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A revised family-level classification of the Polyporales (Basidiomycota)

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ARTICLE INFO

Article history:

Received 21 April 2017

Accepted 30 May 2017

Available online 16 June 2017

Corresponding Editor:

Ursula Peintner

Keywords:

Agaricomycetes

Family-level taxonomy

Phylogeny

PolyPEET

rpb1

ABSTRACT

Polyporales is strongly supported as a clade of Agaricomycetes, but the lack of a consensus higher-level classification within the group is a barrier to further taxonomic revision. We amplified nrLSU, nrITS, and *rpb1* genes across the Polyporales, with a special focus on the latter. We combined the new sequences with molecular data generated during the PolyPEET project and performed Maximum Likelihood and Bayesian phylogenetic analyses. Analyses of our final 3-gene dataset (292 Polyporales taxa) provide a phylogenetic overview of the order that we translate here into a formal family-level classification. Eighteen clades are assigned a family name, including three families described as new (*Cerrenaceae* fam. nov., *Gelatoporiaceae* fam. nov., *Panaceae* fam. nov.) and fifteen others (*Dacryobolaceae*, *Fomitopsidaceae*, *Grifolaceae*, *Hyphodermataceae*, *Incrustoporiaceae*, *Irpicaceae*, *Ischnodermataceae*, *Laetiporaceae*, *Meripilaceae*, *Meruliaceae*, *Phanerochaetaceae*, *Podoscyphaceae*, *Polyporaceae*, *Sparassidaceae*, *Steccherinaceae*). Three clades are given informal names (*/hypochnicium*, */climacocystis* and */fibroporia* + */amyloporia*). Four taxa (*Candelabrochete africana*, *Mycoleptodonoides vassiljevae*, *Auriporia aurea*, and *Tyromyces merulinus*) cannot be assigned to a family within the Polyporales. The classification proposed here provides a framework for further taxonomic revision and will facilitate communication among applied and basic scientists. A survey of morphological, anatomical, physiological, and genetic traits confirms the plasticity of characters previously emphasized in taxonomy of Polyporales.

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<http://dx.doi.org/10.1016/j.funbio.2017.05.010>

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Introduction

Polyporales is one of the most intensively studied clades of Fungi. According to MycoBank, there have been 577 taxonomic proposals in Polyporales from 2010 to 2017, including 42 new genera and one new family, *Fragiliporiaceae* (Zhao et al. 2015). Over the same period, 2183 publications with the keyword 'Polyporales' are recorded in PubMed. As major wood-decay fungi, species of Polyporales are of interest to both fungal ecologists and applied scientists. The first species of *Agaricomycotina* to have its genome sequenced, the model white-rot fungus *Phanerochaete chrysosporium*, is a member of Polyporales (Martinez et al. 2004). The first brown-rot genome, *Rhodonia (Postia) placenta*, was also a polypore (Martinez et al. 2009). At present, there are 46 genomes of Polyporales hosted by the Joint Genome Institute MycoCosm portal (Grigoriev et al. 2013), which is about 22 % of all 212 *Agaricomycotina* genomes, or about 6 % of all 772 fungal genomes. However, with roughly 1800 described species, Polyporales account for only about 1.5 % of all known species of Fungi (Kirk et al. 2008).

Polyporales were sampled extensively in phylogenetic studies using ribosomal RNA (rRNA) genes (Hibbett & Vilgalys 1993; Hibbett & Donoghue 1995; Boidin et al. 1998; Larsson et al. 2004; Binder et al. 2005). From such analyses, four informally named clades of Polyporales were recognized: /antrodia/, core polyporoid, /phlebioid and /residual (the notation is used here to denote clade names; /antrodia is read as '(the) antrodia clade'), but support for these groups, and their interrelationships, was often lacking. Addition of protein-coding genes, including RNA polymerase II subunit 2 (*rpb2*), and translation elongation factor 1- α (*tef1*) was necessary to achieve strong support for monophyly of Polyporales as a whole, and many internal nodes (Matheny et al. 2007).

The PolyPEET project (<http://wordpress.clarku.edu/poly-peet/>), which was active from 2010 to 2016, focused on systematics of Polyporales. PolyPEET supported research on taxonomy of *Trametes* (Justo & Hibbett 2011; Carlson et al. 2014), *Phanerochaete* (Floudas & Hibbett 2015), *Lentinus* (Seelan et al. 2015), and the brown-rot polypores (Ortiz-Santana et al. 2013; Spirin et al. 2013a,b), as well as comparative genomics (Binder et al. 2013; Hibbett et al. 2013; Ruiz-Dueñas et al. 2013; Riley et al. 2014), sapwood and foliar endophytes (which contain a surprising diversity of Polyporales; Martin et al. 2015), and bioremediation (Young et al. 2015).

Binder et al. (2013) presented the most comprehensive phylogenetic analyses for Polyporales so far, including analyses of a 373-species, six-gene supermatrix, containing sequences from genes encoding rRNA (nrLSU, 5.8S, and nrSSU), RNA polymerase II subunits 1 and 2 (*rpb1*, *rpb2*), and *tef1*. Binder et al. also analysed ten Polyporales genomes, and performed phylogenetic informativeness profiling to assess the resolution afforded by individual genes. The analyses of Binder et al. upheld /antrodia/, core polyporoid, /phlebioid and /residual, with varying levels of support. Several lineages outside these major clades were also recovered. Phylogenetic informativeness profiling suggested that the RNA polymerase II large subunit (*rpb1*) is the most informative gene among those traditionally used in Polyporales systematics.

Unfortunately, it also turned out to be the least represented in public databases.

Polyporales is now well accepted as a strongly supported clade of *Agaricomycetes* (Hibbett et al. 2014). However, further taxonomic revision and general communication about Polyporales is hampered by the lack of a consensus classification within the group. As reviewed by Binder et al. (2013), there are forty nomenclaturally valid family names in Polyporales, plus the new *Fragiliporiaceae*, although many names are rarely used. The present study continues where that of Binder et al. (2013) left off and evaluates the status of 37 of the legitimate family names available in the Polyporales. New molecular data were obtained from across the Polyporales, emphasizing *rpb1* and focussing on taxa of phylogenetic and nomenclatural relevance. The new data were combined with sequences generated during the PolyPEET project and from other resources, including genomes, yielding a dataset with 292 species. A classification with eighteen families and four informal unranked clades is proposed, and the distribution of morphological, anatomical, physiological, and genetic characters that have been emphasized in prior taxonomy of Polyporales is reviewed.

Material & methods

Fungal isolates and DNA extraction

Culture collections and specimens were retrieved from the Center for Forest Mycology Research (USDA Forest Service, Madison, Wisconsin, U.S.A.), the Finnish Museum of Natural History at the University of Helsinki (Herbarium H), supplemented with c. 60 new collections and cultures made during the PolyPEET project. Protocols for culture growth and DNA extraction were the same ones outlined in Justo & Hibbett (2011).

PCR amplification and sequencing

The target loci for this study were nrITS, nrLSU, and *rpb1*, with a special focus on *rpb1*. For nrITS the primer pair ITS-1F/ITS4 was used (White et al. 1990; Gardes & Bruns 1993). For nrLSU either the combinations LR0R/LR7 or LR0R/LR5 were used, with additional sequencing primers LR3 and LR5 (Vilgalys Lab, <http://www.biology.duke.edu/fungi/mycolab/primers>). 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 et al. 2002). In some cases the primer *rpb1*-2.2f (Binder et 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 et al. 2005). Expected fragment lengths and degree of primer overlap for *rpb1* are posted at <http://wordpress.clarku.edu/polypeet/datasets/primer-information/>. We used the same PCR protocols outlined in Justo & Hibbett (2011). The PCR products were sequenced using Big-Dye 3.1 terminator sequencing chemistry (Applied Biosystems, Foster City, California, U.S.A.).

Raw data were processed using Sequencher v.4.7 (GeneCodes, Ann Arbor, Michigan, U.S.A.).

Sequence alignment and phylogenetic analyses

To construct the final datasets we combined our newly generated nrITS, nrLSU, and *rpb1* data with all previously generated sequences during the PolyPEET project. We then added *rpb1* sequences of Polyporales available in GenBank (not coming from the PolyPEET project), and retrieved additional *rpb1* data from the genomes available at MycoCosm (Grigoriev et al. 2013) for the following species: *Dichomitus squalens*, *Ganoderma sessile*, *Heterobasidion annosum*, *Phlebia brevispora*, *Sterium hirsutum*, *Wolfiporia cocos*. At this point we excluded all taxa without *rpb1* from further analyses. For taxa represented by multiple nrLSU + nrITS sequences in the nrDNA dataset, only one sequence set per taxon was included in the final 3-gene dataset.

The sequences were aligned using MAFFT v.7 (Katoh & Standley 2013; <http://mafft.cbrc.jp/alignment/server/>). The strategy FFT-NS-i was selected for nrLSU and *rpb1*, and the strategy Q-INS-i for nrITS, as they were deemed the more appropriate given the nature and size of the datasets. The alignments were edited and manually corrected using AliView (Larsson 2014). For the combined datasets each gene was aligned separately and then concatenated. Three different datasets were assembled: *rpb1*-only, nrLSU + nrITS and a combined 3-gene dataset.

For all datasets two different analyses were performed: (i) Maximum likelihood analyses (ML) were performed with RAxML v.8.2.8 (Stamatakis 2014), under a GTR model with one hundred rapid bootstrap replicates; (ii) Bayesian analyses (BY) were performed with MrBayes v.3.2.6 (Ronquist et al. 2012) for 10 million generations, under a GTR model, with four chains, and trees sampled every 100 generations. Convergence of the separate runs was confirmed by checking the average standard deviation of split frequencies (Ronquist et al. 2012). 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, using Tracer (Drummond et al. 2012), this burn-in value was confirmed to be an adequate value for all datasets. A fifty percent majority-rule consensus tree was computed using the remaining trees. Both ML and BY analyses were run at the CIPRES Science Gateway (Miller et al. 2010; <http://www.phylo.org/>). In all analyses *S. hirsutum* and *H. annosum* (Russulales) were used as outgroup taxa.

A search for potential conflicts between the nrDNA (LSU + ITS) dataset, and the *rpb1*-dataset was performed by comparing the resulting trees for each dataset, and looking for strongly supported positive conflict i.e., we looked for alternative topologies for the same taxon, on the different datasets, that were supported by at least 70 % bootstrap and one posterior probability. No strongly supported topological conflicts were detected between the datasets analysed in the present study.

Morphological, physiological, and genetic characters for each family were compiled from the monographic treatments of Bernicchia (2005), Bernicchia & Pérez-Gorjón (2010), Eriksson & Ryvarden (1973, 1975a,b), Eriksson et al. (1978, 1981, 1984), Gilbertson & Ryvarden (1986, 1987), Hjorstam et al. (1987, 1988), Rajchenberg (2011), Reid (1965), Ryvarden (1991, 2010), and Ryvarden & Melo (2014).

Results

New sequences and alignments

A total of 144 *rpb1*, 127 nrITS, and 67 nrLSU were generated in this study. The final *rpb1*-only alignment contains 292 ingroup taxa and 1612 total characters, with 1415 variable positions (87 %). The nrDNA alignment contains 310 ingroup, combined nrLSU + nrITS sequences (some taxa appear more than once), and 2276 characters, with 1482 variable positions (65 %). The 3-gene dataset contains 292 ingroup taxa (no duplicated taxa), and 3888 characters, with 2897 variable positions (74 %).

All newly generated sequences are deposited in GenBank (Table 1). All alignment files, and associated tree files, have been deposited in TreeBASE (<http://purl.org/phylo/treebase/phyloids/study/TB2:S20775>).

Phylogenetic analyses

The best tree from the ML analysis of the 3-gene dataset is presented in Figs 1–9, including support values from the BY consensus tree, which did not differ significantly in topology. Support values mentioned in the text are presented as (ML/BY).

The Polyporales can be subdivided into two main clades (Fig 1): (i) a clade including/phlebioid/residual and *Candelabrochaete africana* (82/1) and (ii) a clade including/core polyporoid/antrodia and satellite lineages (73/1). *Ischnoderma resinum* appears as sister to this second clade, but with no support.

In Fig 2 we give an overview of the families that we recognize in the Polyporales. A family name is assigned to 18 clades recovered in the analyses, including three families described as new here. Three clades are only given informal names (/hypochnium/,/climacocystis and/fibroporia + amyloporia). *Candelabrochaete africana*, *Mycocleptodonoides vassiljevae*, *Auriporia aurea*, and *Tyromyces merulinus* cannot be placed with certainty in any of the recognized families. Comments about the internal topology of each one of these families are given in the Taxonomy section.

Some minor topological differences exist between the trees from the analyses of the ribosomal-only and *rpb1*-only datasets with respect to the 3-gene dataset. These differences involve taxa that are particularly labile in all analyses: *Candelabrochaete africana*, *Caudicicola gracilis*, *T. merulinus*, *M. vassiljevae*, *A. aurea*, and *I. resinum*. In all cases the different placements in the ribosomal-only and *rpb1*-only datasets are not strongly supported. The trees for the ML and BY analyses of the ribosomal-only and *rpb1*-only datasets are available at TreeBASE S20775.

Taxonomy

When deciding on the application of existing family names a pragmatic approach has been chosen, attaching the available names to well-defined and well-supported clades in the phylogenies. For areas of the phylogeny still in need of additional research we have chosen to use family names that are already published (e.g. *Podoscyphaceae*), acknowledging that

Table 1 – Sequences used in this study. (*) Indicates sequences generated in this study.

