade as sister to the clade containing both.

The internal topology of the trametoid clade is much better resolved than in the nLSU+ITS or any of the single gene datasets with 87% of the nodes receiving strong support (Table 2). Five major lineages are recovered. To facilitate the discussion each lineage is here informally named using the oldest generic name available for that group: (i) The pycnoporus clade includes *Pycnoporus* and *T. cubensis*, which are placed as sister to all other members of the clade. (ii) The artolenzites clade includes *Trametes elegans* and the *T. maxima* group. (iii) The coriolopsis clade includes only *Coriolopsis polyzona*. (iv) The lenzites clade includes *L. betulinus*, *T. gibbosa*, *T. pavonia*, and *T. membranacea*. (v) The trametes clade includes *T. villosa*, *T. hirsuta*, *T. suaveolens*, *T. conchifer*, and the *T. versicolor* group. *Coriolopsis polyzona* is placed as sister to the lenzites clade but this relationship does not get significant statistical support. Except for this and the relationship between some members of the *T. versicolor* group all other sister-taxa relationships are well supported.

The polyporus clade is also better resolved in the combined dataset with three well-supported major lineages: (i) the ganoderma clade includes *Ganoderma*, *Amauroderma*, and and some *Coriolopsis* species; (ii) the datronia clade includes *Polyporus* p.p. and *Datronia*; (iii) the lentinus clade includes *Polyporus* p.p., *Lentinus*, *Coriolopsis* p.p., *Daedaleopsis*, and *Earliella*. The ganoderma clade appears as sister to the clade containing the lentinus and datronia clades.

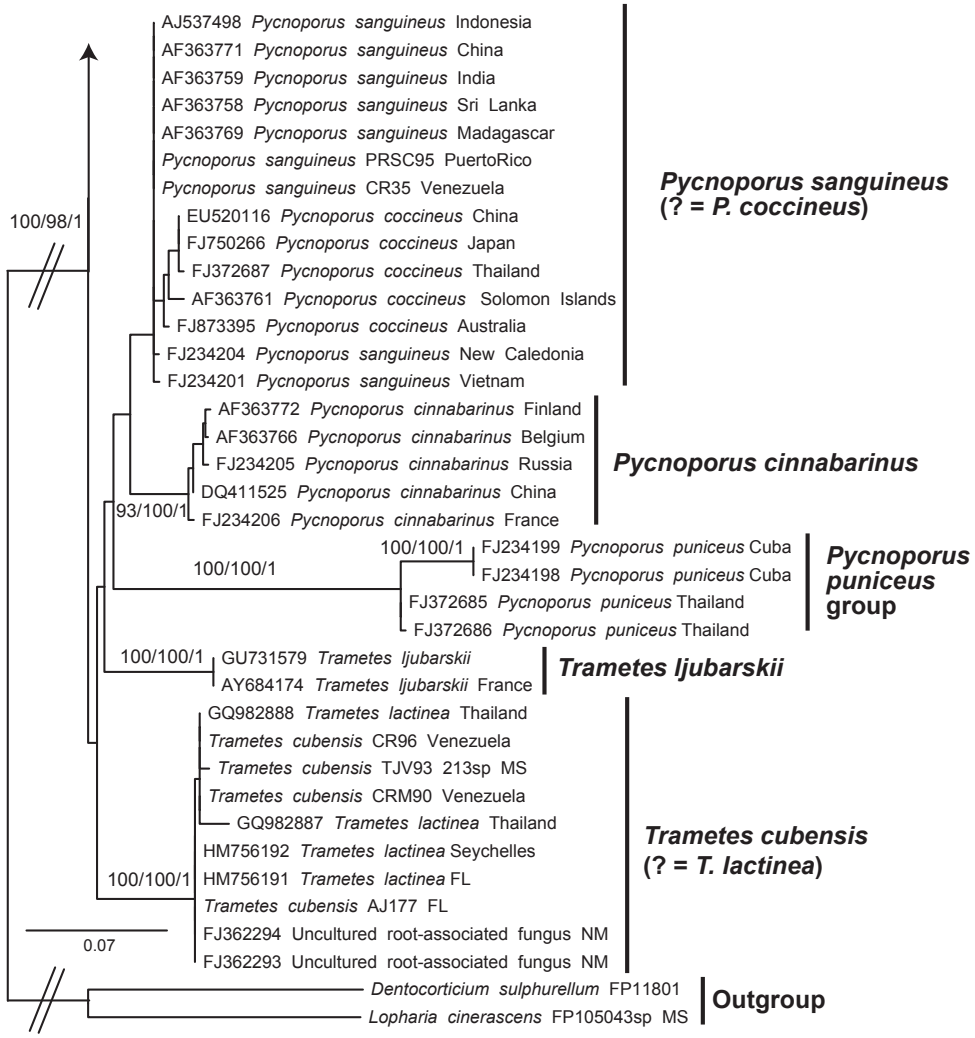

Fig. 3 part 1. Best tree from the ML analysis of the ITS dataset of the trametoid clade. BS values from the ML and MP analyses ≥75 (ML/MP) and PP ≥ 0.95 from the BY analysis for nodes supported in at least two of the analyses are given on or below the branches.

■ DISCUSSION

Taxonomic and nomenclatural overview of the trametoid clade. — Background information on the generic names available for members of the trametoid clade is given here. The phylogenetic placement of the type species of these genera, according to the analysis of the five-marker dataset, is highlighted in Fig. 4.

Trametes Fr., Fl. Scan.: 339. 1836 – Type: *T. suaveolens* (L. : Fr.) Fr., Epicr. Syst. Mycol.: 491. 1838 ≡ *Boletus suaveolens* L., Sp. Pl.: 1177. 1753 ≡ *Polyporus suaveolens* (L. : Fr.) Fr., Syst. Mycol. 1: 366. 1821.

Diagnostic characters. – Basidiocarps annual to perennial, pileate, sessile, dimidiate to fan-shaped, single or imbricate, flexible to hard; upper surface hispid to glabrous, often zonate; pore surface white, cream to pale gray; context white to

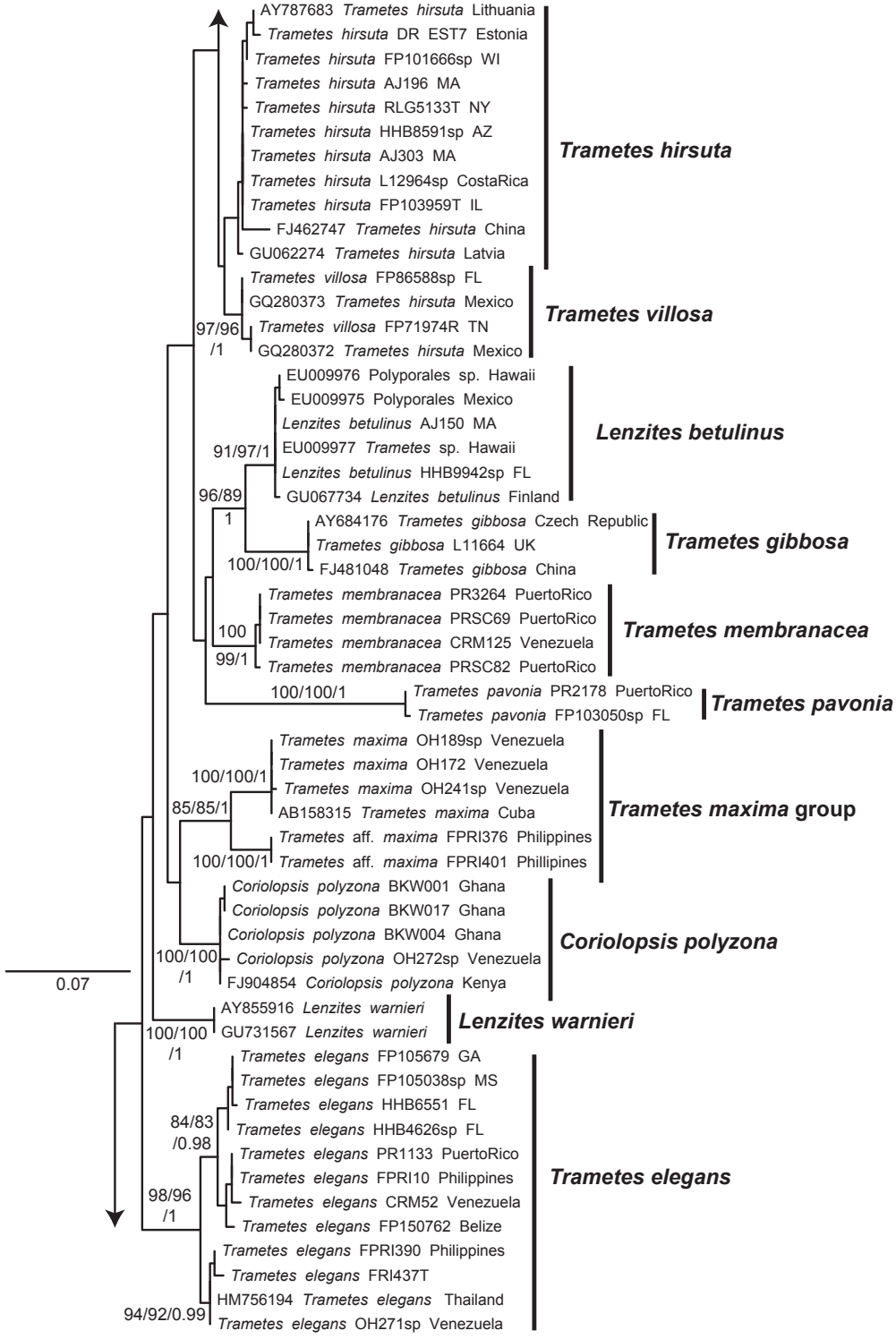

Fig. 3 part 2.

