



Morphological plasticity in brown-rot fungi: *Antrodia* is redefined to encompass both poroid and corticioid species

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ABSTRACT

Most known brown rot-producing species of Polyporales belong to the so-called “Antrodia clade” that largely consists of poroid species. In this study, we use three genetic markers to revise *Antrodia* s. str., the core group of this clade. We show that a corticioid species with a smooth hymenophore, *Phlebia griseoflavescens*, belongs to *Antrodia* s. str. Accordingly, we revise the generic concept of *Antrodia* s. str. to accommodate this species and two recently described poroid taxa, *A. tenerifensis* and *A. multiformis*. In addition, we describe two new poroid species within *Antrodia* s. str., *A. latebrosa* from Africa and *A. peregrina* from East Asia, and provide new documentation for the Southeast Asian species *A. parvula* based on recent collections from the type location.

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INTRODUCTION

Historically, systematic treatments of wood-decomposing basidiomycetes have relied heavily on the morphology of the spore-producing surface of the basidiocarp as a taxonomically decisive trait. Modern molecular analyses have, however, shown that this trait does not carry a stable phylogenetic signal. In recent molecular systematic studies, many genera have been rearranged and redefined and currently comprise species with different hymenophore shapes, in particular, smooth and poroid hymenophores, e.g., *Hymenochaete* Lév., *Steccherinum* Gray, *Xylodon* (Pers.) Fr., *Phlebiopsis* Jülich, and *Phanerochaete* P. Karst. (Wagner and Fischer 2002; Larsson 2007; Miettinen et al. 2012, 2016). In almost all of these cases, a few taxa with a poroid hymenophore (polypores) have been added to a large group containing species with smooth or hydroid hymenial surfaces (corticioids). Here, we reveal yet another exceptional case: this one among the brown-rot fungi, a minority among wood-decomposing Basidiomycota that are widely dominated by polypore species (Gilbertson 1981; Ryvarden 1991).

A vast majority of brown-rot Agaricomycetes belongs to the order Polyporales Gäum. Within this

order, most brown-rot species belong to the so-called “Antrodia clade,” which according to the latest multi-locus analyses, includes four families—Dacrybolaceae Jülich, Fomitopsidaceae Jülich, Laetiporaceae Jülich, and Sparassidaceae Herter—and two unresolved groups including polypore genera such as *Amyloporia* Singer, *Fibroporia* Parmasto, and *Pycnoporellus* Murrill (Justo et al. 2017). At present, there are only few corticioid taxa within this clade. These belong to two genera: *Crustoderma* Parmasto and *Dacryobolus* Fr. Whereas the first forms a distinct phylogenetic lineage separated from the polypore genera in the “Antrodia clade,” the identity of the second, *Crustoderma*, in relation to the polypore genus *Pycnoporellus*, has not yet been properly established (Larsson 2007; Ortiz-Santana et al. 2013; Justo et al. 2017). The core of the “Antrodia clade,” genus *Antrodia* P. Karst., has been shown to comprise poroid species only.

Traditionally, the genus *Antrodia* included brown-rot polypores with tough, pale, resupinate to effused-reflexed basidiocarps with a dimitic hyphal structure, and clamped generative hyphae (e.g., Ryvarden and Gilbertson 1993). Later studies, however, have demonstrated that this genus is polyphyletic consisting of

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several smaller genera (e.g., Kim et al. 2001; Rajchenberg et al. 2011; Bernicchia et al. 2012; Ortiz-Santana et al. 2013). The sole attempt to revise the whole polyphyletic genus has been proposed without providing any new data, adequate phylogenetic analyses, or comparisons with recent taxonomic work and hence was poorly grounded (see Audet 2017). As no phylogenetically reliable taxonomic division has yet been proposed, several studies have for the time being chosen to retain the application of the name in the old polyphyletic sense (e.g., Spirin et al. 2015, 2017). However, *Antrodia* s. str. has been delimited as a small number of species grouped around *Antrodia serpens* (Fr.) P. Karst. (Spirin et al. 2013).

The present study was initiated by two recent collections of the rare brown-rot corticioid fungus *Phlebia griseoflavescens* (Litsch.) J. Erikss. & Hjortstam. Binder et al. (2005) found that this species was related to brown-rot Polyporales based on phylogenetic analysis of nuc rDNA internal transcribed spacer ITS1-5.8S-ITS2 (ITS) and nuc rDNA 28S (28S) sequences from a single sample that originated from a study by Parmasto and Hallenberg (2000). Unfortunately, *P. griseoflavescens* is known from very few collections and thus poorly integrated into subsequent molecular phylogenetic analyses. In the last decade, the species has been collected only twice in Norway and northwest Russia.

Our preliminary morphological observations and phylogenetic analyses showed that *Phlebia griseoflavescens* may belong to *Antrodia* in the strict sense. To arrive at a more clear understanding of the phylogenetic position of this corticioid species, and, accordingly, the borders of *Antrodia* s. str., we performed phylogenetic analyses based on three genetic markers: ITS, 28S, and a portion of the largest subunit of RNA polymerase II (*rpb1*). These markers have been shown to provide optimal genus level resolution within Polyporales (Binder et al. 2013; Justo et al. 2017). Further, to elaborate the understanding of species-level relationships within *Antrodia* s. str., we performed additional analyses including all previously known members of the group and two species that are new and described below. Finally, based on recent collecting in Southeast Asia, we reveal and redescribe one new member in this group. Results and taxonomic conclusions of this study are presented and illustrated below.