Taxon	Collection	<i>rpb1</i>	nrLSU	nrITS
<i>Abortiporus biennis</i>	FD-319	KP134783	KP135195	KP135300
<i>Amylocystis lapponica</i>	FP-105131	KY948873*	KY948879*	KY948805*
<i>Amyloporia carbonica</i>	Zabel-40GLN	KY949013*	KC585065	KC585243
<i>Amyloporia cf. stratosa</i>	GatesFF-461	KY949014*	KY948881*	KY948806*
<i>Amyloporia sinuosa</i>	FP-105386	KY949018*	KC585066	KC585244
<i>Amyloporia xantha</i>	DAOM-16570	KY949016*	KC585076	KC585254
<i>Amyloporia xantha</i>	HHB-8673	KY949017*	KC585084	KC585261
<i>Antella americana</i>	HHB-4100-Sp	KP134885	KP135196	KP135316
<i>Anthoporia albobrunnea</i>	S-4665	KY949020*	KY948880*	KY948808*
<i>Antrodia favesces</i>	FP-103723	KY949009*	KC585092	KC585269
<i>Antrodia heteromorpha</i>	Kosolapov VIII-2003	KY949011*	KC543145	KC543145
<i>Antrodia hyalina</i>	Kotiranta-19668	KY949008*	JQ700284	JQ700284
<i>Antrodia juniperina</i>	SRM-403	KY948991*	KC585109	KC585285
<i>Antrodia malicola</i>	LE208476	KY948992*	JQ700282	JQ700282
<i>Antrodia mellita</i>	Spirin-3315	KY948994*	KC543139	KC543139
<i>Antrodia minuta</i>	Spirin-2680	KY948993*	KC595898	KC595898
<i>Antrodia oleracea</i>	HHB-5988	KY948987*	KC585117	KC585293
<i>Antrodia pulvinascens</i>	Pennanen-1532	KY948995*	JQ700286	JQ700286
<i>Antrodia ramentacea</i>	Spirin-2540	KY949002*	KC595903	KC595903
<i>Antrodia serialiformis</i>	FP-105717	KY949000*	KC585126	KC585302
<i>Antrodia serialis</i>	FP-133692	KY948998*	KC585127	KC585303
<i>Antrodia serpens</i>	Vampola-X-1989	KY949012*	KC543143	KC543143
<i>Antrodia variiformis</i>	FP-104442	KY948997*	KC585134	KC585309
<i>Antrodiella stipitata</i>	FD-136	KP134886	KP135197	KP135314
<i>Aurantiporus albidus</i>	CIEFAP-117	KY948925*	KY948848*	KY948739*
<i>Aurantiporus croceus</i>	Miettinen-16483	KY948927*	KY948901*	KY948745*
<i>Aurantiporus fissilis</i>	HHB-9530-sp	KY948922*	—	KY948774*
<i>Aurantiporus fissilis</i>	Voucher-814	—	HQ729001	—
<i>Auriporia aurea</i>	FP-98524	KY948984*	KC585141	KC585316
<i>Bjerkandera adusta</i>	HHB-12826-Sp	KP134784	KP135198	KP134983
<i>Bjerkandera aff. centroamericana</i>	L-13104-sp	KY948936*	KY948855*	KY948791*
<i>Bulbillomyces farinosus</i>	FP-100488-T	KY948929*	—	KY948802*
<i>Bulbillomyces farinosus</i>	NH-9933	—	DQ681201	—
<i>Butyrea luteoalba</i>	FP-105786-Sp	KP134887	KP135226	KP135320
<i>Byssomerulius corium</i>	FP-102382	KP134802	KP135230	KP135007
<i>Byssomerulius sp.</i>	OMC-1195	KY948962*	—	KY948746*
<i>Candelabrochaete africana</i>	FP-102987-Sp	KP134872	KP135199	KP135294
<i>Candelabrochaete langloisii</i>	FP-110343-sp	KY948981*	KY948886*	KY948793*
<i>Candelabrochaete septocystidia</i>	AS-95	—	EU118609	—
<i>Candelabrochaete septocystidia</i>	RMJ-119-sp	KY948959*	—	KY948783*
<i>Caudicicola gracilis</i>	X-3081	KY415972*	KY415962*	KY415962*
<i>Ceraceomyces serpens</i>	HHB-15692-Sp	KP134785	KP135200	KP135031
<i>Ceraceomyces sp.</i>	Miettinen-16854.3	KY948964*	KY948890*	KY948742*
<i>Ceriporia alachuana</i>	FP-103881-Sp	KP134845	KP135201	KP135341
<i>Ceriporia lacerata</i>	FP-55521-T	KP134805	KP135202	KP135024
<i>Ceriporia purpurea</i>	KKN-223-Sp	KP134788	KP135203	KP135044
<i>Ceriporia reticulata</i>	RLG-11354-Sp	KP134794	KP135204	KP135041
<i>Ceriporia sp.</i>	FP-134993	KP134792	—	KP135048
<i>Ceriporia sp.</i>	HHB-12714	KP134790	—	KP135046
<i>Ceriporia sp.</i>	L-8020	KP134789	—	KP135050
<i>Ceriporia sp.</i>	OMC-1333	KY948958*	KY948887*	KY948779*
<i>Ceriporia spissa</i>	FD-352	KP134793	KP135206	—
<i>Ceriporiopsis aneirina</i>	HHB-15629-Sp	KP134795	KP135207	KP135023
<i>Ceriporiopsis carnegieae</i>	RLG-7277-T	KY948935*	KY948854*	KY948792*
<i>Ceriporiopsis gilvescens</i>	L-3519-sp	KY948919*	—	KY948761*
<i>Ceriporiopsis gilvescens</i>	Niemelä-5516	—	HQ659222	—
<i>Ceriporiopsis pseudoplacenta</i>	Miettinen-18997	KY948926*	KY948902*	KY948744*
<i>Cerrena unicolor</i>	FD-299	KP134874	KP135209	KP135304
<i>Climacocystis borealis</i>	FD-31	KP134882	KP135210	KP135308
<i>Climacodon septentrionalis</i>	AFTOL-767	AY864873	AY684165	AY854082
<i>Corioloopsis cf. byrsina</i>	FP-105050-sp	JN164838	JN164788	JN165001
<i>Corioloopsis cf. caperata</i>	CR-22	JN164837	JN164789	JN164999
<i>Corioloopsis gallica</i>	RLG-7630-sp	JN164821	JN164814	JN165013

(continued on next page)

Table 1 – (continued)

Taxon	Collection	rpb1	nrLSU	nrITS
<i>Corioloopsis trogii</i>	RLG-4286-sp	JN164820	JN164808	JN164993
<i>Crustoderma corneum</i>	HHB-5685	KY949037*	KC585143	KC585318
<i>Crustoderma flavescens</i>	HHB-9359	KY949038*	KC585150	KC585325
<i>Cymatoderma</i> sp.	OMC-1427	KY948971*	KY948872*	KY948826*
<i>Dacryobolus karstenii</i>	Miettinen-18685	KY948955*	KY948900*	KY948743*
<i>Daedalea quercina</i>	FP-56429	KY948989*	KY948883*	KY948809*
<i>Datronia mollis</i>	RLG-6304-sp	JN164818	JN164791	JN165002
<i>Datronia scutellata</i>	RLG-9584-T	JN164817	JN164792	JN165004
<i>Dendrodontia bicolor</i>	FP-150666	KY948983*	KY948878*	KY948710*
<i>Dentocorticium sulphurellum</i>	FP-11801	JN164841	—	—
<i>Dentocorticium sulphurellum</i>	T-609	—	JN164815	JN165015
<i>Dichomitus squalens</i>	LE258894	—	KM411471	KM411455
<i>Dichomitus squalens</i>	LYAD-421 SS1	genome	—	—
<i>Diplomitoporus crustulinus</i>	FD-137	KP134883	KP135211	KP135299
<i>Diplomitoporus overholtsii</i>	HHB-9450-sp	KY948911*	KY948876*	KY948712*
<i>Donkia pulcherrima</i>	OMC-1428	KY948939*	KY948856*	KY948784*
<i>Earliella scabrosa</i>	PR-1209	JN164819	JN164793	JN165009
<i>Efibula americana</i>	FP-102165	KP134808	KP135256	KP135016
<i>Efibula clarkii</i>	FD-228	KP134803	—	KP135019
<i>Efibula gracilis</i>	FD-455	KP134804	—	KP135027
<i>Efibula tuberculata</i>	OM-6707	KP134807	—	KP135017
<i>Epithele macarangae</i>	FP-150881	KY948909*	KY948843*	KY948713*
<i>Etheiaron aff. fimbriatum</i>	FP-102075	KY948950*	KY948864*	KY948821*
<i>Fibroporia gossypium</i>	MR-11443	KY949029*	KY948897*	KY948811*
<i>Fibroporia pseudorennyi</i>	Rivoire 3914	KY949032*	KC595927	KC595927
<i>Fibroporia radiculosa</i>	L-11659	KY949034*	KC585166	KC585341
<i>Fibroporia vaillantii</i>	FP-90877	KY949035*	KC585170	KC585345
<i>Fomitella supina</i>	OMC-1405	KY948910*	KY948841*	KY948711*
<i>Fomitopsis ostreiformis</i>	Miettinen-14311	KY949006*	KC595920	KC595920
<i>Fomitopsis pinicola</i>	AFTOL-770	AY864874	AY684164	AY854083
<i>Fomitopsis rosea</i>	RLG-6954	KY949003*	KC585181	KC585353
<i>Ganoderma boninense</i>	RS	—	X78777	—
<i>Ganoderma boninense</i>	WD-2028 (FFPRI)	KJ143944	—	KJ143905
<i>Ganoderma curtisii</i>	CBS-100131	KJ143946	—	JQ781848
<i>Ganoderma lingzhi</i>	Cui-9166 (BJFC)	JX029982	—	KJ143907
<i>Ganoderma lucidum</i>	Cui-9207 (BJFC)	KJ143949	—	KJ143910
<i>Ganoderma multipileum</i>	Dai-9447 (IFP)	KJ143953	—	KJ143914
<i>Ganoderma oregonense</i>	CBS-265.88	KJ143954	—	JQ781875
<i>Ganoderma resinaceum</i>	CBS-194.76	KJ143956	—	KJ143916
<i>Ganoderma sessile</i>	10597-SS1	genomic	—	—
<i>Ganoderma sessile</i>	JV-1209/9	—	—	KJ143918
<i>Ganoderma tsugae</i>	Dai-12751b (BJFC)	KJ143960	—	—
<i>Ganoderma tsugae</i>	UBC-F23891	—	KJ146707	KJ146707
<i>Ganoderma zonatum</i>	FL-02 (TNM)	KJ143962	—	KJ143921
<i>Gelatoporia subvermispora</i>	FD-354	KP134879	KP135212	KP135312
<i>Gloeoporus dichrous</i>	FP-151129	KP134866	KP135213	KP135058
<i>Gloeoporus pannocinctus</i>	L-15726-Sp	KP134867	KP135214	KP135060
<i>Grammothele aff. fuligo</i>	FP-150657	KY948908*	KY948840*	KY948716*
<i>Grammothele</i> sp.	FP-150285	KY948907*	KY948839*	KY948729*
<i>Grammothele</i> sp.	FP-150289	KY948904*	KY948836*	KY948717*
<i>Grifola frondosa</i>	AFTOL-701	AY864876	AY629318	AY854084
<i>Grifola sordulenta</i>	AFTOL-562	AY864879	AY645050	AY854085
<i>Hapalopilus nidulans</i>	FD-512	KP134809	—	KP135419
<i>Hapalopilus ochraceolateritius</i>	Miettinen-16992.1	KY948965*	KY948891*	KY948741*
<i>Heterobasidium annosum</i>	DAOM-73191	—	AF287866	—
<i>Heterobasidium annosum</i>	TC-32-1	genome	—	—
<i>Heterobasidium annosum</i>	VL-296	—	—	JF440572
<i>Hexagonia tenuis</i>	Niemelä-9032	KY949042*	KY948842*	KY948738*
<i>Hydnophlebia chrysorhiza</i>	FD-282	KP134848	KP135217	KP135338
<i>Hydnophlebia omnivora I</i>	KKN-112	KP134846	KP135216	KP135334
<i>Hydnophlebia omnivora II</i>	ME-497	KP134847	KP135218	KP135332
<i>Hyphoderma litschaueri</i>	FP-101740-Sp	KP134868	KP135219	KP135295
<i>Hyphoderma medioburiense</i>	FD-335	KP134869	KP135220	KP135298
<i>Hyphoderma mutatum</i>	HHB-15479-Sp	KP134870	KP135221	KP135296

Table 1 – (continued)

Taxon	Collection	rpb1	nrLSU	nrITS
<i>Hyphoderma setigerum</i>	FD-312	KP134871	KP135222	KP135297
<i>Hyphodermella rosae</i>	FP-150552	KP134823	KP135223	KP134978
<i>Hypochnicium bombycinum</i>	HHB-12631-sp	KY948930*	—	KY948801*
<i>Hypochnicium karstenii</i>	HHB-9373-sp	KY948931*	—	KY948799*
<i>Hypochnicium karstenii</i>	NH-10924	—	DQ677510	—
<i>Hypochnicium punctulatum</i>	FP-101698-sp	KY948932*	KY948860*	KY948827*
<i>Hypochnicium</i> sp.	FP-110227-sp	KY948944*	KY948862*	KY948804*
<i>Hypochnicium sphaerosporum</i>	RLG-15138-sp	KY948940*	KY948861*	KY948803*
<i>Hypochnicium wakefieldiae</i>	KJM-271-sp	KY948933*	—	KY948828*
<i>Hypochnicium wakefieldiae</i>	NH 11232	—	DQ677512	—
<i>Irpex lacteus</i>	FD-9	KP134806	KP135224	KP135026
<i>Ischnoderma resinosum</i>	FD-328	KP134884	KP135225	KP135303
<i>Jahnoporus hirtus</i>	Spinosa 10-X-2014 (H)	KY949044*	—	KU165784
<i>Jahnoporus hirtus</i>	Vlasák-1108/1	—	KU165782	—
<i>Laetiporus conifericola</i>	CA-8	KY949024*	EU402523	EU402575
<i>Laetiporus persicinus</i>	HHB-9564	KY949027*	EU402513	EU402579
<i>Laetiporus sulphureus</i>	CT-1	KY949025*	EU402532	EU402565
<i>Lentinus badius</i>	JS-0094	KP325691	KP283512	KP283478
<i>Lentinus crinitus</i>	DSH-9243C	KP325687	KP283523	KP283495
<i>Lentinus sajor-caju</i>	FRI-62056	KP325677	KP283509	KP283492
<i>Lentinus squarrosulus</i>	CUI-6513	KP325680	KP283516	KP283482
<i>Lentinus tigrinus</i>	DSH-92D787	KP325689	—	KP283488
<i>Lentinus tigrinus</i>	LE-214778	—	KM411475	—
<i>Leptoporus mollis</i> I (AZ)	RLG-7163	KY948956*	—	KY948794*
<i>Leptoporus mollis</i> II (WA)	TJV-93-174-T	KY948957*	EU402510	KY948795*
<i>Lilaceophlebia livida</i>	FP-135046-sp	KY948917*	KY948850*	KY948758*
<i>Lopharia cinerascens</i>	FP-105043-sp	JN164840	JN164813	JN165019
<i>Meripilus giganteus</i>	FP-135344-Sp	KP134873	KP135228	KP135307
<i>Meruliopsis albostramineus</i>	HHB-10729	KP134787	KP135229	KP135051
<i>Meruliopsis</i> sp.	FD-278	KP134796	KP135205	KP135057
<i>Meruliopsis</i> sp.	FD-497	KP134786	—	KP135054
<i>Merulius tremellosus</i>	FD-323	KP134856	KP135231	—
<i>Mycoacia fuscoatra</i>	HHB-10782-Sp	KP134857	KP135265	KP135365
<i>Mycoacia nothofagi</i>	HHB-4273-Sp	KP134858	KP135266	KP135369
<i>Mycoleptodonoides vassiljevae</i>	Spirin-8033	KY948970*	KY948877*	KY948737*
<i>Neofavolus</i> sp.	MA-672	KP325696	KP283524	KP283506
<i>Neofavolus suavissimus</i>	ADD-7	KP325694	KP283527	KP283501
<i>Obba rivulosa</i>	FP-135416-Sp	KP134878	KP135208	KP135309
<i>Oligoporus balsameus</i>	FP-135372	KY948974*	KC585187	KC585358
<i>Oligoporus sericeomollis</i>	L-15571	KY948977*	KC585192	KC585363
<i>Oxychaete cervinogilvus</i>	Schigel-5216	KX752626*	KX752596*	KX752596*
<i>Panus fragilis</i>	HHB-11042-Sp	KP134877	KP135233	KP135328
<i>Phaeophlebiopsis caribbeana</i>	HHB-6990	KP134810	KP135243	KP135415
<i>Phaeophlebiopsis ignerii</i>	FD-425	KP134811	—	KP135418
<i>Phaeophlebiopsis peniophoroides</i>	FP-150577	KP134813	KP135273	KP135417
<i>Phaeophlebiopsis</i> sp.	HHB-6542-Sp	KP134812	KP135248	KP135413
<i>Phanerochaete</i> ‘krikophora’	HHB-5796-Sp	KP134837	KP135268	KP135164
<i>Phanerochaete allantospora</i>	KKN-111	KP134791	KP135238	KP135038
<i>Phanerochaete arizonica</i>	RLG-10248-Sp	KP134830	KP135239	KP135170
<i>Phanerochaete australis</i>	HHB-7105-Sp	KP134840	KP135240	KP135081
<i>Phanerochaete carnosa</i>	HHB-9195-Sp	KP134831	KP135242	KP135129
<i>Phanerochaete</i> cf. <i>calotriha</i>	Vanhanen-382	KP134826	—	KP135107
<i>Phanerochaete chrysosporium</i> I	AFTOL-776	AY864880	—	AY854086
<i>Phanerochaete chrysosporium</i> II	HHB-6251-Sp	KP134842	KP135246	KP135094
<i>Phanerochaete citrinosa</i>	FP-105385	KP134824	KP135234	KP135100
<i>Phanerochaete ericina</i>	HHB-2288	KP134834	KP135247	KP135167
<i>Phanerochaete exilis</i>	HHB-6988	KP134799	KP135236	KP135001
<i>Phanerochaete laevis</i>	HHB-15519-Sp	KP134836	KP135249	KP135149
<i>Phanerochaete magnoliae</i>	HHB-9829-Sp	KP134838	KP135237	KP135089
<i>Phanerochaete pseudomagnoliae</i>	PP-25	KP135091	KP135250	KP135091
<i>Phanerochaete pseudosanguinea</i>	FD-244	KP134827	KP135251	KP135098
<i>Phanerochaete rhodellum</i>	FD-18	KP135187	KP135258	KP135187
<i>Phanerochaete sanguinea</i>	HHB-7524	KP135101	KP135244	KP135101

(continued on next page)

Table 1 – (continued)