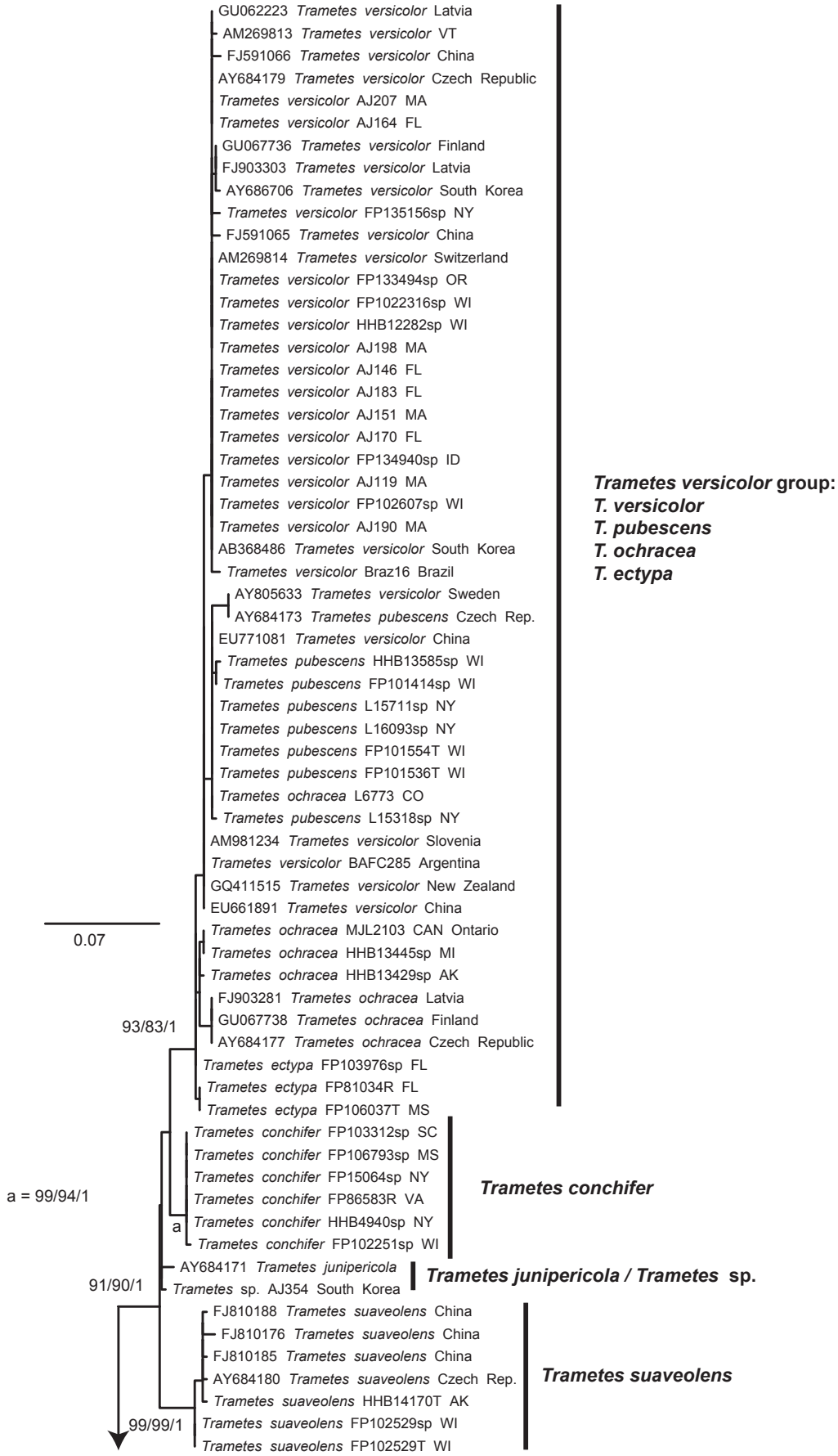
GU062223 Trametes versicolor Latvia
AM269813 Trametes versicolor VT
FJ591066 Trametes versicolor China
AY684179 Trametes versicolor Czech Republic
Trametes versicolor AJ207 MA
Trametes versicolor AJ164 FL
GU067736 Trametes versicolor Finland
FJ903303 Trametes versicolor Latvia
AY686706 Trametes versicolor South Korea
Trametes versicolor FP135156sp NY
FJ591065 Trametes versicolor China
AM269814 Trametes versicolor Switzerland
Trametes versicolor FP133494sp OR
Trametes versicolor FP1022316sp WI
Trametes versicolor HHB12282sp WI
Trametes versicolor AJ198 MA
Trametes versicolor AJ146 FL
Trametes versicolor AJ183 FL
Trametes versicolor AJ151 MA
Trametes versicolor AJ170 FL
Trametes versicolor FP134940sp ID
Trametes versicolor AJ119 MA
Trametes versicolor FP102607sp WI
Trametes versicolor AJ190 MA
AB368486 Trametes versicolor South Korea
Trametes versicolor Braz16 Brazil
AY805633 Trametes versicolor Sweden
AY684173 Trametes pubescens Czech Rep.
EU771081 Trametes versicolor China
Trametes pubescens HHB13585sp WI
Trametes pubescens FP101414sp WI
Trametes pubescens L15711sp NY
Trametes pubescens L16093sp NY
Trametes pubescens FP101554T WI
Trametes pubescens FP101536T WI
Trametes ochracea L6773 CO
Trametes pubescens L15318sp NY
AM981234 Trametes versicolor Slovenia
Trametes versicolor BAFC285 Argentina
GQ411515 Trametes versicolor New Zealand
EU661891 Trametes versicolor China
Trametes ochracea MJL2103 CAN Ontario
Trametes ochracea HHB13445sp MI
Trametes ochracea HHB13429sp AK
FJ903281 Trametes ochracea Latvia
GU067738 Trametes ochracea Finland
AY684177 Trametes ochracea Czech Republic
Trametes ectypa FP103976sp FL
Trametes ectypa FP81034R FL
Trametes ectypa FP106037T MS
Trametes conchifer FP103312sp SC
Trametes conchifer FP106793sp MS
Trametes conchifer FP15064sp NY
Trametes conchifer FP86583R VA
Trametes conchifer HHB4940sp NY
Trametes conchifer FP102251sp WI
AY684171 Trametes junipericola
Trametes sp. AJ354 South Korea
FJ810188 Trametes suaveolens China
FJ810176 Trametes suaveolens China
FJ810185 Trametes suaveolens China
AY684180 Trametes suaveolens Czech Rep.
Trametes suaveolens HHB14170T AK
Trametes suaveolens FP102529sp WI
Trametes suaveolens FP102529T WI
0.07
93/83/1
a = 99/94/1
a
91/90/1
99/99/1
Trametes versicolor group:
T. versicolor
T. pubescens
T. ochracea
T. ectypa
Trametes conchifer
Trametes junipericola / Trametes sp.
Trametes suaveolens

Fig. 3 part 3.