Taxon	Collection	rpb1	nrLSU	nrITS
<i>Phanerochaete sordida</i> I	FD-241	KP135136	KP135252	KP135136
<i>Phanerochaete sordida</i> II	FD-106	KP135070	KP135253	KP135070
<i>Phanerochaete</i> sp.	HHB-11463	KP134797	KP135235	KP134994
<i>Phanerochaete</i> sp.	HHB-18104	KP134798	KP135254	KP135003
<i>Phanerochaete</i> sp.	RLG-13408-Sp	KP134801	KP135257	KP135020
<i>Phanerochaete subceracea</i>	FP-105974-R	KP134835	KP135255	KP135162
<i>Phanerochaete xerophila</i>	HHB-8509-Sp	KP134800	KP135259	KP134996
<i>Phlebia albida</i>	GB-1833	KY948960*	KY948889*	KY948748*
<i>Phlebia aurea</i>	NH-14434	—	AY586691	—
<i>Phlebia aurea</i>	RLG-5075-sp	KY948918*	—	KY948759*
<i>Phlebia brevispora</i>	FBCC1463	—	LN611135	LN611135
<i>Phlebia brevispora</i>	HHB-7030	genome	—	—
<i>Phlebia centrifuga</i>	HHB-9239-Sp	KP134844	KP135262	KP135380
<i>Phlebia cf. griseoflavescens</i>	MR-4310	KY948963*	KY948888*	KY948797*
<i>Phlebia chrysocreas</i>	HHB-6333-Sp	KP134861	KP135263	KP135358
<i>Phlebia coccineofulva</i>	HHB-11466-sp	KY948915*	KY948851*	KY948766*
<i>Phlebia floridensis</i>	HHB-9905	KP134863	KP135264	KP135383
<i>Phlebia hydnoidea</i>	HHB-1993-sp	KY948921*	KY948853*	KY948778*
<i>Phlebia lindtneri</i>	GB-501	KY948923*	KY948847*	KY948772*
<i>Phlebia lividina</i>	HHB-4160-sp	KY948916*	KY948849*	KY948755*
<i>Phlebia ludoviciana</i>	FD-427	KP134849	—	KP135342
<i>Phlebia nantahaliensis</i>	HHB-2816-sp	KY948920*	KY948852*	KY948777*
<i>Phlebia nitidula</i>	Nystroem-020830	—	EU118655	—
<i>Phlebia nitidula</i>	T-407	KY948961*	—	KY948747*
<i>Phlebia radiata</i>	AFTOL-484	AY864881	AF287885	AY854087
<i>Phlebia setulosa</i>	HHB-6891-Sp	KP134864	KP135267	KP135382
<i>Phlebia</i> sp.	HHB-17984	KP134860	KP135261	KP135359
<i>Phlebia</i> sp.	HHB-18295	KP134814	KP135269	KP135405
<i>Phlebia</i> sp.	RLG-10795-sp	KY948937*	KY948857*	KY948785*
<i>Phlebia subochracea</i> I	HHB-8715-sp	KY948913*	KY948846*	KY948770*
<i>Phlebia subochracea</i> II	HHB-8494-sp	KY948912*	KY948845*	KY948768*
<i>Phlebia uda</i>	FP-101544-Sp	KP134859	KP135232	KP135361
<i>Phlebiopsis castanea</i>	Spirin-5295	KX752629*	KX752610*	KX752610*
<i>Phlebiopsis crassa</i>	KKN-86-Sp	KP134820	KP135215	KP135394
<i>Phlebiopsis flavidoalba</i>	FD-263	KP134819	KP135271	KP135402
<i>Phlebiopsis galochroa</i>	FP-102937	KP134822	KP135270	KP135391
<i>Phlebiopsis gigantea</i>	FP-70857-Sp	KP134821	KP135272	KP135390
<i>Phlebiopsis ravenelii</i>	FP-110129	KP134850	KP135274	KP135362
<i>Physisporinus</i> sp.	Miettinen-15239	KY948946*	KY948867*	KY948732*
<i>Physisporinus</i> sp.	Miettinen-16699	KY948947*	KY948863*	KY948733*
<i>Piptoporus betulinus</i>	L-15603	KY949005*	KC585202	KC585373
<i>Pirex concentricus</i>	OSC-41587	KP134843	KP135275	KP134984
<i>Podoscypha parvula</i>	CBS 331.66	—	JN649361	JN649361
<i>Podoscypha parvula</i>	Niemelä-7690	KY948934*	—	—
<i>Polyporellus arcularius</i>	DSH92-132	KP325686	KP283522	KP283489
<i>Polyporus brumalis</i>	PB-4 (EP4)	KP325685	KP283519	KP283490
<i>Polyporus squamosus</i>	AFTOL-704	DQ831023	AY629320	DQ267123
<i>Porogramme albocincta</i>	PR-1478-T	KY948906*	KY948838*	KY948725*
<i>Postia caesia</i>	Kinnunen-5087	KY948978*	KY948885*	KY948814*
<i>Postia lactea</i>	Kotiranta-20058	KY948979*	KC595939	KC595939
<i>Postia lowei</i>	Pennanen-1254	KY948980*	KC595941	KC595941
<i>Pouzaroporia subrufa</i>	Miettinen-14343	KY948972*	KY948896*	KY948736*
<i>Pycnoporellus alboluteus</i>	FP-105074	KY949039*	KC585214	KC585381
<i>Pycnoporellus fulgens</i>	CA-20	KY949040*	KC585218	KC585385
<i>Radulodon casearius</i>	HHB-9567-sp	KY948943*	KY948871*	KY948752*
<i>Rhizochaete americana</i>	FP-102188	KP134815	KP135277	KP135409
<i>Rhizochaete belizensis</i>	FP-150712	KP134817	KP135280	KP135408
<i>Rhizochaete filamentosa</i>	HHB-3169-Sp	KP134818	KP135278	KP135410
<i>Rhizochaete fouquieriae</i>	KKN-121-sp	KY948938*	KY948858*	KY948786*
<i>Rhizochaete radicata</i>	FD-123	KP134816	KP135279	KP135407
<i>Rhodonia placenta</i>	Dietz-7E	KY949028*	KC585223	KC585390
<i>Rigidoporus undatus</i>	Miettinen-13591	KY948945*	KY948870*	KY948731*
<i>Rigidoporus vinctus</i>	ECS-194-R	KY948953*	KY948873*	KY948734*
<i>Rigidoporus vinctus</i>	Miettinen-16136	KY953212*	—	KY953211*

Table 1 – (continued)

Taxon	Collection	rpb1	nrLSU	nrITS
<i>Rigidoporus vinctus</i>	Miettinen-17916	KY948954*	KY948874*	KY948735*
<i>Sarcodontia crocea</i>	OMC-1488	KY948928*	KY948903*	KY948798*
<i>Sarcoporia polyspora</i>	L-14910	KY949022*	KC585226	KC585393
<i>Scopuloides rimosa I</i>	RLG-5104	KP134852	KP135283	KP135351
<i>Scopuloides rimosa II</i>	HHB-7042	KP135350	KP135282	KP135350
<i>Scopuloides rimosa III</i>	HHB-15484	KP134851	KP135281	KP135352
<i>Scopuloides sp.</i>	FP-102935	KP134855	KP135285	KP135353
<i>Scopuloides sp.</i>	FP-150473	KP134854	KP135284	KP135355
<i>Skeletocutis chrysella</i>	L-15957-sp	KY948982*	—	—
<i>Skeletocutis chrysella</i>	X-319	—	FN907916	FN907916
<i>Skeletocutis lilacina</i>	HHB-10522-sp	KY948967*	KY948894*	KY948834*
<i>Skeletocutis nivea</i>	Miettinen-9950	KY953143	KY953045	KY953045
<i>Skeletocutis odora</i>	L-13763-sp	KY949046*	KY948893*	KY948830*
<i>Skeletocutis sp.</i>	L-3291-R	KY948968*	KY948968*	KY948835*
<i>Sparassis radicata</i>	OKM-4756	KY949023*	KF053407	KC987580
<i>Spongipellis delectans</i>	HHB-10489-Sp	KP134876	KP135287	KP135301
<i>Spongipellis pachyodon</i>	FD-314	KP134875	KP135288	KP135302
<i>Spongipellis unicolor</i>	RLG-7638-sp	KY948942*	—	KY948751*
<i>Spongipellis unicolor</i>	RLG-7701-T	—	HQ729016	—
<i>Spongiporus leucospongia</i>	OKM-4335	KY948975*	KC585228	KC585395
<i>Steccherinaceae sp.</i>	OMC-1192	KY949047*	KY948865*	KY948816*
<i>Steccherinum bourdotii</i>	HHB-9743-sp	KY949043*	—	KY948818*
<i>Steccherinum bourdotii</i>	Saarenoksa-10195	—	JN710584	—
<i>Steccherinum laeticolor</i>	FP-102480-sp	KY948948*	KY948868*	KY948823*
<i>Steccherinum nitidum</i>	FP-105195-Sp	KP134888	KP135227	KP135323
<i>Steccherinum oreophilum</i>	HHB-13202-sp	KY948949*	—	KY948824*
<i>Steccherinum oreophilum</i>	Niemelä-7691	—	JN710548	—
<i>Steccherinum sp.</i>	FD-26	KP134889	KP135289	KP135322
<i>Steccherinum sp.</i>	FP-8695	KY948952*	KY948869*	KY948819*
<i>Steccherinum tenue</i>	FP-102082-sp	KY948951*	—	KY948817*
<i>Steccherinum tenue</i>	KHL 12316	—	JN710598	—
<i>Stereum hirsutum</i>	FP-91666	genome	—	—
<i>Stereum hirsutum</i>	FPL-8805	—	AF393078	AY854063
<i>Terana caerulea</i>	FP-104073	KP134865	KP135276	KP134980
<i>Tinctoporellus epimiltinus</i>	CRM-55	KY948905*	KY948837*	KY948720*
<i>Tomophagus cattienensis</i> (as <i>T. colossus</i> in Genbank)	TC-02 (TNM)	KJ143963	—	KJ143923
<i>Trametes aesculi</i>	FP-105679-sp	JN164833	JN164799	JN164944
<i>Trametes betulina</i>	HHB-9942-sp	JN164822	JN164794	JN164983
<i>Trametes cinnabarina</i>	AFTOL-772	JN164843	AY684160	DQ411525
<i>Trametes conchifer</i>	FP-106793-sp	JN164823	JN164797	JN164924
<i>Trametes cubensis</i>	TJV-93-213-sp	JN164834	JN164798	JN164923
<i>Trametes ectypa</i>	FP-106037-T	JN164824	JN164803	JN164929
<i>Trametes gibbosa</i>	L-11664-sp	JN164831	JN164800	JN164943
<i>Trametes hirsuta</i>	RLG-5133-T	JN164829	JN164801	JN164941
<i>Trametes maxima</i>	OH-189-sp	JN164816	JN164804	JN164957
<i>Trametes membranacea</i>	PRSC-82	JN164832	JN164805	JN164945
<i>Trametes meyenii</i>	FPRI-401	JN164836	JN164802	JN164933
<i>Trametes ochracea</i>	HHB-13445-sp	JN164826	JN164812	JN164954
<i>Trametes pavonia</i>	FP-103050-sp	JN164835	JN164806	JN164958
<i>Trametes polyzona</i>	BKW-004	JN164844/JN164846	JN164790	JN164978
<i>Trametes pubescens</i>	FP-101414-sp	JN164827	JN164811	JN164963
<i>Trametes sanguinea</i>	PRSC-95	JN164842	JN164795	JN164982
<i>Trametes suaveolens</i>	FP-102529-sp	JN164828	JN164807	JN164966
<i>Trametes versicolor</i>	FP-135156-sp	JN164825	JN164809	JN164919
<i>Trametes villosa</i>	FP-71974-R	JN164830	JN164810	JN164969
<i>Trametopsis cervina</i>	AJ-185	JN164839	JN164796	JN165020
<i>Tyromyces chioneus</i>	FD-4	KP134891	KP135291	KP135311
<i>Tyromyces galactinus</i>	L-15951-sp	KY948966*	KY948892*	KY948829*
<i>Tyromyces merulinus</i>	CIEFAP-204	KY949045*	KY948875*	KY948740*
<i>Wolfiporia cocos</i>	18176	—	KC585233	—
<i>Wolfiporia cocos</i>	MD-104 SS10	genomic	—	—
<i>Wolfiporia cocos</i>	unknown	—	—	AY728272
<i>Wolfiporia dilatohypha</i>	CS-635913	KY949026*	KC585234	KC585400

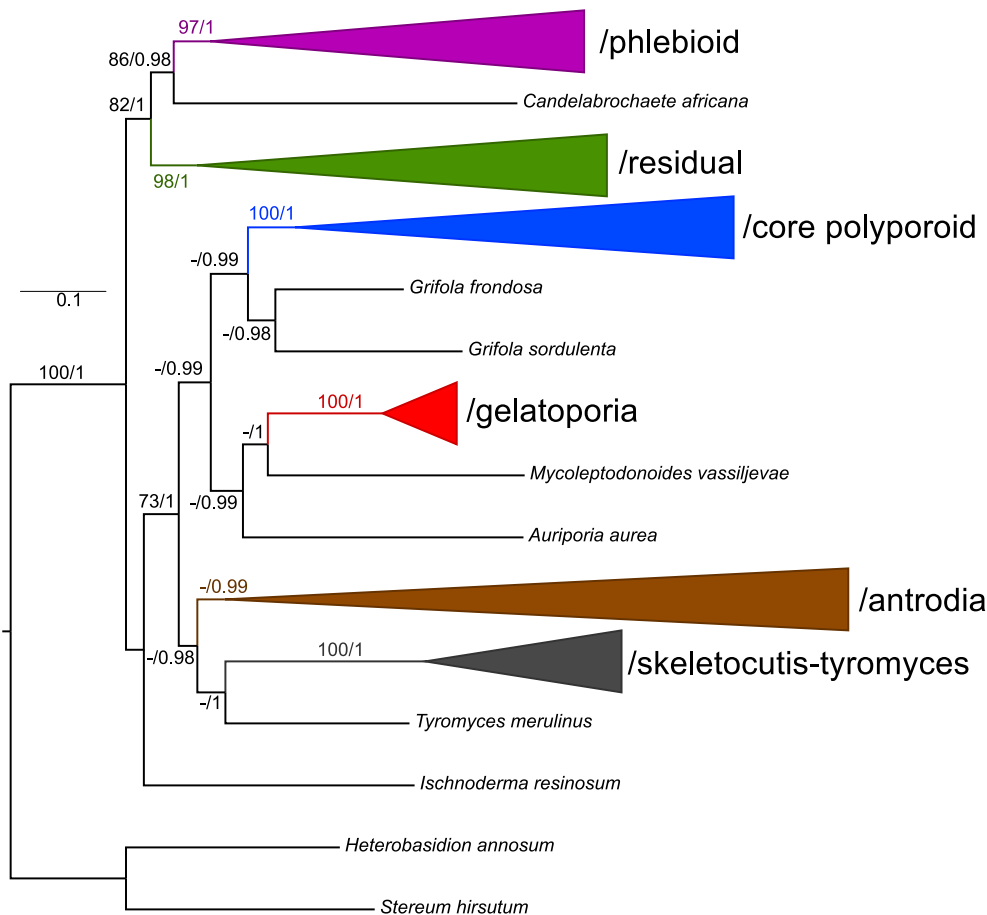


Fig 1 – Overview of the major clades of Polyporales, based on the ML tree from the 3-gene dataset. Support values are given as ML/BY.

defining their limits and composition will need further studies. In cases where no family name is available, or if they cannot be applied with certainty based on the current phylogenetic information (e.g. *Laricifomitaceae*), informal clade names are recommended until a better resolved phylogeny is available (e.g./hypochnicium,/climacocystis,/fibroporia + amyloporia).

Alternative taxonomic arrangements were considered, including adopting more broadly or narrowly defined families for all groups under study. Two representative examples of both cases are discussed in detail under *Podoscyphaceae* and *Polyporaceae*. When multiple family names with equal nomenclatural priority are available for the same clade we have chosen the name that has been more widely used.