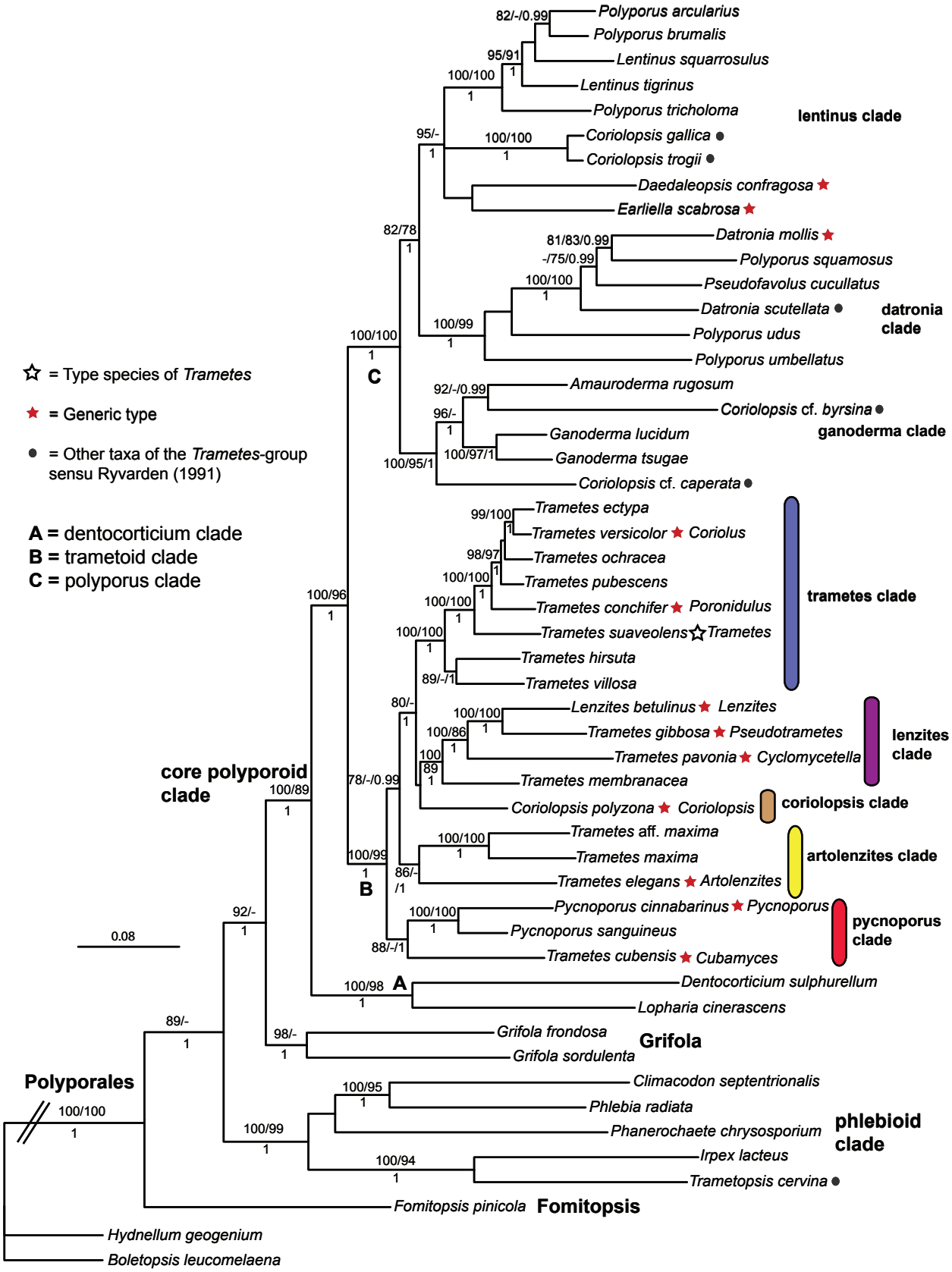

Fig. 4. Fifty percent majority-rule consensus tree from the BY analysis of the nLSU+ITS+RPB1+RPB2+TEF1 dataset of the Polyporales. BS values from the ML and MP analyses ≥75 (ML/MP) and PP ≥ 0.95 from the BY analysis for nodes supported in at least two of the analyses are given on or below the branches.

isabelline, homogeneous or duplex, in some species with a dark line; hyphal system trimitic; generative hyphae hyaline, with clamps; skeletal hyphae straight, thick-walled to solid, hyaline, in some species swelling in KOH; binding hyphae tortuous, solid, hyaline; cystidia absent, in some species pointed ("sword-like") hyphal ends may penetrate the hymenium; spores ellipsoid to allantoid, hyaline, thin-walled, and negative in Melzer's reagent; heterothallic and tetrapolar; causes a white rot in hardwoods, rarely on conifer wood; cosmopolitan genus with many common and widespread species, ca. 50 species worldwide (Gilbertson & Ryvarden, 1987; Ryvarden & Gilbertson, 1994; Kirk & al., 2008).

Observations. – *Trametes elegans*, with a variable hymenophore from poroid to lamellate (Fig. 1F–G), was included in *Lenzites* by Ryvarden & Johansen (1980) but later in *Trametes* by Gilbertson & Ryvarden (1987), despite the fact that the lamellate hymenophore is one of the key characters used by Gilbertson & Ryvarden (1987) to keep *Lenzites* separated from *Trametes*. Both names (*T. elegans* and *L. elegans*) are present in modern treatments of trametoid fungi: e.g., Quanten (1997) as *L. elegans* and Ryvarden (2000) as *T. elegans*.

Lenzites Fr., Fl. Scan.: 339. 1836 – Type: *L. betulinus* (L. : Fr.) Fr., Epicr. Syst. Mycol.: 405. 1838 ≡ *Agaricus betulinus* L., Sp. Pl.: 1176. 1753 ≡ *Agaricus betulinus* L. : Fr., Syst. Mycol. 1: 133. 1821.

Diagnostic characters. – Basidiocarps annual, pileate; upper surface glabrous to hirsute, often in distinct zones; hymenophore lamellate to daedaleoid, white to yellowish; context concolorous, tough and moderately thick; hyphal system trimitic; generative hyphae thin-walled, hyaline, with clamps; binding hyphae hyaline, strongly branched and tortuous, in the trama below the hymenium with long, "sword-like" side branches more or less parallel and pointing towards, and in parts into, the hymenium, but never above it; skeletal hyphae hyaline, thick-walled to solid; spores cylindrical, smooth, thin-walled, hyaline, negative in Melzer' s reagent; heterothallic and tetrapolar; on dead hardwoods, more rarely on conifers, causing a white rot. Cosmopolitan genus, with 3–5 species worldwide. (Gilbertson & Ryvarden, 1987; Ryvarden & Gilbertson, 1993; Kirk & al., 2008).

Observations. – *Lenzites* is separated from *Trametes* on the basis of the distinctly lamellate to daedaleoid hymenophore and the presence of "sword-like" binding hyphae (Fig. 1C–E). However, a lamellate hymenophore is also present in *T. elegans* and "sword-like" binding hyphae are found in *T. cubensis*, a species with poroid hymenophore and otherwise a "typical" member of *Trametes* (Gilbertson & Ryvarden, 1987).

Many polyporoid fungi with lamellate/daedaleoid hymenophore have been recombined in *Lenzites* through the years (e.g., *Daedalea*, *Gloeophyllum*) resulting in more than 200 nomenclatural combinations in the genus but the actual number of species of *Lenzites* sensu Ryvarden (1991) is between 3 and 5 (http://www.MycoBank.org/).

Pycnoporus P. Karst. in Rev. Mycol. 3: 18. 1881 – Type: *P. cinnabarinus* (Jacq. : Fr.) P. Karst. in Rev. Mycol. 3: 18. 1881 ≡ *Boletus cinnabarinus* Jacq., Fl. Austriac. 4: 2. 1776 ≡ *Polyporus cinnabarinus* (Jacq. : Fr.) Fr., Syst. Mycol. 1: 371. 1821.

Diagnostic characters. – Basidiocarps annual, sessile to effused-reflexed, dimidiate; pileus surface and pore surface orange-red to cinnabar, color fading on weathering; pores regular, circular to angular, 3–4 per mm; context reddish orange, coriaceous; hyphal system trimitic; generative hyphae with clamps; tramal hyphae with dextrinoid contents; cystidia absent; basidiospores cylindric, hyaline, smooth, negative in Melzer's reagent; heterothallic and tetrapolar; causing a white rot of dead hardwoods, rarely on conifers. Cosmopolitan genus, with one species (*P. cinnabarinus*) in temperate areas and three (*P. coccineus*, *P. puniceus*, *P. sanguineus*) in tropical and subtropical areas (Gilbertson & Ryvarden, 1987; Ryvarden & Gilbertson, 1994; Kirk & al., 2008).

Observations. – *Pycnoporus* is separated from *Trametes* solely on the basis of the orange-red colors of the basidiocarps (Fig. 1H–I [for color figure see this article online]).

Coriolopsis Murrill in Bull. Torrey Bot. Club 32: 358. 1905 – Type: *C. occidentalis* (Klotzsch) Murrill in Bull. Torrey Bot. Club 32: 358. 1905 ≡ *Polyporus occidentalis* Klotzsch in Linnaea 8: 486. 1833. According to Ryvarden (1972) who studied the type materials this is a synonym of *C. polyzona* (Pers.) Ryvarden ≡ *Polyporus polyzonus* Pers. in Gaudichaud-Beauprét, Voy. Uranie 5: 171. 1827).

Diagnostic characters. – Basidiocarps annual, pileate and sessile, rarely resupinate; pileus velutinate to hirsute, more rarely glabrous, zonate to azonate, yellowish to umber brown, often grayish when hirsute; pore surface concolorous, in some species with a grayish to blue bloom, pores round to entire, small to moderately large; context golden to umber brown, not distinctly delimited toward the pilear cover; hyphal system trimitic; generative hyphae hyaline, thin-walled, with clamps; skeletal hyphae thick-walled to solid, cyanophilous, hyaline, ochraceous to deep golden brown; binding hyphae thick-walled and concolorous with skeletal hyphae, cystidia absent; spores hyaline, cylindrical to oblong-ellipsoid, smooth, thin-walled, negative in Melzer's reagent, on hardwoods, causing a white rot. Cosmopolitan genus but most species are restricted to the tropical zone, ca. 17 species worldwide (Gilbertson & Ryvarden, 1986; Ryvarden & Gilbertson, 1993; Kirk & al., 2008).

Observations. – *Coriolopsis* is separated from *Trametes* mainly by the colored hyphae that give the context a brown color (Fig. 1J–K). The presence of cyanophilic skeletal hyphae has also been cited as a diagnostic character but it has not been demonstrated for all the species currently placed in *Coriolopsis* (Ryvarden, 1991).

In addition to *Trametes*, *Lenzites*, *Pycnoporus*, and *Coriolopsis*, currently accepted as separate, there are other six legitimate and validly published generic names for taxa included in the trametoid clade (Fig. 4). None of these generic names, except *Coriolus*, have been widely used by polypore taxonomists during the 20th century (Ryvarden, 1991), mostly because the morphological separation from the four main trametoid genera discussed above is very difficult, if not impossible in some

cases. They are listed here because they are relevant for the nomenclatural and taxonomic discussion of the trametoid clade.

Artolenzites Falck, Hausschwamm-Forschungen 3: 37. 1909 – Type: *Daedalea repanda* Pers. in Gaudichaud-Beauprét, Voy. Uranie 5: 168. 1827 (= *Trametes elegans* (Spreng. : Fr.) Fr., Epicr. Syst. Mycol.: 492. 1838).

Artolenzites elegans (Spreng. : Fr.) Teixeira is the only nomenclatural combination made in this genus.

Coriolus Quél., Enchir. Fung.: 175. 1886 – Type: *Coriolus versicolor* (L. : Fr.) Quél., Enchir. Fung.: 175. 1886 ≡ *Boletus versicolor* L., Sp. Pl.: 1176. 1753 ≡ *Polyporus versicolor* (L. : Fr.) Fr., Observ. Mycol. 2: 260. 1818 (sanctioned in Syst. Mycol. 1: 368. 1821.) ≡ *Trametes versicolor* (L. : Fr.) Lloyd, Mycol. Writings 6: 1045. 1920.