The list of taxa belonging to each family (or clade) is based on the results presented here (Figs 1–9), as well as the phylogenies of Binder et al. (2013), Floudas & Hibbett (2015), Miettinen et al. (2012, 2016), Ortiz-Santana et al. (2013) and Sjökvist et al. (2012). Additional relevant references are mentioned under the comments for each family. Under ‘additional taxa’ we list species of uncertain generic placement that have been confirmed to belong in each family. The study of the genus-level taxonomy within each family falls out of the scope of the present paper, but in some particularly problematic cases

(e.g. *Phlebia* s. lato,/antrodia) some comments are given, and generic types are highlighted in the respective figures.

We provide a short morphological characterization for each family, that is intended to apply to the majority of the species included in that family, but exceptions do occur in most cases. A morphological overview of all families recognized here is given in Table 2.

Phanerochaetaceae Jülich 1981 (Fig 3)

Synonym. *Hapalopilaceae* Jülich 1981.

Synonym. *Bjerkanderaceae* Jülich 1981.

Type genus: *Phanerochaete* P. Karst.

Mostly corticioid species; hyphal system monomitic; hyphae without clamp-connections; spores thin-walled, smooth, hyaline; cystidia often present. More rarely polypores and/or dimitic and/or clamp-connections present. Producing a white-rot.

Genera: *Bjerkandera* P. Karst, *Donkia* Pilát, *Hapalopilus* P. Karst, *Hyphodermella* J. Erikss. & Ryvarden, *Oxychaete* Miettinen, *Phaeophlebiopsis* Floudas & Hibbett, *Phanerina* Miettinen, *Phlebiopsis* Jülich (including *Castanoporus* Ryvarden, see Miettinen et al. 2016), *Pirex* Hjortstam & Ryvarden, *Porostereum* Pilát, *Rhizochaete* Gresl., Nakasone & Rajchenb., *Riopa* D.A. Reid, *Terana* Adans.

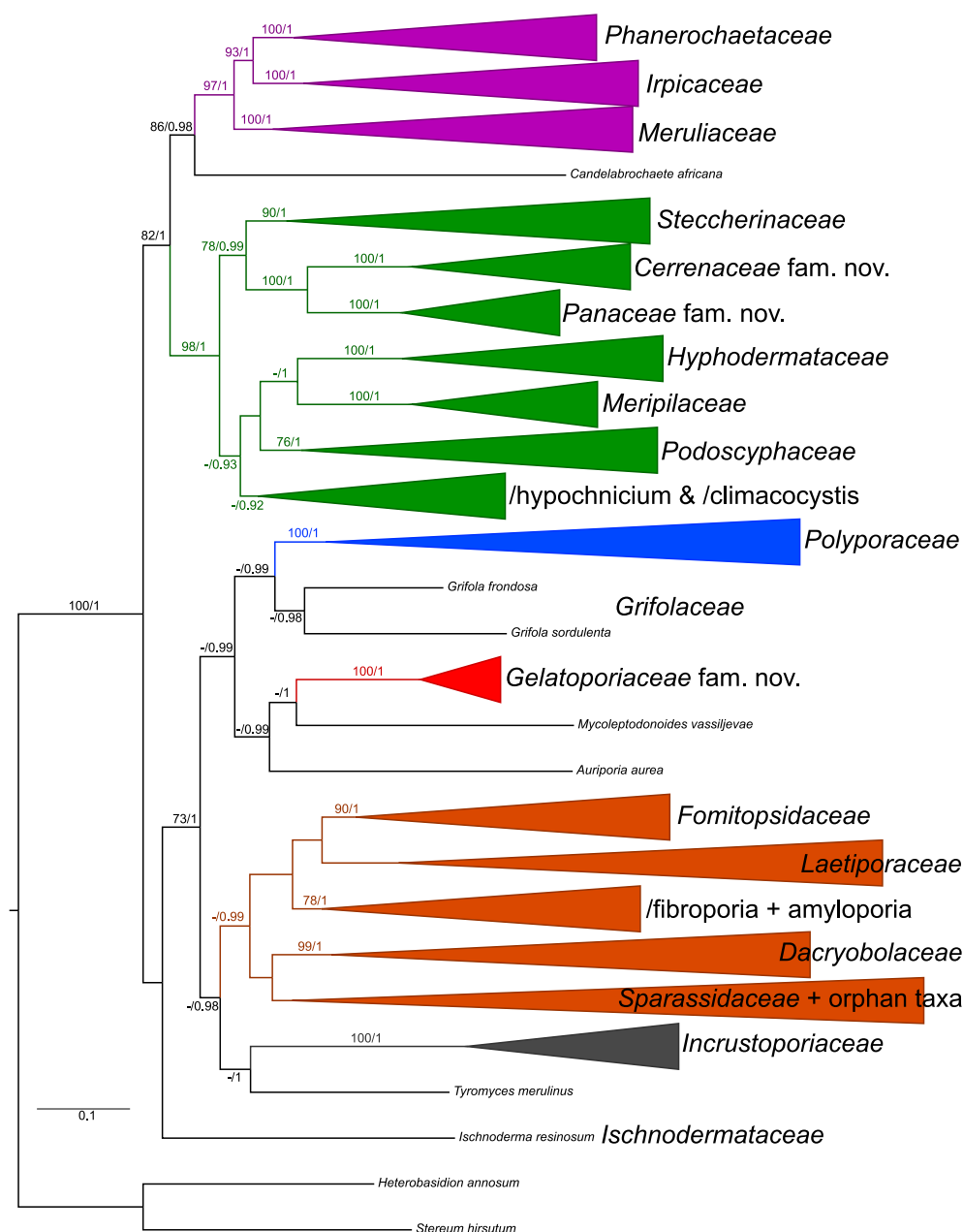


Fig 2 – Overview of the families and clades recognized here, based on the ML tree from the 3-gene dataset. Support values are given as ML/BY.

Additional taxa: *Ceriporiopsis carnegieae* (D.V. Baxter) Gilb. & Ryvariden, *Phanerochaete lamprocystidiata* Sheng H. Wu, *Phanerochaete lutea* (Sheng H. Wu) Hjortstam, *Phlebia bresadolae* Parmasto, *Phlebia deflectens* (P. Karst.) Ryvariden, *Phlebia firma* J. Erikss. & Hjortstam, *Phlebia lilascens* (Bourdot) J. Erikss. & Hjortstam, *Phlebia unica* (H.S. Jacks. & Dearden) Ginns, *Phlebiopsis himalayensis* Dhingra, *Phlebiopsis roumeguerii* (Bres.) Jülich & Stalpers.

Comments: The names *Hapalopilaceae* and *Bjerkanderaceae* have equal nomenclatural priority, but are placed here as synonyms of *Phanerochaetaceae*. A comprehensive overview of the genus *Phanerochaete* and related taxa has been recently published (Floudas & Hibbett 2015), combining morphological

and molecular data. Although the limits of *Phanerochaete* s. stricto are now clearly defined, many species still await proper generic placement (see additional taxa above), and generic concepts in the family are in need of additional research (Miettinen et al. 2016).

Irpicaceae Spirin & Zmitr. 2003 (Fig 4)

Type genus: *Irpe* Fr.

Corticoid species or polypores; hyphal system monomitic; hyphae without clamp-connections; spores thin-walled, smooth, hyaline; cystidia often absent. More rarely dimittic and/or with cystidia and/or clamp-connections present. Producing a white-rot, except for one brown-rot genus (*Leptoporus*).

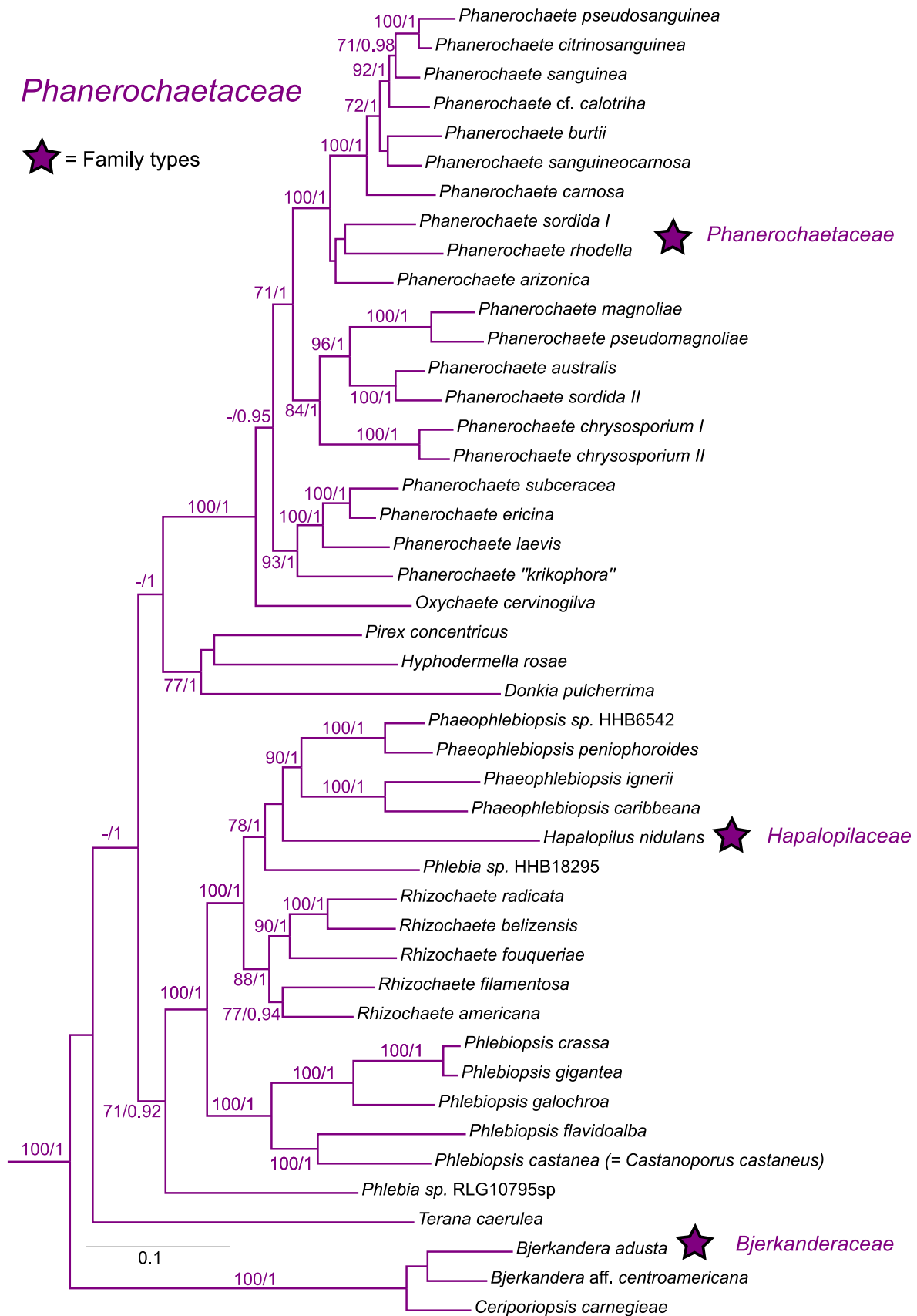


Fig 3 – *Phanerochaetaceae*, based on the ML tree from the 3-gene dataset. Support values are given as ML/BY. Stars indicate the type genus of a family.

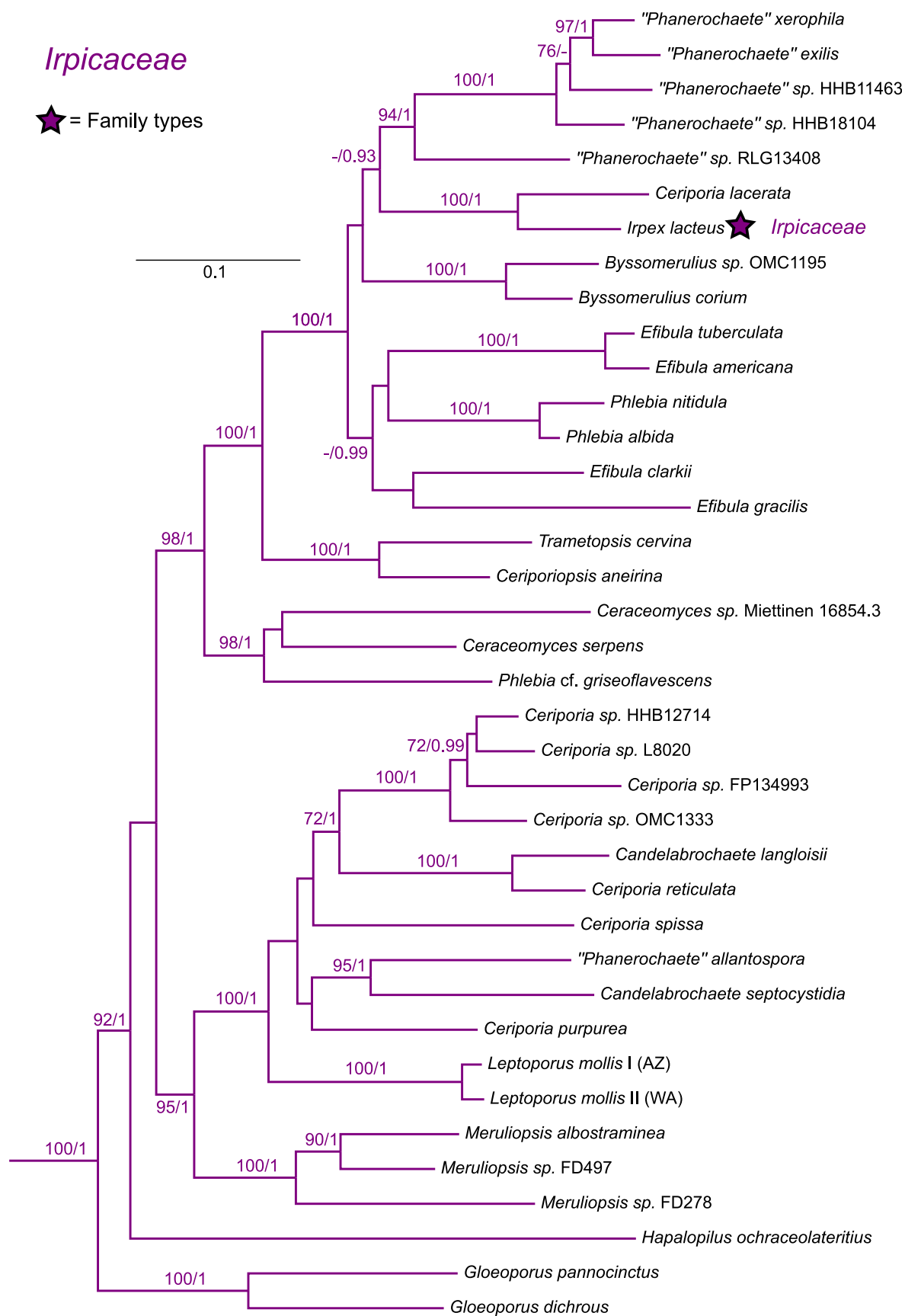


Fig 4 – Irpicaceae, based on the ML tree from the 3-gene dataset. Support values are given as ML/BY. Stars indicate the type genus of a family.

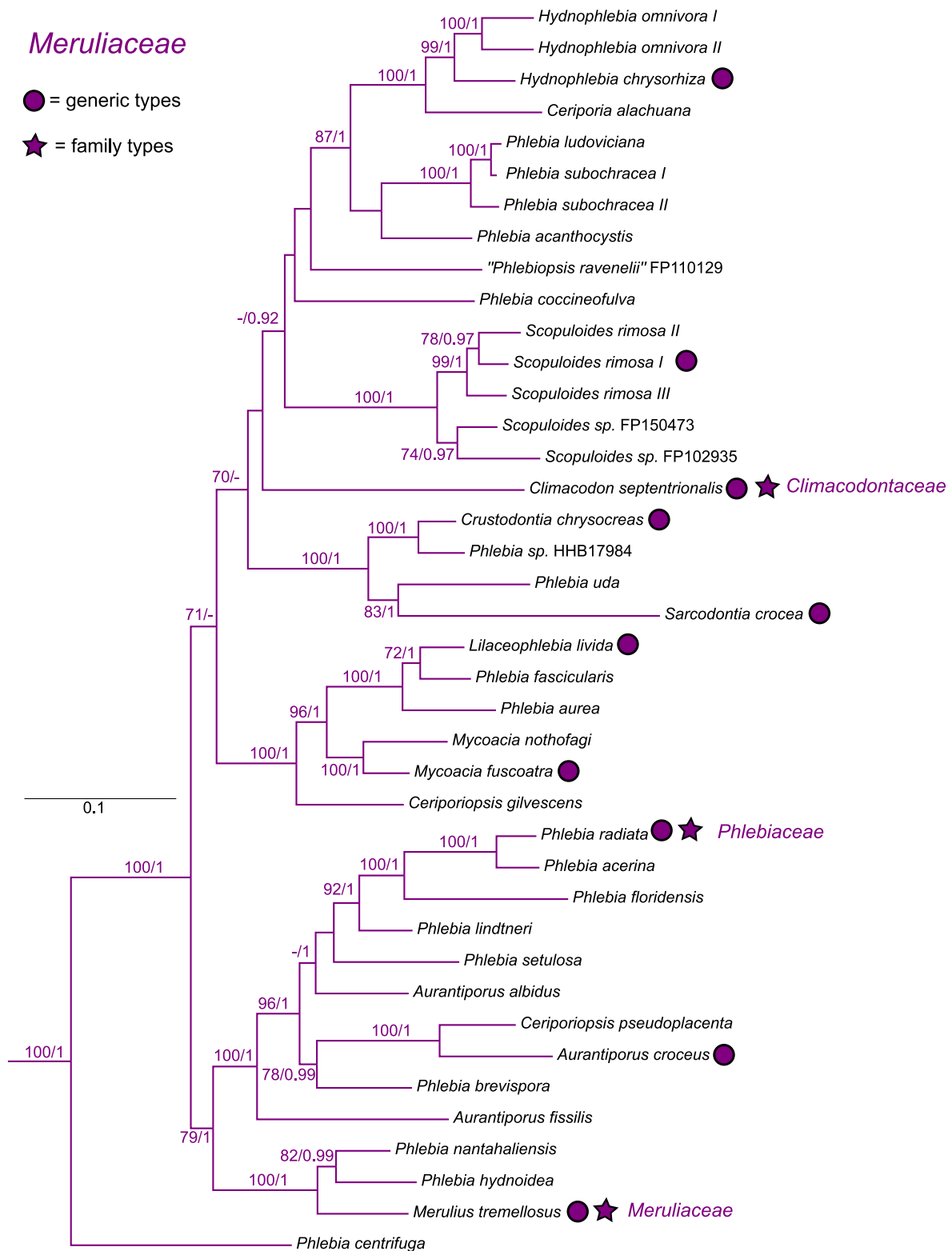
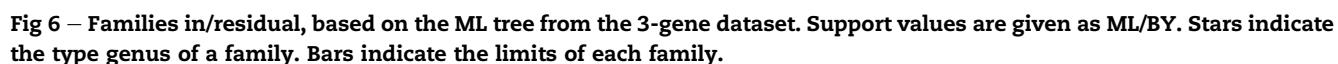


Fig 5 – Meruliaceae, based on the ML tree from the 3-gene dataset. Support values are given as ML/BY. Stars indicate the type genus of a family. Circles indicate the type species of a genus.



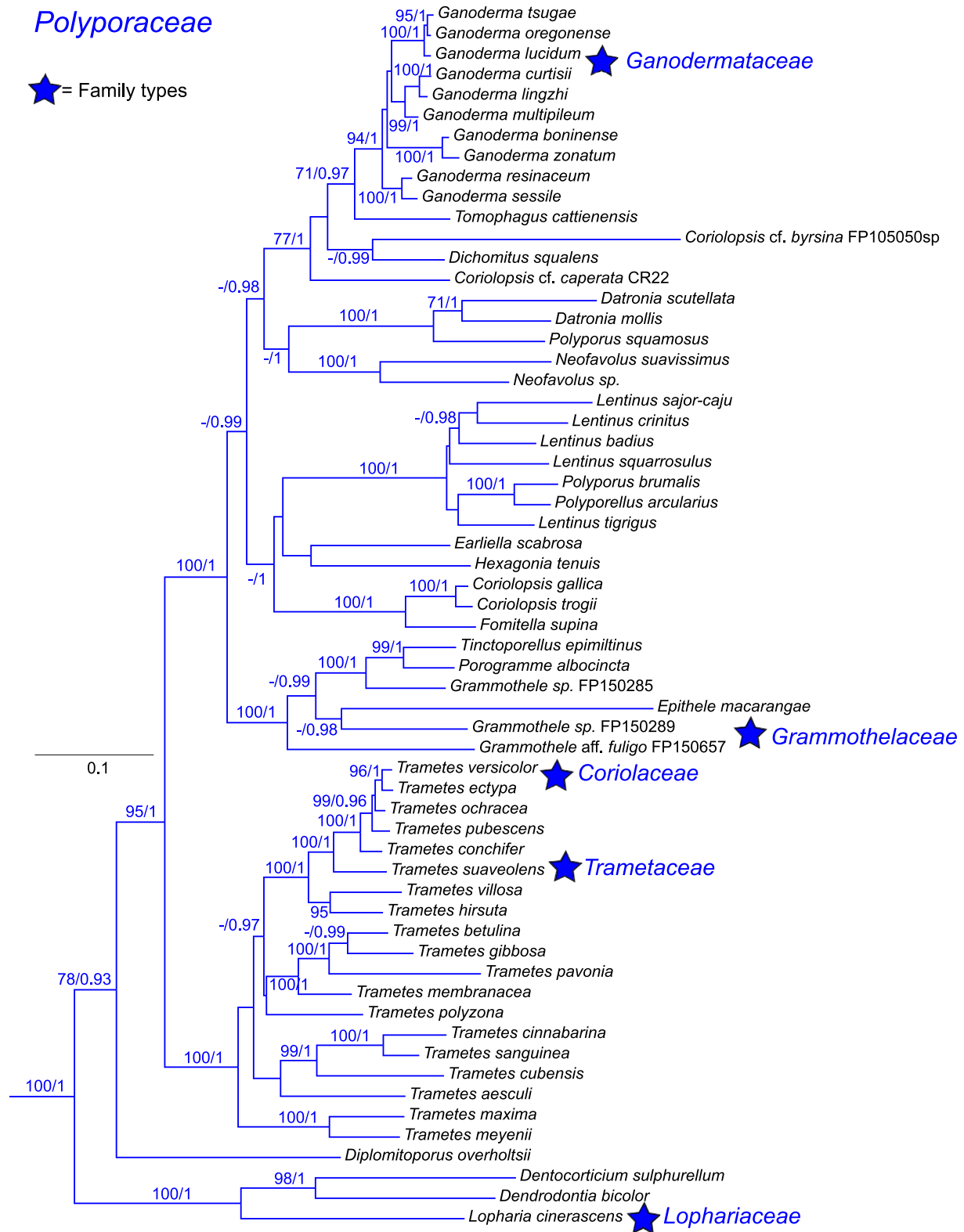


Fig 7 – Polyporaceae, based on the ML tree from the 3-gene dataset. Support values are given as ML/BY. Stars indicate the type genus of a family.

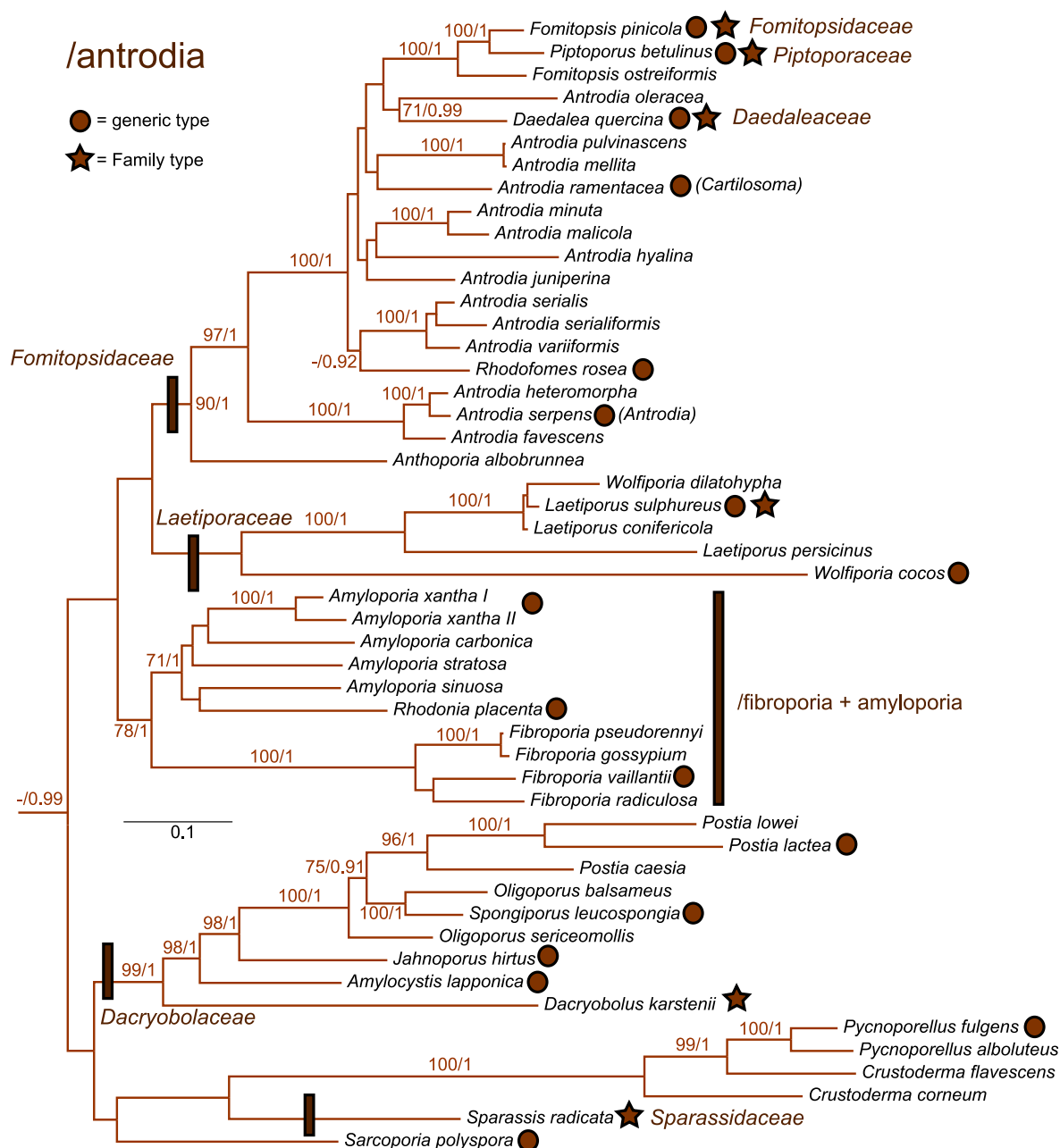


Fig 8 – Families in/antrodia, based on the ML tree from the 3-gene dataset. Support values are given as ML/BY. Stars indicate the type genus of a family. Circles indicate the type species of a genus. Bars indicate the limits of each family.

Genera: *Byssomerulius* Parmasto, *Ceriporia* Donk, *Cyrtidiella* Pouzar, *Efibula* Sheng H. Wu, *Emmia* Zmitr., *Spirin* & Malysheva, *Flavodon* Ryvarden, *Gloeoporus* Mont., *Hydnopolyporus* D.A. Reid, *Leptoporus* Qué., *Meruliopsis* Bondartsev, *Trametopsis* Tomšovský.

Additional taxa: *Candelabrochaete langloisii* (Pat.) Boidin, *Candelabrochaete septocystidia* (Burt) Burds., *Ceraceomyces eludens* K.H. Larss., *Ceraceomyces microsporus* K.H. Larss., *Ceraceomyces serpens* (Tode) Ginns, *Ceriporia lacerata* N. Maek., *Suhara* & R. Kondo, *Ceriporiopsis aneirina* (Sommerf.) Domański, *Ceriporiopsis resinascens* (Romell) Domański, *Hapalopilus ochraceolateritius* (Bondartsev) Bondartsev & Singer, *Phanerochaete allantopora*

Burds. & Gilb., *Phanerochaete angustocystidiata* Sheng H. Wu, *Phanerochaete exilis* (Burt) Burds., *Phanerochaete ginnsii* Sheng H. Wu, *Phanerochaete intertexta* Sheng H. Wu, *Phanerochaete leptoderma* Sheng H. Wu, *Phanerochaete xerophila* Burds., *Phlebia albida* H. Post, *Phlebia albomellea* (Bondartsev) Nakasone, *Phlebia nitidula* (P. Karst.) Ryvarden.

Comments: *Irpicaceae* encompasses a great variation of basidiome and hymenophore types, with typical polypore and corticioid morphologies intermixing with each other. These morphological transitions have occurred repeatedly within this lineage (Floudas & Hibbett 2015; Miettinen et al. 2016); recognizing smaller, well-supported clades as independent

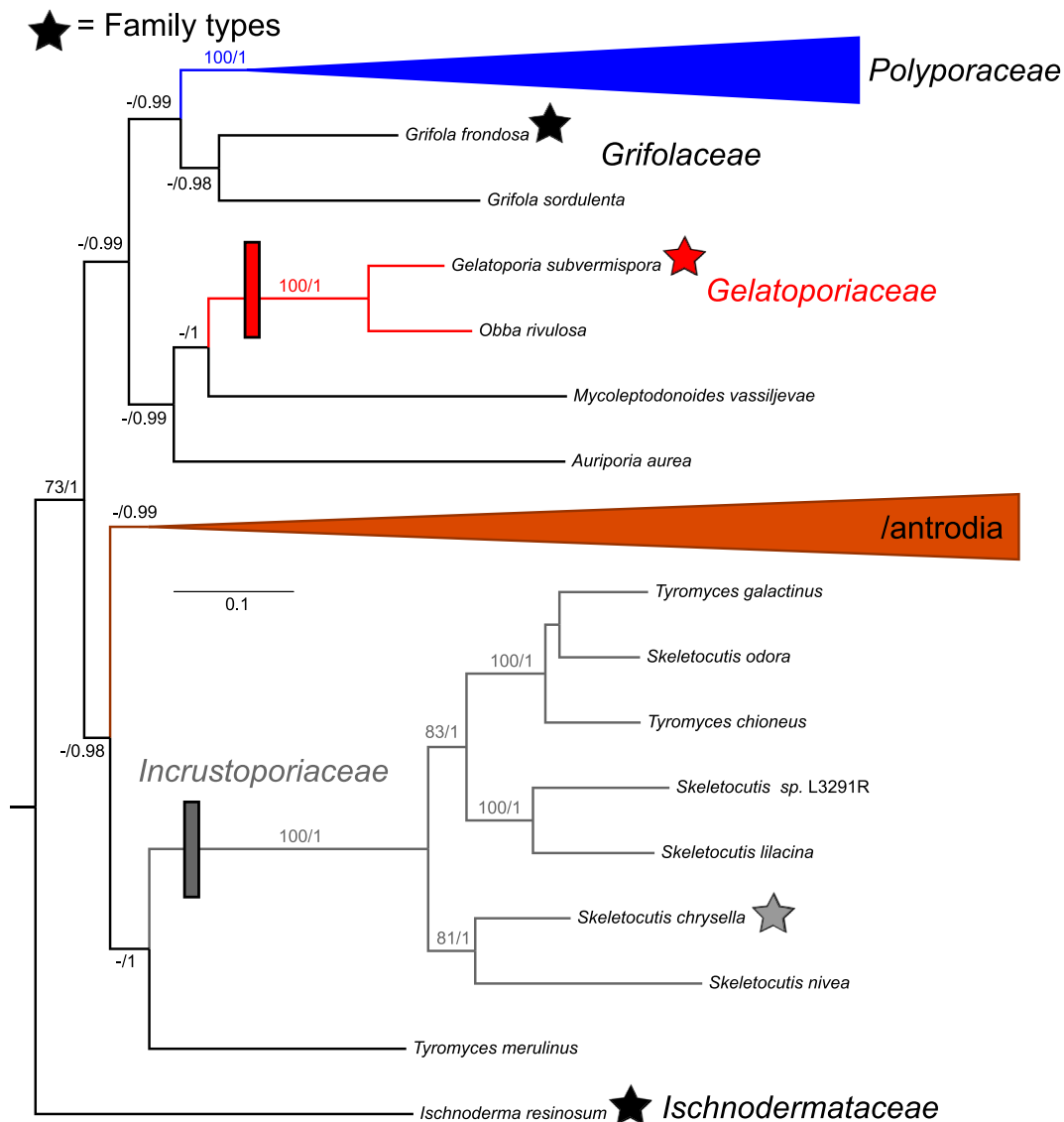


Fig 9 – Grifolaceae, Gelatoporiaceae, Incrustoporiaceae, Ischnodermataceae, and un-assigned taxa, based on the ML tree from the 3-gene dataset. Support values are given as ML/BY. Bars indicate the limits of each family.

families would not result in a more straightforward morphological grouping of these taxa. Microscopically, most members of the family are rather nondescript, with smooth hyaline spores, monomitic hyphal systems, non-clamped septa, and lack of cystidia, however exceptions to this pattern do exist (e.g. cystidia in *Irpex*, *Emmia* and others; clamp-connections in *Gloeoporus* and others), and this combination of characters occurs also outside the *Irpiceae*.