Coriolus has been considered by some authors as separate from *Trametes* because of the presence of a thin black line between the tomentum and the context, but recent authors (e.g., Gilbertson & Ryvarden, 1987) have considered this character to be very variable and of no taxonomic significance on the generic level. The genus *Cellularia* Bull. (Bulliard, 1789: pl. 414) is typified by *Cellularia cyathiformis* Bull., which is cited by MycoBank (http://www.MycoBank.org) and Index Fungorum (http://www.indexfungorum.org) as a synonym of *Coriolus versicolor* (= *T. versicolor*). However, if this synonymy is accepted *Coriolus* would become an illegitimate name as *Cellularia* is almost 100 years older. A formal proposal to conserve *Coriolus* against *Cellularia* made by Hawksworth (1984) was rejected by the Committee of Fungi (Korf, 1988), because the actual synonymy of *Coriolus versicolor* and *Cellularia cyathiformis* was considered doubtful. Since this synonymy remains as doubtful now as it did at the time of Hawksworth's proposal the genus *Cellularia* will not be considered in the nomenclatural discussion.

Cyclomycetella Murrill in Bull. Torrey Bot. Club 31: 722. 1904 – Type: *Cyclomycetella pavonia* (Hook.) Murrill in Bull. Torrey Bot. Club 31: 722. 1904 ≡ *Boletus pavonius* Hook. in Kunth, Syn. Pl. 1: 10. 1822 ≡ *Trametes pavonia* (Hook.) Ryvarden in Norweg. J. Bot. 19: 237. 1972 [illegitimate because of the existence of *Trametes pavonia* (Berk.) Fr., a taxonomic synonym of *T. elegans*].

Cyclomycetella pavonia is the only nomenclatural combination made in this genus.

Cubamyces Murrill in Bull. Torrey Bot. Club 32: 480. 1905 – Type: *Cubamyces cubensis* (Mont.) Murrill in Bull. Torrey Bot. Club 32: 480. 1905 ≡ *Polyporus cubensis* Mont. in Ann. Sci. Nat., Bot., ser 2, 8: 364. 1837 ≡ *Trametes cubensis* (Mont.) Sacc., Syll. Fung. 9: 198. 1891.

Cubamyces cubensis is the only nomenclatural combination made in this genus.

Poronidulus Murrill in Bull. Torrey Bot. Club 31: 425. 1904 – Type: *Poroninulus conchifer* (Schwein. : Fr.) Murrill in Bull. Torrey Bot. Club 31: 425. 1904 ≡ *Boletus conchifer* Schwein. in Schriften Naturf. Ges. Leipzig 1: 98. 1822 ≡ *Polyporus conchifer* (Schwein. : Fr.) Fr., Elench. Fung. 1: 96. 1828 ≡ *Trametes conchifer* (Schwein. : Fr.) Pilát, Atlas Champ. Eur., Polypor., B 3: 264. 1939.

In its more typical form *Poronidulus conchifer* is easy to recognize because of the cup-shaped structures in the basidiocarps that produce asexual propagules. However, this character is not always present and Gilbertson & Ryvarden (1987) did not consider it important enough to maintain *T. conchifer* in a separate genus. The only other taxon in the genus is *Poronidulus bivalvis* Höhn., but the actual identity of this species is doubtful.

Pseudotrametes Bondartsev & Singer ex Singer in Mycologia 36: 68. 1944 – Type: *Pseudotrametes gibbosus* (Pers. : Fr.) Bondartsev & Singer ex Singer in Mycologia 36: 68. 1944 ≡ *Merulius gibbosus* Pers. in Ann. Bot. (Usteri) 15: 21. 1795 ≡ *Daedalea gibbosa* (Pers. : Fr.) Pers., Syn. Meth. Fung.: 501: 1801 (sanctioned in Syst. Mycol. 1: 338. 1821) ≡ *Trametes gibbosa* (Pers. : Fr.) Fr., Epicr. Syst. Mycol.: 492. 1838.

Pseudotrametes was created to accommodate *T. gibbosa*, characterized by the radially elongated pores. It is the only species of the genus.

In view of the results from the phylogenetic analyses and the nomenclatural and taxonomic history of this group we discuss below different taxonomic scenarios for *Trametes* and related genera.

Phylogenetic classification of the trametoid clade. — We conclude that all members of the trametoid clade should be classified under one single generic name (*Trametes*). The morphological concept of *Trametes* of Gilbertson & Ryvarden (1987) would only have to be slightly expanded to allow species with orange-red basidiocarps (*Pycnoporus*) and/or colored hyphae and context (*Pycnoporus*, *C. polyzona*) to be included in *Trametes*. Ascription of unsampled and newly described taxa to this "new" *Trametes* will be easier than in any of the alternative taxonomic scenarios considered here and not more complicated than with the current morphological concept of *Trametes*. This solution is straightforward, but it is not totally free of problems.

The morphological separation of the genus *Trametes* and some taxa currently placed in *Coriolopsis* will still be problematical. In all phylogenetic analyses *Coriolopsis* is clearly polyphyletic (Figs. 2, 4), with two lineages in the polyporus clade not closely related to each other and away from the type species (*C. polyzona*) that will become a member of *Trametes*. Morphological characters such as spore length (e.g., above 10 µm in *C. aspera*, *C. byrsina*, *C. gallica*, and *C. trogii*) or the tomentose-strigose pileus surface of many species can help to separate these taxa from *Trametes*, especially from *Trametes polyzona*. This difficult morphological separation is not a consequence of the new taxonomic concept of *Trametes* but the result of the lack of diagnostic morphological features in the group of trimitic polypores (Ryvarden, 1991).

Of all the generic names available for taxa in the trametoid clade, *Lenzites* and *Trametes* have equal nomenclatural priority

as they were published on the same year and on the very same page of the same book (Fries, 1836: 339). For these cases Art. 11.5 of the *ICBN*. (McNeill & al., 2006) dictates that the first author treating *Lenzites* and *Trametes* as synonyms should be followed in his choice of name. Pilát (Kavina & Pilát, 1939) was the first to do so, choosing *Trametes* over *Lenzites*, and thus recombining the type species of *Lenzites* (*L. betulinus*) under *Trametes*. While some species of *Trametes* have been alternatively classified under *Lenzites* (e.g., *T. elegans*, *T. gibbosa*) the type species (*T. suaveolens*) has never been recombined in *Lenzites*. The name *Trametes betulina* (L. : Fr.) Pilát should be used for *Lenzites betulinus*.

Nomenclatural combinations in *Trametes* already exist for all species currently placed in *Pycnoporus*: *Trametes cinnabarina* (Jacq. : Fr.) Fr. (= *Pycnoporus cinnabarinus*), *Trametes punicea* Fr. (= *Pycnoporus puniceus*), and *Trametes sanguinea* (L. : Fr.) Lloyd (= *Pycnoporus sanguineus*). Corner (1989) recombined *Coriolopsis polyzona* in *Trametes* but failed to provide a full and direct reference to its basionym therefore his name is not validly published under Art. 33.4 of the *ICBN* (McNeill & al., 2006). The new combination is proposed here:

Trametes polyzona (Pers.) Justo, **comb. nov.** ≡ *Polyporus polyzonus* Pers. in Gaudichaud-Beaupré, Voy. Uranie 5: 171. MycoBank 561896

In the case of *L. warnieri* and *Lenzites vespacea* (Pers.) Pat. new combinations in *Trametes* would be necessary but the separation of these taxa from each other and from *Lenzites acuta* Berk. is at present doubtful based on morphological characters (Ryvarden & Johansen,1980) and molecular data are only available for *L. warnieri*. Considering that there are already over 120 nomenclatural and taxonomic synonyms for *L. acuta* and *L. vespacea* listed in MycoBank (http://www.MycoBank.org) we refrain from proposing any new nomenclatural combination for these taxa until molecular data are available for the three species.

Alternatives to using the name *Trametes* for all members of the trametoid clade were also considered (Fig. S4). The most obvious one would be to recognize the five well-supported lineages recovered in the five-marker dataset analysis (Fig. 4) at the generic level: *Trametes*, *Lenzites*, *Coriolopsis*, *Artolenzites*, and *Pycnoporus*. If this option is adopted it would be necessary to transfer some species currently placed in *Trametes* to *Lenzites* (*T. gibbosa*, *T. pavonia*, *T. membranacea*) or *Pycnoporus* (*T. cubensis*) and to "resurrect" the name *Artolenzites* to accommodate *T. elegans* and the *T. maxima* group. Reasons not to adopt this option can be readily recognized: (i) These five genera would be indistinguishable from each other based on morphology, ecology, and/or geographical distribution. (ii) Given the homoplasious nature of some important characters used in the generic distinction of this group (e.g., lamellate vs. poroid hymenophore, presence of "sword-like" binding hyphae, nature and distribution of the pigments in the basidiocarps) it is not possible to determine, based on morphology alone, the taxonomic position of species not sampled here. (iii) It will not be possible to ascribe newly described species to any of these five genera without generating molecular data and even then if only rDNA is available (e.g., *T. pocas*, *T. ljubarskii*, *L. warnieri*) it may not be enough for a confident generic classification.

We also considered a third taxonomic scenario: to recognize the genera *Trametes*, *Coriolopsis* (only *C. polyzona*), *Lenzites*, and *Pycnoporus* as defined by Gilbertson & Ryvarden (1987), without transferring any species into them, and adopting new generic names for the taxa that fall outside these genera. The generic names *Pseudotrametes*, *Cyclomycetella*, *Artolenzites*, and *Cubamyces* would accommodate only their respective type species and two new genera would have to be created for *T. membranacea* and the *T. maxima* group. With the current sampling a total of ten genera would have to be accepted for taxa in the trametoid clade (Fig. S4). However the same problems just outlined for the five-genera option will be even more serious with this option and very likely the number of genera in the trametoid clade would increase as new taxa are sampled for molecular analyses.