Meruliaceae Rea 1922 (Fig 5)

Synonym. *Climacodontaceae* Jülich 1981.

Synonym. *Phlebiaceae* Jülich 1981.

Type genus: *Merulius* Fr.

Corticoid species or polypores, commonly with a waxy appearance when dry; hyphal system monomitic and tightly arranged; hyphae with clamp-connections; spores thin-walled, smooth, hyaline; cystidia often present. More rarely

dimitic and/or without cystidia and/or without clamp-connections. Producing a white-rot.

Genera: *Aurantipileus* Ginns, D.L. Lindner & T.J. Baroni, *Aurantiporus* Murrill, *Climacodon* P. Karst., *Crustodontia* Hjortstam & Ryvarden, *Hydnophlebia* Parmasto, *Lilaceophlebia* (Parmasto) Spirin & Zmitr., *Luteoporia* F. Wu, Jia J. Chen & S.H. He, *Mycoacia* Donk, *Mycoaciella* J. Erikss. & Ryvarden, *Phlebia* Fr., *Phlebioporia* Jia J. Chen, B.K. Cui & Y.C. Dai, *Sarcodontia* Schulzer, *Scopuloides* (Masse) Höhn. & Litsch.

Additional taxa: *Ceriporia alachuana* (Murrill) Hallenb., *Ceriporiopsis gilvenscens* (Bres.) Domański, *Ceriporiopsis guidella* Bernicchia & Ryvarden, *Ceriporiopsis pseudoplacenta* Vlasák & Ryvarden, *Phanerochaete ontoidea* Sheng H. Wu, *Phanerochaete subglobosa* Sheng H. Wu, *Phanerochaete subontoidea* Sheng H. Wu, *Phlebia acanthocystis* Gilb. & Nakasone, *Phlebia aurea* (Fr.) Nakasone, *Phlebia centrifuga* P. Karst., *Phlebia*

Table 2 – Overview of morphological, anatomical, physiological, and genetic characters of the families of Polyporales. Symbols: + indicates the character is common in the family, but not necessarily present in all species; (+) indicates the character is present in only a few species.

Taxon	Basidiome			Hymenophore				Type or rot	
	Pileate	Stipitate	Resupinate	Poroid ^a	Daedaleoid/Lamellate ^b	Smooth ^c	Hydnoid ^d	White	Brown
<i>Cerrenaceae</i>	+		+	+	(+)		+	+	
<i>Dacryobolaceae</i>	+	(+)	+	+		(+)	(+)		+
<i>Fomitopsidaceae</i>	+		+	+	(+)				+
<i>Gelatoporiaceae</i>			+	+				+	
<i>Grifolaceae</i>	+	+		+				+	
<i>Hyphodermataceae</i>			+			+	(+)	+	
<i>Incrustoporiaceae</i>	+		+	+				+	
<i>Irpicaceae</i>	(+)		+	+	(+)	+	(+)	+	(+)
<i>Ischnodermataceae</i>	+			+				+	
<i>Laetiporaceae</i>	+	+	(+)	+	(+)				+
<i>Meripilaceae</i>	+	+	+	+				+	
<i>Meruliaceae</i>	(+)		+	+		+	+	+	
<i>Panaceae</i>	+	+			+	+		+	
<i>Phanerochaetaceae</i>	(+)		+	(+)	(+)	+	(+)	+	
<i>Podoscyphaceae</i>	+	+	+	(+)	(+)	+		+	
<i>Polyporaceae</i>	+	+	+	+	+	(+)	(+)	+	
<i>Sparassidaceae</i>	spathulate					+			+
<i>Steccherinaceae</i>	+	(+)	+	+	(+)		+	+	
Character present in 'n' families	15	8	14	15	9	9	8	14	5

Taxon	Spores					Cystidia		
	Amyloid	Dextrinoid	Ornamented	Pigmented	Thick-walled	Smooth	Ornamented	Thick-walled
<i>Cerrenaceae</i>					(+)	+	(+)	(+)
<i>Dacryobolaceae</i>	(+)		(+)		(+)	+	(+)	(+)
<i>Fomitopsidaceae</i>				(+)				
<i>Gelatoporiaceae</i>								
<i>Grifolaceae</i>								
<i>Hyphodermataceae</i>						+	(+)	(+)
<i>Incrustoporiaceae</i>					(+)		(+)	
<i>Irpicaceae</i>						(+)	(+)	(+)
<i>Ischnodermataceae</i>						(+)		
<i>Laetiporaceae</i>								
<i>Meripilaceae</i>					+		+	+
<i>Meruliaceae</i>					(+)	+	+	+
<i>Panaceae</i>						+	(+)	+
<i>Phanerochaetaceae</i>						+	+	+
<i>Podoscyphaceae</i>			(+)		(+)	+	(+)	+
<i>Polyporaceae</i>		(+)	(+)	(+)	+	(+)	(+)	(+)
<i>Sparassidaceae</i>						(+)		
<i>Steccherinaceae</i>						(+)	+	+
Character present in 'n' families	1	1	3	2	7	12	12	11

Taxon	Hyphae	Hyphal system			Mating system		
	Clamps	Monomitic	Dimitic	Trimitic	Homothallic	Bipolar	Tetrapolar
<i>Cerrenaceae</i>	+	+	+	(+)		+	+
<i>Dacryobolaceae</i>	+	+	+	(+)			+
<i>Fomitopsidaceae</i>	+	(+)	+	+	+	+	
<i>Gelatoporiaceae</i>	+	+	(+)			+	+
<i>Grifolaceae</i>	+		+				+
<i>Hyphodermataceae</i>	+	+				+	
<i>Incrustoporiaceae</i>	+	(+)	+				+
<i>Irpicaceae</i>	+	+	(+)		(+)?		(+)
<i>Ischnodermataceae</i>	+		+			+	
<i>Laetiporaceae</i>		(+)	+			+	
<i>Meripilaceae</i>		+	(+)		?	?	?
<i>Meruliaceae</i>	+	+	(+)			+	
<i>Panaceae</i>	+		+				+

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Table 2 – (continued)

Taxon	Hyphae	Hyphal system			Mating system		
	Clamps	Monomitic	Dimitic	Trimitic	Homothallic	Bipolar	Tetrapolar
<i>Phanerochaetaceae</i>	(+)	+				+	
<i>Podoscyphaceae</i>	+	+	+	(+)			+
<i>Polyporaceae</i>	+	(+)	+	+			+
<i>Sparassidaceae</i>	(+)	+				+	
<i>Steccherinaceae</i>	+	+	+				+
Character present in 'n' families	16	15	15	5	1–3	9–10	10–11

Taxon	Nuclear Behaviour			
	Normal	Heterocytic	Astatocoenocytic	Holocoenocytic
<i>Cerrenaceae</i>		+	+	
<i>Dacryobolaceae</i>	+			
<i>Fomitopsidaceae</i>	+		(+)	
<i>Gelatoporiaceae</i>			+	
<i>Grifolaceae</i>	?	?	?	?
<i>Hyphodermataceae</i>	?	?	?	?
<i>Incrustoporiaceae</i>		+	+	
<i>Irpicaceae</i>		+		+
<i>Ischnodermataceae</i>			+	
<i>Laetiporaceae</i>				+
<i>Meripilaceae</i>	?	?	?	?
<i>Meruliaceae</i>	?	?	?	?
<i>Panaceae</i>	?	?	?	?
<i>Phanerochaetaceae</i>		+	(+)	
<i>Podoscyphaceae</i>	+			
<i>Polyporaceae</i>	+	(+)	(+)	
<i>Sparassidaceae</i>	?	?	?	?
<i>Steccherinaceae</i>	+			
Character present in 'n' families	5–11	5–11	7–13	2–8

a Regular round to angular pores.

b Irregular, sinuous, daedaleoid pores or lamellae.

c Surface smooth or with small grains, rounded projections, folds, wrinkles.

d Surface with tooth-like projections, aculei, rigid hairs, spine-like structures.

coccineofulva Schwein., *Phlebia fascicularis* (Rick) Nakasone & Burds., *Phlebia hydnoidea* Schwein., *Phlebia ludoviciana* (Burt) Nakasone & Burds., *Phlebia nantahaliensis* Nakasone & Burds., *Phlebia subochracea* (Bres.) J. Erikss. & Ryvarden, *Phlebia uda* (Fr.) Nakasone, *Scopuloides hydnoidea* (Cooke & Masee) Hjortstam & Ryvarden.

Comments: Species currently classified in *Phlebia* can be found in three different families: *Phanerochaetaceae*, *Irpicaceae*, and *Meruliaceae*. The proposed synonymy of *Phlebia* and *Merulius* (Nakasone & Burdsall 1984) needs to be re-evaluated. A generic concept of *Phlebia* that includes *Merulius* would also need to include *Aurantiporus*, *Aurantiopileus*, and *Ceriporiopsis pseudoplacenta*, based on the current phylogenetic results. The proposed synonymies of *Mycoacia* (Nakasone 1997) and *Mycoaciella* (Nakasone 2002) with *Phlebia* also need further attention. The generic type of *Mycoacia* appears in a more inclusive clade with *Ceriporiopsis gilvescens*, *Lilaceophlebia livida*, and several *Phlebia* species, not related to the *Phlebia*/*Merulius* clade (Fig 5). The genus *Mycoaciella* appears in an unsupported position together with *Phlebia uda* and *Crustodontia chrysocreas* in the analyses of Binder et al. (2013). Additional available generic names for *Phlebia* s. lato include *Crustodontia*, *Sarcodontia*, and *Lilaceophlebia*. Extensive molecular sampling is essential to establish sound generic concepts in *Phlebia* s. lato. A

representative example of the current inadequacy of generic concepts is the genus *Lilaceophlebia*. Of the 16 species recombined in this genus (Spirin & Zmitrovich 2004), only one, *Phlebia tuberculata*, has been shown to be close to the type of *Lilaceophlebia*, and the two species that do appear close to the type in the phylogenies, *Phlebia fascicularis* and *Phlebia aurea* (Fig 5), were never included in *Lilaceophlebia*.

Steccherinaceae Parmasto 1968 (Fig 6)

Synonym. *Mycorrhaphiaceae* Jülich 1981.

Type genus: *Steccherinum* Gray.

Polypores or species with hydroid hymenophores; hyphal system dimitic; hyphae with clamp-connections; spores mostly thin-walled and rather small, smooth, hyaline; cystidia often present. More rarely monomitic and/or without clamp-connections. Producing a white-rot.

Genera: *Antella* Miettinen, *Antrodiella* Ryvarden & I. Johans., *Atraporilla* Ryvarden, *Austeria* Miettinen, *Butyrea* Miettinen, *Cabalodontia* M. Piątek, *Caudicicola* Miettinen, *Kotir.* & Kulju, *Citripora* Miettinen, *Chaetoporus* P. Karst., *Etheiroduon* Banker, *Flabellophora* G. Cunn., *Flaviporus* Murrill, *Frantisekia* Spirin & Zmitr., *Junghuhnia* Corda, *Lamelloporus* Ryvarden, *Loweomyces* (Kotl. & Pouzar) Jülich, *Metuloidea* G. Cunn., *Mycorrhaphium* Maas Geest., *Niemelaea* Zmitr., *Ezhov* et Khimich., *Nigroporus* Murrill, *Trulla* Miettinen & Ryvarden, *Xanthoporus* Audet.

Table 3 – Genome sampling of Polyporales in MycoCosm^a as of Apr., 2017.

clade	family/clade	genomes (one/species unless noted)		
/phlebioid	Irpicaceae	Cytidiella melzeri		
		Hydnopolyporus fimbriatus		
		Irpex lacteus		
	Meruliaceae	Trametopsis cervina		
		Phlebia brevispora		
		Phlebia centrifuga		
	Phanerochaetaceae	Bjerkandera adusta		
		Phanerochaete carnosa		
		Phanerochaete chrysosporium		
Phlebiopsis gigantea				
/residual	Cerrenaceae	Cerrena unicolor		
	Hyphodermataceae	none		
	Meripilaceae	none		
	Panaceae	Panus rudis		
	Podoscyphaceae	none		
	Steccherinaceae	none		
	/climacocystis	Climacocystis borealis		
	/hypochnicium	none		
/core polyporoid	Polyporaceae	Artolenzites elegans (2)		
		Dichomitus squalens (4)		
		Ganoderma sp.		
		Leiotrametes sp		
		Lentinus tigrinus (3)		
		Polyporus arcularius		
		Polyporus brumalis		
		Pycnoporus cinnabarinus		
		Pycnoporus coccineus		
		Pycnoporus puniceus		
		Pycnoporus sanguineus		
		Trametes cingulata		
		Trametes gibbosa		
		Trametes ljubarskyi		
		Trametes pubescens		
		Trametes versicolor		
		inc. sed. near/core polyporoid	Gelatoporiaceae	Gelatoporia (Ceriporiopsis)
				subvermispora
				Obba rivulosa
		/antrodia	Grifolaceae	none
Dacryobolaceae	none			
Fomitopsidaceae	Daedalea quercina			
	Fomitopsis pinicola			
Laetiporaceae	Laetiporus sulphureus			
	Wolfiporia cocos			
Sparassidaceae	Sparassis latifolia			
/amyloporia	Antrodia sinuosa			
	Rhodonia (Postia) placenta			
/fibroporia	Fibroporia radiculosa			
inc. sed. near/antrodia	Incrustoporiaceae	none		
	Ischnodermataceae	none		
a http://genome.jgi.doe.gov/programs/fungi/index.jsf .				

^a <http://genome.jgi.doe.gov/programs/fungi/index.jsf>.

Additional taxa: *Antrodiella perennis* B.K. Cui & Y.C. Dai, *Fibri-cium subceraceum* (Hallenb.) Bernicchia, *Junghuhnia micropora* Spirin, Zmitr. & Malysheva, '*Mellipora constricta*' nom. prov., *Mycoacia columellifera* (G. Cunn.) Hjortstam, *Skeletocutis novae-zelandiae* (G. Cunn.) P.K. Buchanan & Ryvarden, *Steccherinum aridum* Svrček, *Steccherinum laeticolor* (Berk. & M.A. Curtis) Banker, *Steccherinum litschaueri* (Bourdot & Galzin) J. Erikss., *Steccherinum oreophilum* Lindsey & Gilb., *Steccherinum robustius*

(J. Erikss. & S. Lundell) J. Erikss., *Steccherinum straminellum* (Bres.) Melo.

Comments: For a detailed discussion of the taxa in this family see Miettinen et al. (2012) and Miettinen & Ryvarden (2016). The recently described *Caudicicola* (Kotiranta et al. 2017) appears as sister to all other members of the *Steccherinaceae* (Fig 6).

Cerrenaceae Miettinen, Justo & Hibbett, fam. nov. (Fig 6)

MycoBank No.: 820826

Diagnosis. Basidiomes resupinate, effused-reflexed or pileate. Hymenophore poroid, daedaleoid or hydroid. Hyphal system mono- or dimitic, rarely trimitic. Clamp-connections usually present. Spores hyaline, smooth, non-amyloid, non-dextrinoid, thin- or thick-walled. Thin-walled hymenial cystidia (gloeocystidia) present, also thick-walled encrusted cystidia in one genus. Mating system heterothallic, bi- or tetrapolar. Nuclear behaviour heterocytic or astatocoenocytic (as far as is known). Producing a white-rot, also parasitic.

Type genus: *Cerrena* Gray, A natural arrangement of British plants 1: 649, 1821.