Species recognition in *Trametes*. — The results of the ITS (Fig. 3) and five-marker analyses (Fig. 4) offer some insights about the species-level taxonomy of *Trametes*.

The separation of the species group around *T. versicolor* (*T. ectypa*, *T. ochracea*, *T. pubescens*) is unclear in the ITS dataset. Morphological separation of these taxa is also difficult given the variability of morphological characters used for their delimitation (Gilbertson & Ryvarden, 1987; Ryvarden & Gilbertson, 1994). However there are different lines of evidence like (i) the results from the five-marker dataset (Fig. 4), (ii) separate ITS analyses of this complex and the presence of molecular polymorphisms in the ITS unique to each one of these taxa (data available at http://wordpress.clarku.edu/polypeet/datasets/), and (iii) the intercompatibility tests performed by Tomšovský & Homolka (2004) that suggest that they may actually be different biological species or at least they are currently undergoing speciation. The ITS data also suggest the possible synonymy of *Pycnoporus sanguineus* and *Pycnoporus coccineus*, as already proposed by Ryvarden & Johansen (1980) and of *T. cubensis* and *T. lactinea*. There is also evidence of intercontinental distribution of some species of *Trametes* (e.g., *T. betulina*, *T. suaveolens*, *T. versicolor*) as well as their ability to survive under very different climate conditions, e.g., *T. betulina* occurs in boreal (Finland), temperate (Massachusetts, U.S.A.) and tropical (Hawaii) ecosystems. A more exhaustive multi-gene analysis of *Trametes* is in preparation to address these questions in detail.

Morphological separation of *Trametes* species, as recognized in the phylogenetic analyses, relies on characters such as the consistency of the basidiocarps, nature of the hymenophore (poroid vs. lamellate, color, morphology of the pores, number of pores per mm), surface and colors of pileus, presence of red-orange or dark brown pigments in some parts of the basidiocarps, spore size and shape and, to a lesser extent, presence of specialized structures (e.g., "sword-like" binding hyphae, cystidioles, asexual propagules).

Final overview of the *Trametes*-group and remaining questions. — With the inclusion of the generic type (*Coriolopsis polyzona*) in *Trametes* the name *Coriolopsis* becomes

a synonym of *Trametes*. A change of type species could be proposed to keep the name *Coriolopsis* for the *C. gallica* group. Alternatively, the name *Funalia* Pat. could be adopted for the *C. gallica* group but no molecular data are available for the type species of *Funalia*, viz. *Polyporus mons-veneris* Jungh. (= *Trametes leonina* (Klotzsch) Imazeki, = *Funalia leonina* (Klotzsch) Pat.). Morphological characters of *F. leonina*, especially the spore length above 10 µm and the strigose pileus (Ryvarden & Johansen, 1980), suggest a relationship with the *C. gallica* group. The generic name *Trametella* Pinto-Lopes, typified by *Trametes hispida* (= *C. gallica*) is also available. Molecular data for *Funalia leonina* are critical for making a final decision for this group of species.

The other two species of *Coriolopsis* sampled in this study (*Coriolopsis* cf. *byrsina*, *Coriolopsis* cf. *caperata*) are closely related to *Ganoderma* and *Amauroderma* and according to the results of the combined dataset (Fig. 4) they are not grouped together. In both cases the species-level identification is tentative as no reliable molecular data are available for comparison. A preliminary analysis of all ITS sequences of *Coriolopsis* available in GenBank and sequences generated here indicates that the 64 ITS sequences deposited in GenBank as "*Coriolopsis caperata"* represent at least three different, not closely related, species and the available ITS sequence of "*C. byrsina"* represents *Earliella scabrosa* (Fig. S5).

The current knowledge about the phylogenetic placement of the other genera in the *Trametes*-group sensu Ryvarden (1991), including the results from the present study (Figs. 2, 4) is summarized in Table 1. *Daedaleopsis*, *Earliella*, *Hexagonia*, *Megasporoporia*, and *Microporus* appear as separate genera from each other and from *Trametes*. The genus *Datronia*, and also *Lentinus*, appear intermixed with species of *Polyporus* s.l. This result was already reported by Sotome & al. (2008) and confirmed in our five-marker dataset but a formal taxonomic proposal involving these genera has yet to be made.

■ ACKNOWLEDGEMENTS

Financial support from the NSF through the PolyPEET grant (DEB 0933081) is gratefully acknowledged. Dimitrios Floudas, Loreen Meyer, Claudia Osorio, David Marcano, Kim Pivorunas, Nathan Kallen, and Drew Minnis collected some of the specimens and helped producing some of the molecular data presented here. Zheng Wang originally designed the PCR protocol used for protein-coding genes. Beatriz Ortiz-Santana, Dan Lindner, and the personnel at Forest Products Lab (Madison, Wisconsin) are thanked for managing the loans of specimens and culture collections. Comments from two reviewers were very helpful for improving the manuscript.

■ LITERATURE CITED

Benson, D.A., Karsch-Mizrachi, I., Lipman, D.J., Ostell, J. & Sayers, E.W. 2011. GenBank. *Nucl. Acids Res.* 39: D32–D327.

Bernicchia, A. 2005. *Polyporaceae s.l.* Fungi Europaei 10. Alassio: Ed. Candusso.

Binder, M., Hibbett, D.S., Larsson, K.-H., Larsson, E. & Langer, E. 2005. The phylogenetic distribution of resupinate forms in the homobasidiomycetes. *Syst. Biodivers.* 3: 113–157.

Binder, M., Larsson, K.-H., Matheny, P.B. & Hibbett, D.S. 2010. Amylocorticiales ord. nov. and Jaapiales ord. nov.: Early-diverging clades of Agaricomycetidae were dominated by corticioid forms. *Mycologia* 102: 865–880.

Bulliard, J.B.F. 1789. *Herbier de la France*, vol. 9. Paris.

Corner, E.J.H. 1989. Ad Polyporaceas VI. The genus *Trametes*. *Beih. Nova Hedwigia* 97: 1–197.

Crous, P.W., Gams, W., Stalpers, J.A., Robert, V. & Stegehuis, G. 2004. MycoBank: An online initiative to launch mycology into the 21st century. *Stud. Mycol.* 50: 19–22.

Fries, E.M. 1836 ('1835'). *Corpus florarum provincialium Sueciae. I. Floram scanicam*, partic. 22. Uppsala: Palmblad, Sebell & C.

Frøslev, T.G., Matheny, P.B. & Hibbett, D.S. 2005. Lower level relationships in the mushroom genus *Cortinarius* (Basidiomycota, Agaricales): A comparison of RPB1, RPB2, and ITS phylogenies. *Molec. Phylogenet. Evol.* 37: 602–618.

García-Sandoval, R., Wang, Z., Binder, M. & Hibbett, D.S. 2011. Molecular phylogenetics of the Gloeophyllales and relative ages of clades of Agaricomycotina producing a brown rot. *Mycologia* 103: 510–524.

Gardes, M. & Bruns, T.D. 1993. ITS primers with enhanced specificity for basidiomycetes application to the identification of mycorrhizae and rusts. *Molec. Ecol.* 2: 113–118.

Gilbertson, R.L. & Ryvarden, L. 1986. *North American polypores,* vol. 1. Synopsis Fungorum Special Volume. Oslo: Fungiflora.

Gilbertson, R.L. & Ryvarden, L. 1987. *North American polypores,* vol. 2. Synopsis Fungorum Special Volume. Oslo: Fungiflora.

Hawksworth, D.L. 1984. (758–774) Proposals for nomina nonservanda and rejicienda for names of Hymenomycetes necessary as a result of the change in starting point date for the nomenclature of Fungi. *Taxon* 34: 730–736.

Hibbett, D.S. & Donoghue, M.J. 1995. Progress toward a phylogenetic classification of the Polyporaceae through parsimony analyses of ribosomal DNA sequences. *Canad. J. Bot.* 73(Suppl. 1): S853–S861.

Hibbett, D.S. & Donoghue, M.J. 2001. Analysis of correlations among wood decay mechanisms, mating systems, and substrate ranges in homobasidiomycetes. *Syst. Biol.* 50: 215–242.

Katoh, K. & Toh, H. 2008. Recent developments in the MAFFT multiple sequence alignment program. *Briefings Bioinf.* 9: 286–298.

Kavina, C. & Pilát, A. 1939. *Atlas des Champignons de l'Europe*, vol. 3, *Polyporaceae*. Praha.

Kirk, P.M., Cannon, P.F., Minter, M.W. & Stalpers, J.A. 2008. *Dictionary of the Fungi,* 10th ed. Wallingford, U.K.: CAB International.

Ko, K.S. & Jung, H.S. 1999a. Phylogenetic re-evaluation of *Trametes consors* based on mitochondrial small subunit ribosomal DNA sequences. *F. E. M. S. Microbiol. Lett.* 170: 181–186.

Ko, K.S. & Jung, H.S. 1999b. Molecular phylogeny of *Trametes* and related genera. *Antonie van Leeuwenhoek* 75: 191–199.

Korf, R.P. 1988. Reports (N.S. 1) of the Committee for Fungi and Lichens on proposals to conserve and/or reject names. *Taxon* 37: 450–463.

Larsson, K.-H., Larsson, E. & Kõljalg, U. 2004. High phylogenetic diversity among corticioid homobasidomycetes. *Mycol. Res.* 108: 983–1002.

Larsson, K.-H., Parmasto, E., Fischer, M., Langer, E., Nakasone, K.N. & Redhead, S.A. 2006. Hymenochaetales: A molecular phylogeny for the hymenochaetoid clade. *Mycologia* 98: 926–936.

Lee, J.S. & Lim, Y.W. 2010. *Cerrena aurantipora* sp. nov. (Polyporaceae) from eastern Asia. *Mycologia* 102: 211–216.

Liu, Y.L., Whelen, S. & Hall, B.D. 1999. Phylogenetic relationships among ascomycetes: Evidence from an RNA polymerase II subunit. *Molec. Biol. Evol.* 16: 1799–1808.

Maddison, D.R. & Maddison, W.P. 2002. MacClade4: Analysis of phylogeny and character evolution. Sunderland, Massachusetts: Sinauer.

Matheny, P.B. 2005. Improving phylogenetic inference of mushrooms with RPB1 and RPB2 nucleotide sequences (*Inocybe*; Agaricales). *Molec. Phylogenet. Evol.* 35: 1–20.

Matheny, P.B., Liu, Y.J., Ammirati, J.F. & Hall, B.D. 2002. Using RPB1 sequences to improve phylogenetic inference among mushrooms (*Inocybe*, Agaricales). *Amer. J. Bot.* 89: 688–698.

Matheny, P.B., Wang, Z., Binder, M., Curtis, J.M., Lim, Y.W., Nilsson, H.R., Hughes, K.W., Hofstetter, V., Ammirati, J.F., Schoch, C., Langer, E., Langer, G., McLaughlin, D.J., Wilson, A.W., Frøslev, T.G., Ge, Z.W., Yang, Z.L., Baroni, T.J., Fischer, M., Hosaka, K., Matsuura, K., Seidl, M.T., Vauras, J. & Hibbett D.S. 2007. Contributions of *rpb2* and *tef1* to the phylogeny of mushrooms and allies (Basidiomycota, Fungi). *Molec. Phylogenet. Evol.* 43: 430–451.

McNeill, J., Barrie, F.R., Burdet, H.M., Demoulin, V., Hawksworth, D.L., Marhold, K., Nicolson, D.H., Prado, J., Silva, P.C., Skog, J.E., Wiersema, J.H., & Turland, N.J. (eds.) 2006. *International Code of Botanical Nomenclature (Vienna Code): Adopted by the Seventeenth International Botanical Congress Vienna, Austria, July 2005*. Regnum Vegetabile 146. Ruggell: Gantner.

Miller, M.A., Pfeiffer, W. & Schwartz, T. 2010. Creating the CIPRES Science Gateway for inference of large phylogenetic trees. Pp. 1–8 in: *Proceedings of the Gateway Computing Environments Workshop (GCE)*. New Orleans: GCE.

Quanten, E. 1997. *The polypores of Papua New Guinea*. Opera Botanica Belgica 11. Meise: National Botanic Garden of Belgium.

Rehner, S.A. & Buckley, E. 2005. A *Beauveria* phylogeny inferred from nuclear ITS and EF1-a sequences: Evidence for cryptic diversification and links to *Cordyceps* teleomorphs. *Mycologia* 97: 84–98.

Ronquist, F. & Huelsenbeck, J.P. 2003. MrBayes3: Bayesian phylogenetic inference under mixed models. *Bioinformatics* 19: 1572–1574.

Ryvarden, L. 1972. A critical checklist of the Polyporaceae in tropical East Africa. *Norweg. J. Bot.* 19: 229–238.

Ryvarden, L. 1991. *Genera of polypores: Nomenclature and taxonomy.* Synopsis Fungorum 5. Oslo: Fungiflora.

Ryvarden, L. 2000. Studies in Neotropical polypores 8. Poroid fungi from Jamaica, a preliminary checklist. *Mycotaxon* 76: 349–360.

Ryvarden, L. & Gilbertson, R.L. 1993. *European polypores,* vol. 1. Synopsis Fungorum 6. Oslo: Fungiflora.

Ryvarden, L. & Gilbertson, R.L. 1994. *European polypores,* vol. 2. Synopsis Fungorum 7. Oslo: Fungiflora.

Ryvarden, L. & Johansen, I. 1980. *Preliminary polypore flora of East Africa*. Synopsis Fungorum Special Volume. Oslo: Fungiflora.

Sotome, K., Hattori, T., Ota, Y., To-anun, C., Salleh, B. & Kakishima, M. 2008. Phylogenetic relationships of *Polyporus* and morphologically allied genera. *Mycologia* 100: 603–615.

Stamatakis, A., Hoover, P. & Rougemont, J. 2008. A rapid bootstrap algorithm for the RAxML web-servers. *Syst. Biol.* 75: 758–771.

Stiller, J.W. & Hall, B.D. 1997. The origin of red algae: Implications for plastid evolution. *Proc. Natl. Acad. Sci. U.S.A.* 94: 4520–4525.

Swofford, D.L. 2002. PAUP*: Phylogenetic analysis using parsimony (*and other methods), version 4.0 Beta. Sunderland, Massachusetts: Sinauer.

Tomšovský, M. 2008. Molecular phylogeny and taxonomic position of *Trametes cervina* and description of a new genus *Trametopsis*. *Czech Mycol.* 60: 1–11.

Tomšovský, M. & Homolka L. 2004. Mating tests among geographically separated collections of the *Trametes versicolor* (Fr.) Pilat (Basidiomycetes, Polyporales) group. *Nova Hedwigia* 79: 425–431.

Tomšovský, M., Kolařík, M., Pažoutová, S. & Homolka L. 2006. Molecular phylogeny of European *Trametes* (Basidiomycetes, Polyporales) species based on LSU and ITS (nrDNA) sequences. *Nova Hedwigia* 82: 269–280.

White, T.J., Bruns, T., Lee, S.S. & Taylor, J. 1990. Amplification and direct sequencing of fungal ribosomal RNA genes for phylogenetics. Pp. 315–322 in: Innis, M.A., Gelfand, D.H., Sninsky, J.J. & White, T.J. (eds), *PCR protocols: A guide to methods and applications*. New York: Academic Press.

Appendix. GenBank accession numbers for the sequences used in the phylogenetic analyses. For the 117 new isolates studied here the following information is given: Geographic origin, *collector* and *collection number* (herbarium, if different from the Forest Product Lab, Madison, U.S.A.). Nomenclatural authorities are given after the first mention of a taxon. Preexisting GenBank sequences are marked with an asterisk (*). Sequences are given in the following order: nrLSU, nrITS, RPB1, RPB2, and TEF1.