Genera: *Irpiciporus* Murrill, *Pseudolagarobasidium* J.C. Jang & T. Chen, *Radulodon* Ryvarden.

Additional taxa: *Rigidoporus vinctus* (Berk.) Ryvarden, *Spongipellis delectans* (Peck) Murrill, *Spongipellis litschaueri* Lohwag, *Spongipellis pachyodon* (Pers.) Kotl. & Pouzar, *Spongipellis unicolor* (Schwein.) Murrill.

Comments: *Spongipellis spumea* (Sowerby) Pat., the type species of *Spongipellis*, appears in an isolated position within/residual (Tomšovský 2012; Binder et al. 2013), not related to other species of the genus. The genus *Rigidoporus* is also polyphyletic, with the species-complex around *R. vinctus* placed in the *Cerrenaceae* and the type species, *R. lineatus*, and related taxa in the *Meripilaceae*. The *Cerrenaceae* is strongly supported as the sister group to the *Panaceae* (Fig 6). Both *Cerrena* (Enebak & Blanchette 1989) and *Pseudolagarobasidium* (Hallenberg et al. 2008) have demonstrated abilities to act as parasites of living plants.

Panaceae Miettinen, Justo & Hibbett, fam. nov. (Fig 6)

MycoBank No.: 820827

Diagnosis. Basidiomes pileate-stipitate. Hymenophore lamellate or smooth. Hyphal system dimitic. Clamp-connections present. Spores hyaline, smooth, non-amyloid, non-dextrinoid, thin-walled. Cystidia present as gloeocystidia or thick-walled cystidia. Mating system heterothallic and tetrapolar. Producing a white-rot.

Type genus: *Panus* Fr., *Epicrisis Systematis Mycologici*: 396, 1838.

Genera: *Cymatoderma* Jungh.

Comments: The phylogenies of Sjökvist et al. (2012) recovered a polyphyletic *Cymatoderma*, with some species closely related to *Podoscypha*, and a second group, including the type *C. elegans*, on a distant position within/residual. The species of *Cymatoderma* sampled in our analyses is closely related to *C. elegans* and *C. caperatum*, based on nrLSU and nrITS sequences (data not shown), indicating that *Cymatoderma* s. stricto belongs in the *Panaceae*. The genus *Panus* represents an independent origin of the agaricoid habit in the *Polyporales*, the others being *Lentinus* and *Neofavolus* in the *Polyporaceae* (Seelan et al. 2015).

Hyphodermataceae Jülich 1981 (Fig 6)

Type genus: *Hyphoderma* Fr.

Corticoid species; hyphal system monomitic; hyphae with clamp-connections; spores thin-walled, smooth, hyaline; cystidia present in most species. Producing a white-rot.

Genera: *Hyphoderma*.

Comments: The genus *Hyphoderma* as traditionally defined is polyphyletic, with c. 20 species now classified in *Peniophorella* in the *Hymenochaetales* (Larsson 2007). The genera *Hypochnicum* and *Bulbillomyces* are consistently recovered as separate from *Hyphoderma* in our analyses: 3-gene (Fig 6), ribosomal-only and *rpb1*-only (TreeBASE S20775). Alternative topologies for these genera have been recovered in the study of Larsson (2007).

Meripilaceae Jülich 1981 (Fig 6)

Synonym. *Rigidoporaceae* Jülich 1981.

Type genus: *Meripilus* P. Karst.

Polypores; hyphal system monomitic or dimitic; hyphae without clamp-connections; spores thin-walled to slightly thick-walled, often subglobose, smooth, hyaline; cystidia often present. Producing a white-rot.

Genera: *Physisporinus* P. Karst., *Rigidoporus* Murrill.

Comments: Additional species of *Rigidoporus* are placed in the *Cerrenaceae*. The names *Meripilaceae* and *Rigidoporaceae* have equal nomenclatural priority; the former is chosen here.

Podoscyphaceae D.A. Reid 1965 (Fig 6)

Type genus: *Podoscypha* Pat.

Pileate species with smooth, ridged, or poroid hymenophore; hyphal system dimitic or trimitic; hyphae with clamp-connections; spores thin-walled, smooth, hyaline; cystidia often present. Producing a white-rot. In the broad sense adopted here (see comments) it also includes corticioid species, with monomitic hyphal systems, no clamp-connections, and thick-walled, ornamented spores.

Genera: *Abortiporus* Murrill, *Pouzaroporia* Vampola.

Additional taxa: *Cymatoderma dendriticum* (Pers.) D.A. Reid, *Cymatoderma pallens* Berthet & Boidin, *Hypochnicum punctulatum* (Cooke) J. Erikss., *Hypochnicum sphaerosporum* (Höhn. & Litsch.) J. Erikss., *Hypochnicum wakefieldiae* (Bres.) J. Erikss.

Comments: The limits and composition of *Podoscyphaceae* need further study. As accepted here the family receives moderate to high support in the 3-gene analyses (73/1). In the ribosomal-only analyses the same topology is recovered but without strong support. In the *rpb1*-only analyses a similar topology is recovered, again without strong support, and *Pouzaroporia* is placed outside the family (TreeBASE S20775). The species of *Hypochnicum* included in the *Podoscyphaceae* do not appear closely related to the type species *H. bombycinum*. The name *Podoscyphaceae* could be adopted to include all families in/residual (Fig 6) but the morphological characterization of such a group would be even more problematic than the individual definition of each of the families recognized here. The extreme morphological variation within the *Steccherinaceae* (Miettinen et al. 2012) makes it very difficult to characterize the family by means other than phylogeny and a certain predominance of morphological characters. However, recognizing the *Steccherinaceae* as a discrete group allows us to recognize several smaller families in/residual that are relatively easier to characterize in terms of morphology.

Additional/residual lineages (Fig 6)

Genera: *Bulbillomyces* Jülich, *Climacocystis* Kotl. & Pouzar, *Diplomitoporus* Domański, *Hypochnicum* J. Erikss., *Rickiopora* Westphalen, Tomšovský & Rajchenb.

Additional taxa: *Phlebia bresadolae* Parmasto.

Comments: Two well-supported clades, *hypochnicum* (*Hypochnicum*, *Bulbillomyces*) and *climacocystis* (*Climacocystis*, *Diplomitoporus*), appear as sister-taxa but without strong support (Fig 6). The relative position of these two clades is never well supported in the ribosomal-only, *rpb1*-only or 3-gene analyses, therefore we refrain from proposing any formal family-level placement at this time. Based on the results of Binder et al. (2013) *Phlebia bresadolae* belongs in *climacocystis*. The recently described genus *Rickiopora* is probably related to *Climacocystis* (Westphalen et al. 2016).

Polyporaceae Corda 1939 (Fig 7)

Synonym. *Ganodermataceae* (Donk) Donk 1948.

Synonym. *Coriolaceae* Singer 1961.

Synonym. *Cryptoporaceae* Jülich 1981.

Synonym. *Echinochaetaceae* Jülich 1981.

Synonym. *Fomitaceae* Jülich 1981.

Synonym. *Grammotheleaceae* Jülich 1981.

Synonym. *Haddowiacae* Jülich 1981.

Synonym. *Microporaceae* Jülich 1981.

Synonym. *Pachykytosporaceae* Jülich 1981.

Synonym. *Perenniporiaceae* Jülich 1981.

Synonym. *Sparsitubaceae* Jülich 1981.

Synonym. *Lophariaceae* Boidin, Mugnier & Canales 1998.

Synonym. *Trametaceae* Boidin, Mugnier & Canales 1998.

Type genus: *Polyporus* P. Micheli ex Adans.

Polypores, rarely corticioid species; hyphal system mostly dimitic or trimitic, some monomitic species also present, and those usually with dendroid hyphal elements in the hymenium; hyphae with clamp-connections, exceptionally simple-septate; spores thin to thick-walled, smooth to ornamented, relatively big for Polyporales, hyaline to brown; cystidia mostly absent. Producing a white-rot.

Genera: *Abundisporus* Ryvarden, *Amauroderma* Murrill, *Cerarioporia* F. Wu, L.W. Zhou & J. Si, *Colospora* Miettinen & Spirin, *Cryptoporus* (Peck) Shear, *Datronia* Donk, *Datroniella* B.K. Cui, Hai J. Li & Y.C. Dai, *Dendrodontia* Hjortstam & Ryvarden, *Dentocorticium* (Parmasto) M.J. Larsen & Gilb., *Dichomitus* D.A. Reid, *Donkioporia* Kotl. & Pouzar, *Earliella* Murrill, *Echinochaete* D.A. Reid, *Epithele* (Pat.) Pat., *Favolus* P. Beauv., *Fomes* (Fr.) Fr., *Fomitella* Murrill, *Ganoderma* P. Karst., *Grammothele* Berk. & M.A. Curtis, *Grammothelopsis* Jülich, *Hexagonia* Fr., *Haploporus* Bondartsev & Singer ex Singer, *Hornodermoporus* Teixeira, *Lentinus* Fr., *Lignosus* Lloyd ex Torrend, *Lopharia* Kalchbr. & MacOwan, *Megasporia* B.K. Cui, Y.C. Dai & Hai J. Li, *Megasporoporia* Ryvarden & J.E. Wright, *Melanoderma* B.K. Cui & Y.C. Dai, *Microporellus* Murrill, *Microporus* P. Beauv., *Neodatronia* B.K. Cui, Hai J. Li & Y.C. Dai, *Neofavolus* Sotome & T. Hatt., *Pachykytospora* Kotl. & Pouzar, *Perenniporia* Murrill, *Perenniporiella* Decock & Ryvarden, *Pseudofavolus* Pat., *Pyrofomes* Kotl. & Pouzar, *Tinctoporellus* Ryvarden, *Tomophagus* Murrill, *Trametes* Fr., *Truncospora* Pilát ex Pilát, *Vanderbylia* D.A. Reid, *Yuchengia* B.K. Cui & Steffen.

Additional taxa: *Coriolopsis byrsina* (Mont.) Ryvarden, *Coriolopsis caperata* (Berk.) Murrill, *Coriolopsis gallica* (Fr.) Ryvarden, *Coriolopsis glabro-rigens* (Lloyd) Núñez & Ryvarden, *Coriolopsis*

rigida (Berk. & Mont.) Murrill, *Corioloopsis sanguinaria* (Klotzsch) Teng, *Corioloopsis strumosa* (Fr.) Ryvarden, *Corioloopsis trogii* (Berk.) Domański, *Diplomitoporus overholtsii* (Pilát) Gilb. & Ryvarden, *Funalia subgallica* Hai J. Li & S.H. He.

Comments: A central, unresolved, problem for the generic-level taxonomy of the Polyporaceae is the typification of *Polyporus*. Krüger & Gargas (2004) made a convincing case as to why *Polyporus brumalis* should be considered the type of *Polyporus*, instead of *Polyporus tuberaster*, as has been accepted by most modern authors (Ryvarden 1991; Sotome et al. 2008). That creates a nomenclatural problem for the delimitation of the *P. brumalis* group (*Polyporellus*) and *Lentinus*. Sotome et al. (2008) published the first large phylogeny of *Polyporus*, and they acknowledged the problems with the typification of the genus, but for practical purposes considered *P. tuberaster* as the type species, and mentioned that the typification of *Polyporus* would be addressed in a future paper. Zmitrovich & Kovalenko (2016) gave a phylogenetic overview of the polyporoid and lentinoid genera, and recognized seven genera to accommodate these taxa in the Polyporaceae. However, these authors assume that *P. tuberaster* is the type of *Polyporus*, which is not correct under Article 9 of the International Code of Nomenclature for Algae, Fungi and Plants (McNeill et al. 2012). *Polyporus*, as traditionally defined, is polyphyletic so name changes are bound to happen one way or the other. However, it is our opinion that strict application of the nomenclature rules here will result in disadvantageous changes, as *Polyporus* and *Lentinus*, two names with long established usages and central to the taxonomic arrangement of the Polyporaceae, will be in direct conflict. We suggest that the best way to move forward is to formally propose the conservation of *Polyporus* with a conserved type, as allowed by Article 14. 9 (McNeill et al. 2012), preferably not *P. brumalis* to avoid conflict with *Lentinus*.

The genus *Trametes* is accepted in the sense of Justo & Hibbett (2011), including the type of *Corioloopsis* Murrill. This leaves the majority of species formerly placed in *Corioloopsis* in need of new generic placements. The genus *Funalia* Pat. could accommodate some of these species, as proposed by Li et al. (2016), but molecular data from the type species *Funalia mons-veneris* (Jungh.) Pat., are still lacking. Suitable modern collections of this species should be sequenced to settle the status of *Funalia*. Alternative taxonomic arrangements of the Polyporaceae were considered. Taking the approach of narrowly defining a family, because of its unique set of morphological characters, can lead to a more problematic taxonomic scenario. The *Ganodermataceae* stands out morphologically because of the yellow, ornamented spores with a double spore-wall. However, recognizing the *Ganodermataceae* as an independent taxon would create a cascading effect in the Polyporaceae, and at least four additional families would have to be adopted to accommodate the taxa currently placed in the Polyporaceae (Fig 7). In this scenario, considering the results presented here and those of Binder et al. (2013) the following families would be recognized: *Grammothelaceae*, *Fomitaceae*/*Microporaceae*, *Lophariaceae*, *Polyporaceae*, and *Corioloraceae*. The number of families would only increase as additional taxa are sampled for *rpb1* data. These segregated families would all be distinct from the *Ganodermataceae* on morphological grounds, but for the most part indistinguishable from each other.

Fomitopsidaceae Jülich 1981 (Fig 8)

Synonym. *Daedaleaceae* Jülich 1981.

Synonym. *Piptoporaceae* Jülich 1981.

Polypores; hyphal system dimitic or trimitic, more rarely monomitic; hyphae with clamp-connections; spores thin-walled, smooth, hyaline; cystidia absent, sometimes skeletal hyphal ends protruding into the hymenium. Producing a brown-rot.

Type genus: *Fomitopsis* P. Karst. (including *Piptoporus* P. Karst.)
Genera: *Anthoporia* Karasiński & Niemelä, *Antrodia* P. Karst., *Buglossoporus* Kotl. & Pouzar, *Cartilosoma* Teixeira, *Daedalea* Pers., *Fragifomes* B.K. Cui, M.L. Han & Y.C. Dai, *Melanoporia* Murrill, *Neolentiporus* Rajchenb., *Niveoporofomes* B.K. Cui, M.L. Han & Y.C. Dai, *Rhodofomes* Kotl. & Pouzar, *Rhodofomitopsis* B.K. Cui, M.L. Han & Y.C. Dai, *Rubellofomes* B.K. Cui, M.L. Han & Y.C. Dai, *Ungulidaedalea* B.K. Cui, M.L. Han & Y.C. Dai.

Additional taxa: *Antrodia hyalina* Spirin, Miettinen & Kotir., *Antrodia juniperina* (Murrill) Niemelä & Ryvarden, *Antrodia macrospora* Bernicchia & De Dominicis, *Antrodia malicola* (Berk. & M.A. Curtis) Donk, *Antrodia mellita* Niemelä & Penttilä, *Antrodia minuta* Spirin, *Antrodia oleracea* (R.W. Davidson & Lombard) Ryvarden, *Antrodia pulvinascens* (Pilát) Niemelä, *Antrodia serialiformis* Kou' & Vlasák, *Antrodia serialis* (Fr.) Donk, *Antrodia taxa* T.T. Chang & W.N. Chou, *Antrodia variiformis* (Peck) Donk.

Comments: The names *Daedaleaceae* and *Piptoporaceae*, with equal nomenclatural priority, are considered here as synonyms of *Fomitopsidaceae*. The recent studies of Ortiz-Santana et al. (2013) and Spirin et al. (2013a,b) have defined the limits of *Antrodia*, but many species traditionally classified in *Antrodia* still await proper generic placement (see additional taxa above).

Fomitopsis, as traditionally defined, is polyphyletic and has been the subject of a recent study by Han et al. (2016). These authors have proposed to subsume *Piptoporus* into *Fomitopsis* sensu stricto, while they place other *Fomitopsis* species in the genera *Fragifomes*, *Niveoporofomes*, *Rhodofomes*, *Rhodofomitopsis*, *Rubellofomes*, and *Ungulidaedalea*. The genus *Piptoporellus*, also introduced by Han et al. (2016), falls outside the *Fomitopsidaceae*, and its relations with other members of/antrodia remain unresolved.

Laetiporaceae Jülich 1981 (Fig 8)

Synonym. *Phaeolaceae* Jülich 1981.

Type genus: *Laetiporus* Murrill.

Polypores; hyphal system dimitic, more rarely monomitic; hyphae without clamp-connections; spores thin-walled, smooth, hyaline; cystidia mostly absent. More rarely monomitic and cystidia present. Producing a brown-rot.

Genera: *Phaeolus* (Pat.) Pat., *Wolfiporia* Ryvarden & Gilb.

Comments: Based on the phylogenies of Ortiz-Santana et al. (2013), Binder et al. (2013), and Han et al. (2016) *Phaeolus* is closely related to *Laetiporus* and *Wolfiporia*, therefore the name *Phaeolaceae* is placed here in synonymy with *Laetiporaceae*. Mycobank cites *Laetiporaceae* Jülich as an invalid name, but after consulting the original publication (Jülich 1981) we have found no reasons to consider the name invalid. The delimitation of *Laetiporus* vs. *Wolfiporia* needs further study.

/fibroporia + amyloporia (Fig 8)

Polypores, almost all resupinate; hyphal system mostly dimitic; hyphae with clamp-connections; spores thin-to

slightly thick-walled, smooth, hyaline; cystidia mostly absent. Producing a brown-rot.

Genera: *Amyloporia* Bondartsev & Singer ex Singer, *Fibroporia* Parmasto, *Rhodonina* Niemelä.

Comments: The results presented here place *Amyloporia* and *Fibroporia* outside the *Fomitopsidaceae*, but the relations to each other and to the rest of/antrodia are not fully resolved at the moment. In previous studies different topologies have been recovered for both genera: (i) *Fibroporia* as sister to most of/antrodia, and *Amyloporia* included in the *Fomitopsidaceae* (Ortiz-Santana et al. 2013); (ii) *Fibroporia* and *Amyloporia* as sister-taxa, and grouped with *Laricifomes* Kotl. & Pouzar and *Antrodia albobrunnea* (Binder et al. 2013); (iii) *Amyloporia*, together with *Laricifomes*, *Ryvardenia* Rajchenb. and *Gilbertsonia* Parmasto in an unsupported position as sister to *Fomitopsidaceae*, and *Fibroporia* as sister to *Piptoporellus* (Han et al. 2016; nuclear ribosomal + *rpb2* dataset); (iv) *Amyloporia* and *Fibroporia* together with species of *Postia* s. lato (Han et al. 2016, nuclear ribosomal + mitochondrial ribosomal + *rpb2* + *tef1* dataset). For the time being we refrain from proposing any family-level placement for *Amyloporia*, *Fibroporia*, *Laricifomes*, *Ryvardenia*, *Gilbertsonia*, and *Piptoporellus*. The name *Laricifomitaceae* Jülich, typified by *Laricifomes*, is available. The type species of *Rhodonina* (*R. placenta*) appears nested within *Amyloporia* s. lato, but at the moment it is not clear what is the best taxonomic solution for this group (one or multiple genera).

Dacryobolaceae Jülich 1981 (Fig 8)

Type genus: *Dacryobolus* Fr.

Polypores or corticioid species; hyphal system monomitic, more rarely di- or trimitic; hyphae with clamp-connections; spores thin- to thick-walled, smooth or rarely ornamented, hyaline; cystidia present or absent. Producing a brown-rot.

Genera: *Amylocystis* Bondartsev & Singer ex Singer, *Jahnporus* Nuss, *Oligoporus* Bref., *Postia* Fr., *Spongiporus* Murrill.

Comments: In the phylogenies presented by Ortiz-Santana et al. (2013) and Binder et al. (2013) the genera *Auriporia* Ryvarden, *Sarcoporia* P. Karst., and *Taiwanofungus* Sheng H. Wu, Z.H. Yu, Y.C. Dai & C.H. Su, appear sometimes related to the genera here accepted as part of the *Dacryobolaceae*. In the present study *Auriporia* appears outside/antrodia (Fig 9) and *Sarcoporia* does not appear as closely related to the *Dacryobolaceae* (Fig 8). The placement of these genera and *Taiwanofungus*, not sampled here, needs further study.

Sparassidaceae Jülich 1981 (Fig 8)

Type genus: *Sparassis* Fr.

Basidiomes consist of branched flabellae arising from a central core; hyphal system monomitic, with gloeoplerous hyphae; hyphae with scattered clamp-connections; spores thin- to slightly thick-walled, smooth, hyaline; cystidia mostly absent. Producing a brown-rot.

Comments: The genus *Sparassis* appears as sister to the *Laetiporaceae* in the analyses of Ortiz-Santana et al. (2013) and Binder et al. (2013), while in our analyses it appears in a more inclusive clade as sister to the *Dacryobolaceae* (Fig 8), but neither placement is strongly supported. The genera *Crustoderma* Parmasto, *Pycnoporellus* Murrill, and *Sarcoporia* appear in our analysis in the same clade as *Sparassis*, but without strong support, and their placement in or out the *Sparassidaceae* needs to be confirmed in future studies.

Grifolaceae Jülich 1981 (Fig 9)

Type genus: *Grifola* Fr.

Polypores (stipitate-imbricate); hyphal system monomitic; hyphae with scattered clamp-connections; spores thin-walled, smooth, hyaline; cystidia absent. Producing a white-rot and acting as root parasites.

Comments: *Grifola* consistently appears as sister to the *Polyporaceae*, although without strong support (Justo & Hibbett 2011; Binder et al. 2013). The name *Grifolaceae* is accepted here to accommodate this genus.

Gelatoporiaceae Miettinen, Justo & Hibbett, fam. nov. (Fig 9)

Mycobank No.: 820828

Diagnosis. Basidiomes resupinate. Hymenophore poroid. Hyphal system monomitic, rarely dimitic. Clamp-connections present. Spores hyaline, smooth, non-amyloid, non-dextrinoid, thin-walled, rarely slightly thick-walled. Cystidia absent, but characteristic cystidioles may be present. Mating system heterothallic, bi- or tetrapolar. Nuclear behaviour astatocoenocytic (as far as is known). Producing a white-rot.

Type genus: *Gelatoporia* Niemelä, *Karstenia* 25: 22, 1985.

Genera: *Cinereomyces* Jülich, *Obba* Miettinen & Rajchenb., *Sebiopora* Miettinen.

Comments: Miettinen & Rajchenberg (2012) introduced the name 'Cinereomyces clade' to accommodate a small group of white-rot polypores of uncertain position within the *Polyporales*. Further analyses by Binder et al. (2013) and the data presented here confirm that this clade represents a separate lineage from the *Polyporaceae*, which is formally described here as the family *Gelatoporiaceae*. For a detailed study of the genera in this family see Miettinen & Rajchenberg (2012).

In our analyses *Mycocleptodonoides vassiljevae* and *Auriporia aurea* appear close to the *Gelatoporiaceae* but without strong support. If the position of *Auriporia* is confirmed in future studies it would represent a third independent origin of brown-rot in the *Polyporales*, other than/antrodia and *Leptoporus* in the *Irpicaceae*.

Incrustoporiaceae Jülich 1981 (Fig 9)

Type genus: *Incrustoporia* Domański.

Polyporoid species; hyphal system dimitic, more rarely monomitic; hyphae with clamp-connections, rarely simple-septate; spores thin-walled, smooth, hyaline, relatively small; cystidia usually absent, but tips of generative hyphae at tube mouths commonly with rose-thorn encrustation. Producing a white-rot.

Genera: *Piloporia* Niemelä, *Skeletocutis* Kotl. & Pouzar, *Tyromyces* P. Karst.

Comments: The generic limits of *Incrustoporia*, *Skeletocutis*, and *Tyromyces* are not currently settled, and additional sampling of this clade is needed before a taxonomic arrangement can be put forward. *Tyromyces merulinus* (Berk.) G. Cunn. appears as sister to the *Incrustoporiaceae*, but this position only receives support in the Bayesian analyses and alternative placements for this species have been recovered.

Ischnodermataceae Jülich 1981 (Fig 9)

Type genus: *Ischnoderma* P. Karst.

Polypores; hyphal system dimitic, with hyphae tightly arranged; hyphae with clamp-connections; spores thin-walled, smooth, hyaline; cystidia absent. Producing a white-rot.

Comments: Our analyses confirm the rather isolated position of the genus *Ischnoderma* within the Polyporales recovered in previous phylogenies (Binder et al. 2013). The monotypic family *Ischnodermataceae* is adopted here for this genus.

Additional family names putatively belonging in the Polyporales

Diachanthodaceae Jülich, 1981. No molecular data are available for the type species of the type genus, *Diachanthodes novo-gui-neensis* (Hennings) O. Fidalgo.

Fragiliporiaceae Y.C. Dai, B.K. Cui & C.L. Zhao, 2015. This family was recently introduced (Zhao et al. 2015) to accommodate the newly described genus *Fragiliporia*. The molecular phylogenies of these authors recover *Fragiliporia* in an isolated position within the Polyporales, possibly related to/phlebioid and/residual, but not included in either clade. We performed an analysis on an alternate version of our ribosomal-only dataset to include *Fragiliporia*, and it was recovered in an isolated, unsupported position as sister to *Candelabrochaete africana* (tree available at TreeBASE S20775). *Fragiliporia* is characterized by resupinate basidiomes; tubes being very soft when fresh, becoming brittle when dry (become almost powdery when bruised); monomitic hyphal system; common clamp-connections; and thin-walled, hyaline basidiospores (Zhao et al. 2015). Future studies should include *rpb1* data to address the relations of *Fragiliporia* with *Candelabrochaete africana* and its position within the Polyporales.

Hymenogrammeaceae Jülich, 1981. The corticioid/poroid type species, *Hymenogramme javensis* Mont. & Berk., has few distinct morphological characters and has not been sequenced, leaving placement of this family as uncertain.

Nigrofomitaceae Jülich, 1981. Currently there is only one nrITS sequence available (GenBank KT156704.1) for the type species of the type genus, *Nigrofomes melanoporus* (Mont.) Murrill. A BLAST search of this sequence does not yield any close relative in the Polyporales. Additional *Nigrofomes* sequences from Southeast Asia (Miettinen, unpublished data) indicate that this family belongs in the *Hymenochaetales*.

Phaeotrametaceae Popoff ex Piatek, 2005. No molecular data are available for the type species of the type genus, *Phaeotrametes decipiens* (Berk.) J.E. Wright.

Discussion

The classification of Polyporales presented here integrates results from prior analyses by members of the PolyPEET consortium (Justo & Hibbett 2011; Miettinen et al. 2012, 2016; Ortiz-Santana et al. 2013; Floudas & Hibbett 2015) with those of many other research groups (Krüger & Gargas 2004; Spirin & Zmitrovich 2004; Sotome et al. 2008; Zhao et al. 2015; Han et al. 2016; Li et al. 2016). The combination of *rpb1* and ribosomal RNA genes provides robust resolution of many clades, including eighteen that are recognized here as families, but some nodes remain weakly supported and numerous taxa have yet to be sampled. In future studies addressing the family-level organization of the Polyporales, data for protein-coding genes, especially *rpb1*, should be routinely included. The classification proposed here provides a nomenclatural as well as phylogenetic framework that will facilitate further

revision at all taxonomic levels within Polyporales, following the principles elucidated by Vellinga et al. (2015).

Increased genome sampling will be necessary to resolve many nodes in Polyporales. It is hoped that this classification will help guide such efforts, such as the 1000 Fungal Genomes Project, which aims to sample at least two representatives of all families of fungi (Grigoriev et al. 2013). Leaving aside the non-equivalence of taxa classified at the same rank, it is clear that genome sampling in Polyporales to date has not maximized phylogenetic diversity; the 46 Polyporales genomes currently available on the JGI MycoCosm portal represent only ten of the 18 families recognized here and three unplaced clades (Table 3). Nine families or clades are represented by only one or two genomes, while the *Polyporaceae* is represented by 22 genomes (16 species).

In developing this classification, an effort has been made to name clades that can be recognized or described easily. However, many of the characters emphasized in prior taxonomy exhibit homoplasy and are poor predictors of higher-level evolutionary relationships within the Polyporales (Table 2). Macromorphology of fruiting bodies, which was coded with three states for basidiomes form (pileate, stipitate or resupinate) and with four states for hymenophore configuration (poroid, daedaleoid/lamellate, smooth, or hydroid), is particularly variable. Fourteen families have two or three different basidiome types, with twelve containing both pileate (sessile) and resupinate forms. Fifteen families contain species with poroid hymenophores, which is the most common configuration, whereas daedaleoid/lamellate and smooth hymenophores each occur in nine families; twelve families have at least two different hymenophore types. Similar variation is evident in the diversity of hyphal systems (monomitic, dimitic, or trimitic), which affect the consistency and longevity of fruiting bodies. Fifteen families contain dimitic or trimitic hyphal systems, which confer tough, resilient fruiting bodies, but fifteen families contain monomitic forms, and eleven families have at least two kinds of hyphal systems. The fruiting bodies of Polyporales may be massive or minute, ephemeral or perennial, and they can be produced in diverse locations, including the tops, sides, or bottoms of fallen logs, on standing tree trunks, small woody debris, or soil. The diversity of macromorphology and hyphal construction in Polyporales reflects a dynamic history of morphological evolution, as lineages have adapted to the challenges of spore dispersal under different environmental conditions and on diverse substrates.

Decay mode is one of the most stable characters in Polyporales, and has been used as the basis for segregating genera (Gilbertson & Ryvarden 1986; Ryvarden 1991). The majority of Polyporales produce a white-rot, which is the plesiomorphic condition for the group (Floudas et al. 2012), with only two confirmed transitions to a brown-rot (/antrodia and *Leptoporus*), and a possible third represented by *Auriporia* (Fig 9). The eight brown-rot genomes currently available all represent members of/antrodia. It will be interesting to see if the dramatic reduction in the lignocellulolytic apparatus observed in *Rhodonia* (*Postia*) *placenta* and other brown-rot members of/antrodia also occurs in *Leptoporus* and *Auriporia*.

Rot type can be inferred from direct examination of wood substrates or from cultural tests, and it is regularly reported for species of Polyporales and other wood-decay fungi (Nobles

1965; Gilbertson & Ryvarden 1986). In contrast, determination of mating systems requires laborious crossing experiments using single-spore isolates, and this character is not nearly as well documented as decay mode. Nevertheless, even with limited taxon sampling, mating type appears to be highly labile; nine or ten families include bipolar species, ten or eleven families contain tetrapolar species, and two or three families have both modes represented (Table 2). James et al. (2013) described the genetic architecture underlying tetrapolar and bipolar mating systems based on a sample of ten Polyporales genomes representing seven of the eighteen families recognized here. Expanded genome sampling will make it possible to test the generality of their conclusions, including the putative irreversibility of transitions from tetrapolar to bipolar mating systems.

Nuclear behaviour in the Polyporales has been analysed in detail by Rajchenberg (2011), and it includes the number of nuclei present in a fungus at different phases of its life cycle, the production of basidiospores, the production of germinating basidiospores, production of the hyphal cells of the primary (monosporic) mycelium, production of the hyphal cells of the secondary (polyspore or tissue) mycelium and the variation in number of nuclei under different oxygen pressures. Other characters that have been discussed in the context of Polyporales taxonomy include features of spores (staining, pigmentation, wall thickness, and ornamentation), cystidia, and clamp connections (Table 2). The genetic bases and selective significance of these characters are obscure.

Acknowledgements

This is the final paper of the PolyPEET project, which was supported by the U. S. National Science Foundation Partnerships for Enhancing Expertise in Taxonomy Program (DEB-0933081). Research under PolyPEET was complemented by projects on genomics of wood-decay fungi conducted by the U.S. Department of Energy Joint Genome Institute, a DOE Office of Science User Facility, supported by the Office of Science of the U.S. Department of Energy under Contract No. DE-AC02-05CH11231. The authors are grateful to many collaborators and former members of the Hibbett lab at Clark University for their support of PolyPEET, including Manfred Binder, Alexis Carlson, Romina Gazis, Rachael Martin, Mitchell Nuhn, Laszlo Nagy, and Jaya Seelan. We gratefully acknowledge the support and advice of Harold H. Burdsall during the PolyPEET project. Mario Rajchenberg and Viacheslav Spirin provided invaluable material for this study.

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