Amauroderma rugosum (Blume & T. Nees) Torrend; AB368061*, AB509712*, –, AB368119*, –. ***Boletopsis leucomelaena*** (Pers.) Fayod; DQ154112*, DQ484064*, GU187494*, GU187820*, GU187763*. ***Cerrena aurantiopora*** J.S. Lee & Y.W. Lim; FJ821521*, FJ821532*, –, –, –. ***Cerrena consors*** (Berk.) K.S. Ko & H.S. Jung; FJ821517*, FJ821528*, –, –, –. ***Cerrena unicolor*** (Bull. : Fr.) Murrill; FJ821524*, FJ821534*, –, –, –. ***Climacodon septentrionalis*** (Fr. : Fr.) P. Karst; AY684165*, AY854082*, AY864872*, AY780941*, AY885151*. ***Coriolopsis aspera*** (Jungh.) Teng; AY351956*, –, –, –, –. ***Coriolopsis*** cf. ***byrsina*** (Mont.) Ryvarden; U.S.A. (MS), *R.W. Davidson, FP-105050-Sp*, JN164788, JN165001, JN164838, JN164871, JN164879. ***Coriolopsis*** cf. ***caperata*** (Berk.) Murrill; Venezuela, *C. Rodríguez, CR-22*, JN164789, JN164999, JN164837, JN164870, JN164880. ***Coriolopsis*** cf. ***caperata***; Venezuela, *C. Rodríguez, CRM-77*, –, JN165000, –, –, –. ***Coriolopsis gallica*** (Fr. : Fr.) Ryvarden; U.S.A. (AZ), *R.L. Gilbertson, RLG-7630-sp*, JN164814, JN165013, JN164821, JN164869. ***Coriolopsis gallica***; U.S.A. (IL), *C. Thoms, FP-66249-T*, –, JN165011, –, –, –. ***Coriolopsis gallica***; U.S.A. (MS), *E.R. Toole, T328*, –, JN165010, –, –, –. ***Coriolopsis gallica***; U.S.A. (NM), *H.H. Burdsall, Jr., HHB-1207sp*, –, JN165014, –, –, –. ***Coriolopsis gallica***; U.S.A. (OR), *J. Hunt, FP-91633-T*, –, JN165012, JN164845, JN164868, –. ***Coriolopsis gallica***; U.S.A. (OK), *A. Pakula, MC-42*, –, JN164998, –, –, –. ***Coriolopsis gallica***; U.S.A. (WI), *T.J. Volk & T.W. Darmono, FP-102596A-Sp*, –, JN164997, –, –, –. ***Coriolopsis polyzona*** (Pers.) Ryvarden; Ghana, *B. Kumi-Woode, BKW-001*, –, JN164980, –, –, –. ***Coriolopsis polyzona***; Ghana, *B. Kumi-Woode, BKW-004*, JN164790, JN164978, JN164844 & JN164846, JN164856, JN164881. ***Coriolopsis polyzona***; Ghana, *B. Kumi-Woode, BKW-017*, –, JN164977, –, –, –. ***Coriolopsis polyzona***; Venezuela, *O. Holmquist, OH-272-Sp*, –, JN164979, –, –, –. ***Coriolopsis sanguinaria*** (Klotzsch) Teng; AY351950*, –, –, –, –. ***Coriolopsis trogii*** (Berk.) Domanski; U.S.A. (MI), *M.J. Larsen, MJL-3721-Sp*, –, JN164994, –, –, –. ***Coriolopsis trogii***; U.S.A. (MI), *M.J. Larsen, MJL-3725-Sp*, –, JN164995, –, –, –. ***Coriolopsis trogii***; U.S.A. (MN), *R.L. Gilbertson, RLG-9577-R*, –, JN164996, –, –, –. ***Coriolopsis trogii***; U.S.A. (NY), *R.L. Gilbertson, RLG-4286-Sp*, JN164808, JN164993, JN164820, JN164867, JN164898. ***Cryptoporus volvatus*** (Peck) Shear; AF393050*, –, –, –, –. ***Daedalea quercina*** (L. : Fr.) Pers.; AF518613*, FJ403212*, –, –, –. ***Daedaleopsis confragosa*** (Bolton : Fr.) J. Schröt.; AB368062*, GU731549*, –, AB368120*, –. ***Datronia mollis*** (Sommerf. : Fr.) Donk; U.S.A. (MI), *H.H. Burdsall, Jr., HHB-3480*, –, JN165005, –, –, –. ***Datronia mollis***; U.S.A. (MT), *R.L. Gilbertson, RLG-6304-Sp*, JN164791, JN165002, JN164818, JN164872, JN164901. ***Datronia mollis***; U.S.A. (NY), *R.L. Gilbertson, RLG-5624-Sp*, –, JN165007, –, –, –. ***Datronia scutellata*** (Schwein.) Gilb. & Ryvarden; U.S.A. (MN), *D.W. French, RLG-9584-R*, –, JN165003, –, –, –. ***Datronia scutellata***; U.S.A. (MN), *D.W. French, RLG-9584-T*, JN164792, JN165004, JN164817, JN164873, JN164902. ***Dentocorticium sulphurellum*** (Peck) M.J. Larsen & Gilb.; Canada (QC), *J.H. Ginns, T609*, JN164815, JN165015, –, JN164875, –. ***Dentocorticium sulphurellum***; U.S.A., *collector unknown, FP-11801*, –, JN165018, JN164841, JN164876, JN164903. ***Dentocorticium sulphurellum***; U.S.A. (NY), *J.L. Lowe, L14474*, –, JN165016, –, –, –. ***Dentocorticium sulphurellum***; U.S.A. (NY), *P. Roskin, PR52*, –, JN165017, –, –, –. ***Earliella scabrosa*** (Pers.) Gilb. & Ryvarden; Puerto Rico, *C. Rodríguez, PR-1209*, JN164793, JN165009, JN164819, JN164866, JN164894. ***Earliella scabrosa***; Venezuela, *C. Rodríguez, CR-45*, –, JN164992, –, –, –. ***Earliella scabrosa***; Venezuela, *C. Rodríguez, CR-95*, –, JN165008, –, –, –. ***Earliella scabrosa***; Venezuela, *C. Rodríguez, CR-Irel*, –, JN165006, –, –, –. ***Fomitopsis pinicola*** (Sw. : Fr.) P. Karst.; AY684164*, AY854083*, AY864874*, AY786056*, AY885152*. ***Ganoderma lucidum*** (Curtis : Fr.) P. Karst.; AB368068*, EU021460*, –, AB368126*, –. ***Ganoderma tsugae*** Murrill; AY684163*,

Appendix. Continued.

DQ206985*, –, DQ408116*, DQ059048*. ***Grifola frondosa*** (Dickson : Fr.) Gray; AY629318*, AY854084*, AY864876*, –, AY885153*. ***Grifola sordulenta*** (Mont.) Singer; AY645050*, AY854085*, AY864877*, AY786058*, AY885154*. ***Hexagonia hirta*** (P. Beauv. : Fr.) Fr.; AY351944*, –, –, –, –. ***Hydnellum geogenium*** (Fr.) Banker; AY631900*, DQ218304*, –, DQ408133*, DQ059053*. ***Irpex lacteus*** (Fr. : Fr.) Fr.; EU522839*, AB079264*, –, DQ408117*, –. ***Lentinus squarrosulus*** Mont.; AB368071*, GU001951*, –, AB368129*, –. ***Lentinus tigrinus*** (Bull. : Fr.) Fr.; AB368072*, AF516520*, –, AB368130*, –. ***Lenzites betulinus*** (L. : Fr.) Fr.; U.S.A. (FL), *H.H. Burdsall, Jr., HHB-9942-Sp*, JN164794, JN164983, JN164822, JN164860, JN164895. ***Lenzites betulinus***; U.S.A. (MA), *A. Justo, AJ150* (CUW), –, JN164915, –, –, –. ***Lignosus rhinocerotis*** (Cooke) Ryvarden; AB368074*, FJ380871*, –, –, –. ***Lopharia cinerascens*** (Schwein.) G. Cunn.; U.S.A. (MS), *R.W. Davidson, FP-105043-sp*, JN164813, JN165019, JN164840, JN164874, JN164900. ***Megasporoporia setulosa*** (Henn.) Rajchenb.; GU566007*, –, –, –, –. ***Microporus vernicipes*** (Berk.) Imazeki; AY351929*, AB531465*, –, –, –. ***Microporus xanthopus*** (Fr. : Fr.) Kuntze, AB368075*, AJ698132*, –, –, –. ***Phanerochaete chrysosporium*** Burdsall; AF287883*, AY854086*, AY864880*, –, AY885155*. ***Phlebia radiata*** Fr. : Fr.; AF287885*, AY854087*, AY864881*, AY218502*, AY885156*. ***Polyporus arcularius*** (Batsch : Fr.) Fr.; AB368081*, AF516523*, –, AB368138*, –. ***Polyporus brumalis*** (Pers. : Fr.) Fr.; AB368084*, FJ596883*, –, AB368141*, –. ***Polyporus squamosus*** (Huds. : Fr.) Fr.; AY629320*, DQ267123*, DQ831023*, DQ408120*, DQ028601*. ***Polyporus tricholoma*** Mont.; AB368100*, AF516555*, –, AB368157*, –. ***Polyporus udus*** Jungh.; AB368108*, AF518756*, –, AB368165*, –. ***Polyporus umbellatus*** (Pers. : Fr.) Fr.; AB368109*, EU442276*, –, AB368166*, –. ***Pseudofavolus cucullatus*** Mont.; AB368114*, AF516601*, –, AB368170*, –. ***Pycnoporus cinnabarinus*** (Jacq. : Fr.) P. Karst.; China, *Zheng Wang, ZW 02-30* (CUW), AY684160*, DQ411525*, JN164843 & JN164847, DQ408121*, DQ02860*. ***Pycnoporus puniceus*** (Fr.) Ryvarden; FJ372708*, FJ372686*, –, –, –. ***Pycnoporus sanguineus*** (L. : Fr.) Murrill; Puerto Rico, *S.A. Cantrell, PR-SC-95*, JN164795, JN164982, JN164842, JN164858, JN164897. ***Pycnoporus sanguineus***; Venezuela, *C. Rodríguez, CR-35*, –, JN164981, –, –, –. ***Trametes*** aff. ***maxima*** (Mont.) A. David & Rajchenb.; Philippines, *M.A. Eusebio, FPRI-376*, –, JN164918, –, –, –. ***Trametes*** aff. ***maxima***; Philippines, *E.M. Mendoza, FPRI-401*, JN164802, JN164933, JN164836, JN164863, JN164884. ***Trametes conchifer*** (Schwein. : Fr.) Pilát; U.S.A. (MS), *P.L. Lentz, FP-106793-Sp*, JN164797, JN164924, JN164823, JN164849, JN164887. ***Trametes conchifer***; U.S.A. (NY), *H.H. Burdsall, Jr., HHB-4940-Sp*, –, JN164988, –, –, –. ***Trametes conchifer***; U.S.A. (NY), *J.L. Lowe, L-15064-Sp*, –, JN164926, –, –, –. ***Trametes conchifer***; U.S.A. (SC), *A.S. Rhoads, FP-103312-Sp*, –, JN164925, –, –, –. ***Trametes conchifer***; U.S.A. (VA), *F. Berry, FP-86583-R*, –, JN164939, –, –, –. ***Trametes conchifer***; U.S.A. (WI), *Poulle & Dorworth, FP-102251-Sp*, –, JN164987, –, –, –. ***Trametes cubensis*** (Mont.) Sacc.; U.S.A. (FL), *A. Justo, AJ177* (CUW), JN164787, JN164905, –, –, –. ***Trametes cubensis***; U.S.A. (MS), *T.J. Volk, TJV-93-213-Sp*, JN164798, JN164923, JN164834, JN164865, JN164883. ***Trametes cubensis***; Venezuela, *C. Rodríguez, CR-96*, –, JN164922, –, –, –. ***Trametes cubensis***; Venezuela, *C. Rodríguez, CRM-90*, –, JN164989, –, –, –. ***Trametes ectypa*** (Berk. & M.A. Curtis) Gilb. & Ryvarden; U.S.A. (FL), *A.S. Rhoads, FP-103976-Sp*, –, JN164961, –, –, –. ***Trametes ectypa***; U.S.A. (FL), *G.G. Hedgcock, FP-81034-R*, –, JN164930, –, –, –. ***Trametes ectypa***; U.S.A. (MS), *E.R. Toole, FP-106037-T*, JN164803, JN164929, JN164824, JN164848, JN164888. ***Trametes elegans*** (Spreng. : Fr) Fr.; Belize, *K.K. Nakasone, FP-150762*, –, JN164928, –, –, –. ***Trametes elegans***; country unknown, *collector unknown, FRI-437-T*, –, JN164985, –, –, –. ***Trametes elegans***; Philippines, *L. Lodderau, FPRI-10*, –, JN164973, –, –, –. ***Trametes elegans***; Philippines, *M.A. Eusebio,* FPRI-390, –, JN164921, –, –, –. ***Trametes elegans***; Puerto Rico, *D.J. Lodge & L. Fish, PR-1133*, –, JN164937, –, –, –. ***Trametes elegans***; U.S.A. (FL), *H.H. Burdsall, Jr., HHB-4626-Sp*, –, JN164950, –, –, –. ***Trametes elegans***; U.S.A. (FL), *H.H. Burdsall, Jr., HHB-6551-Sp*, –, JN164938, –, –, –. ***Trametes elegans***; U.S.A. (GA), *R.W. Davidson, FP-105679-Sp*, JN164799, JN164944, JN164833, JN164861, JN164899. ***Trametes elegans***; U.S.A. (MS), *R.W. Davidson, FP-105038-Sp*, –, JN164951, –, –, –. ***Trametes elegans***; Venezuela, *C. Rodríguez, CRM-52*, –, JN164986, –, –, –. ***Trametes elegans***; Venezuela, *O. Holmquist, OH-271-Sp*, –, JN164936, –, –, –. ***Trametes gibbosa*** (Pers. : Fr.) Fr.; UK, *J.L. Lowe, L-11664-Sp*, JN164800, JN164943, JN164831, JN164859, JN164896. ***Trametes hirsuta*** (Wulfen : Fr.) Pilát; U.S.A. (MA), *A. Justo, AJ196* (CUW), –, JN164916, –, –, –. ***Trametes hirsuta***; U.S.A. (MA), *A. Justo, AJ303* (CUW), –, JN164917, –, –, –. ***Trametes hirsuta***; Costa Rica, *J.L. Lowe, L-12964-Sp*, –, JN164935, –, –, –. ***Trametes hirsuta*****,** Estonia, *D.R. Richter, DR-EST-7*, –, JN164934, –, –, –. ***Trametes hirsuta***; U.S.A. (AZ), *H.H. Burdsall, Jr., HHB-8591-Sp*, –, JN164953, –, –, –. ***Trametes hirsuta***; U.S.A. (IL), *H.H. McKay, FP-103959-T*, –, JN164952, –, –, –. ***Trametes hirsuta***; U.S.A. (NY), *R.L. Gilbertson, RLG-5133-T*, JN164801, JN164941, JN164829, JN164854, JN164891. ***Trametes hirsuta***; U.S.A. (WI), *M.J. Larsen, FP-101666-Sp*, –, JN164942, –, –, –. ***Trametes junipericola*** Manjón, G. Moreno & Ryvarden; AY855915*, AY684171*, –, –, –. ***Trametes ljubarskii*** Pilát; AY855911*, AY684174*, –, –, –. ***Trametes maxima*** (Mont.) A. David & Rajchenb.; Venezuela, *O. Holmquist, OH-172-Sp*, –, JN164932, –, –, –. ***Trametes maxima***; Venezuela, *O. Holmquist, OH-189-Sp*, JN164804, JN164957, JN164816, JN164864, JN164885. ***Trametes maxima***; Venezuela, *O. Holmquist, OH-241-Sp*, –, JN164940, –, –, –. ***Trametes membranacea*** (Sw. : Fr.) Kreisel; Puerto Rico, *E. Horak, PR-3264*, –, JN164946, –, –, –. ***Trametes membranacea***; Puerto Rico, *R. Petersen & S.A. Cantrell, PR-SC-69*, –, JN164927, –, –, –. ***Trametes membranacea***; Puerto Rico, *R. Petersen & S.A. Cantrell, PR-SC-82*, JN164805, JN164945, JN164832, JN164857, JN164893. ***Trametes membranacea***; Venezuela, *C. Rodríguez, CRM-125*, –, JN164956, –, –, –. ***Trametes ochracea*** (Pers.) Gilb. & Ryvarden; Canada (ON), *M.J. Larsen, MJL-2103*, –, JN164948, –, –, –. ***Trametes ochracea***; U.S.A. (AK), *H.H. Burdsall, Jr., HHB-13429-Sp*, –, JN164976, –, –, –. ***Trametes ochracea***; U.S.A. (CO), *J.L. Lowe, L-6773-R*, –, JN164971, –, –, –. ***Trametes ochracea***; U.S.A. (MI), *T.J. Volk, HHB-13445-Sp*, JN164812, JN164954, JN164826, JN164852, JN164904. ***Trametes pavonia*** (Hook.) Ryvarden; Puerto Rico, *E. Setliff, PR-2178*, –, JN164959, –, –, –. ***Trametes pavonia***; U.S.A. (FL), *A.S. Rhoads, FP-103050-Sp*, JN164806, JN164958, JN164835, JN164862, JN164886. ***Trametes pocas*** (Berk.) Ryvarden, AY351919*, –, –, –, –. ***Trametes pubescens*** (Schumach. : Fr.) Pilát; U.S.A. (NY), *J.L. Lowe, L-15318-Sp*, –, JN164949, –, –, –. ***Trametes pubescens***; U.S.A. (NY), *J.L. Lowe, L-15711-Sp*, –, JN164972, –, –, –. ***Trametes pubescens***; U.S.A. (NY), *J.L. Lowe, L-16093-Sp*, –, JN164964, –, –, –. ***Trametes pubescens***; U.S.A. (WI), *F.F. Lombard & R.G. Payne, FP-101414-Sp*, JN164811, JN164963, JN164827, JN164851, JN164889. ***Trametes pubescens***; U.S.A. (WI), *Nishijima & Evans, FP-101536-T*, –, JN164960, –, –, –. ***Trametes pubescens***; U.S.A. (WI), *Burdsall & Leslie, FP-101554-T*, –, JN164962, –, –, –. ***Trametes pubescens***; U.S.A. (WI), *H.H. Burdsall, Jr. & T.J. Volk, HHB-13585-Sp*, –, JN164947, –, –, –. ***Trametes*** **sp.**; South Korea, *A.M. Minnis, AJ354* (CUW), –, JN164990, –, –, –. ***Trametes suaveolens*** (L. : Fr.) Fr.; U.S.A. (AK), *H.H. Burdsall, Jr., HHB-14170-T*, –, JN164968, –, –, –. ***Trametes suaveolens***; U.S.A. (WI), *H.H. Burdsall, Jr. & T.J. Volk, FP-102529-Sp*, JN164807, JN164966, JN164828, JN164853, JN164890. ***Trametes suaveolens***; U.S.A. (WI), *H.H. Burdsall, Jr. & T.J. Volk, FP-102529-T*, –, JN164967, –, –, –. ***Trametes versicolor*** (L : Fr.) Lloyd; U.S.A. (FL), *A. Justo, AJ146* (CUW), –, JN164912, –, –, –. ***Trametes versicolor***; U.S.A. (FL), *A. Justo, AJ164* (CUW), –, JN164909, –, –, –. ***Trametes versicolor***; U.S.A. (FL), *A. Justo, AJ170* (CUW), –, JN164907, –, –, –. ***Trametes versicolor***; U.S.A. (FL), *A. Justo, AJ183* (CUW), –, JN164911, –, –, –. ***Trametes versicolor***; U.S.A. (MA), *A. Justo, AJ119* (CUW), –, JN164914, –, –, –. ***Trametes versicolor***; U.S.A. (MA), *A. Justo, AJ151* (CUW), –, JN164913, –, –, –. ***Trametes versicolor***; U.S.A. (MA), *A. Justo, AJ190* (CUW), –, JN164908, –, –, –. ***Trametes versicolor***; U.S.A. (MA), *A. Justo, AJ198* (CUW), –, JN164906, –, –, –. ***Trametes versicolor***; U.S.A. (MA), *A. Justo, AJ207* (CUW), –, JN164910, –, –, –. ***Trametes versicolor***; Brazil (SP), *A.R. Teixeira, Braz-16*, –, JN164975, –, –, –. ***Trametes versicolor***; U.S.A. (ID), *M.J. Larsen, FP-134940-Sp*, –, JN164920, –, –, –. ***Trametes versicolor***; U.S.A. (NY), *M.J. Larsen, FP-135156-Sp*, JN164809, JN164919, JN164825, JN164850, JN164878. ***Trametes versicolor***; U.S.A. (OR), *M.J. Larsen, FP-133494-Sp*, –, JN164931, –, –, –. ***Trametes versicolor***; U.S.A. (WI), *T.J. Volk & al., FP-102607-Sp*, –, JN164955, –, –, –. ***Trametes versicolor***; U.S.A. (WI), *E.B. Dorworth, FP102316sp*, –, JN164984, –, –, –. ***Trametes versicolor***; U.S.A. (WI), *M.T. Banik, HHB-12282-Sp*, –, JN164974, –, –, –. ***Trametes versicolor***; Argentina, *H. Lenko, BAFC-285*, –, JN164965, –, –, –. ***Trametes villosa*** (Sw.) Kreisel, U.S.A. (FL), *A.S. Rhoads, FP-86588-Sp*, –, JN164970, –, –, –. ***Trametes villosa*** (Sw.) Kreisel, U.S.A. (TN), *B.S. Crandall, FP-71974-R*, JN164810, JN164969, JN164830, JN164855, JN164892. ***Trametopsis cervina*** (Schwein.) Tomsovský; U.S.A. (FL), *A. Justo, AJ185* (CUW), –, JN164991, –, –, –. ***Trametopsis cervina***; U.S.A. (FL), *A. Justo, AJ189* (CUW), –, JN165021, –, –, –. ***Trametopsis cervina***; U.S.A. (MS), *T.J. Volk, TJV-93-216-Sp*, JN164796, JN165020, JN164839, JN164877, JN164882.