MATERIALS AND METHODS

Specimen vouchers and morphological analysis.—Collections and type specimens from herbaria H, O, S, TAAM, TU, LE, BPI, PRM, and GB, as well as from the private herbarium of the author JV, were studied.

Herbarium abbreviations followed Thiers [continuously updated]. Macroscopic descriptions followed Spirin et al. (2013, 2017), and micromorphological analyses followed Miettinen et al. (2018). In short, all microscopical structures were measured with 1250× magnification (oil immersion) and phase-contrast illumination using cotton blue in lactic acid (CB). The following abbreviations were used in the taxonomic descriptions and tables: L = mean basidiospore length; W = mean basidiospore width; Q' = length/width ratio; Q = mean length/width ratio; n = total number of measurements per specimens measured; section = cross-section of the basidiocarp.

DNA extraction, PCR, and sequencing.—DNA extraction, polymerase chain reaction (PCR), and sequencing of the target loci for this study (ITS, 28S, and *rpb1*) followed protocols described by Tamm and Pöldmaa (2013) and Spirin et al. (2013). The ITS region was amplified using primers ITS1F (Gardes and Bruns 1993) and ITS4 (White et al. 1990), and the D1–D2 domains of the 28S region using primers CTB6 (Garbelotto et al. 1997) and LR7 (Vilgalys and Hester 1990) or LBW (Tedersoo et al. 2008). The area between conserved domains A and C of *rpb1* (ca. 1400 bp) was amplified using primers *rpb1*-gAf and *rpb1*-fCr (Stiller and Hall 1997; Matheny et al. 2002). PCR products were sequenced at MacroGen (Amsterdam, the Netherlands) or at the Genomics laboratory of the Biology Centre, Academy of Sciences of the Czech Republic (České Budějovice, Czech Republic). Sequences were edited and assembled in Sequencher 5.1 (Gene Codes, Ann Arbor, Michigan).

Taxon sampling for phylogenetic analyses.—We compiled four data sets for phylogenetic analyses. Each one was aligned in the online version of MAFFT 7 (Kato et al. 2017) using the G-INS-i algorithm followed by manual adjustment in AliView (Larsson 2014).

The aim of the first three data sets was to assess genus placement of “*Phlebia*” *griseoflavescens* within the “*Antrodia* clade.” These data sets contained a selection of sequences of brown-rot species belonging to *Antrodia* s. str. (Spirin et al. 2013) and sequences representing all major groups in the “*Antrodia* clade” sensu Justo et al. (2017), including Dacrybolaceae, Fomitopsidaceae, Laetiporaceae, and all still unresolved groups. *Skeletocutis chrysella* Niemelä, a representative of the neighboring “*Skeletocutis*/*Tyromyces*” clade (Justo et al. 2017), was used as an outgroup. The data sets included (i) a combined ITS+28S+*rpb1* alignment, (ii) an ITS+28S-only alignment, and (iii) a *rpb1*-only alignment. The separate ITS+28S and *rpb1* data sets

were used to check for strongly supported positive topological conflicts (>70% bootstrap and 1.0 posterior probability), i.e., strongly supported alternative topologies for the same species in the different data sets. Before analyses, 56 uninformative base pairs in the beginning of 28S region were removed from the data because this region was absent from several combined sequences. The final data sets consisted of 34 sequences representing 34 taxa (2–4 taxa from each larger group in the “*Antrodia* clade” and 8 from *Antrodia* s. str. and closely related taxa). Gblocks (Castresana 2000) was used to select those regions of the sequences that were confidently aligned to be included in analyses. The length of the final data sets was as follows: combined three-gene data set, 2465 base pairs (1955 included in the analyses); ITS+28S, 1462 base pairs (1134 included); and *rpb1*, 1003 base pairs (819 included).

The aim of the fourth data set was to assess the species-level relationships within *Antrodia* s. str. This data set was taxonomically more restricted and contained the ITS+28S sequences representing *Phlebia griseoflavescens* and all the known species in *Antrodia* s. str.: 11 species, including the two new species described in this paper, the recently described *Antrodia neotropica* Kaipper-Figueiró, Robledo & Drechsler-Santos (Kaepernick-Figueiró et al. 2016) and *A. subserpens* B.K. Cui & Yuan Y. Chen (Chen and Cui 2016), and *A. parvula* (Bres.) Ryvardeen, which was sequenced for the first time in this study. In addition, sequences representing *A. multififormis* Vlasák and *A. tenerifensis* Kout & Vlasák, the two recently described species close to *Antrodia* s. str. (Kout et al. 2017), were added to the data set. Based on analyses of data sets i, ii, and iii, *Fomitopsis pinicola* (Sw.) P. Karst. and *Anthoporia albobrunnea* (Romell) Karasiński & Niemelä were used as an outgroup in data set iv. As in data sets i and ii, 56 sites from the 28S region were removed from the combined data sets, resulting in a final data set consisting of 32 sequences (11 produced for this study), with a length of 1367 base pairs.

Data for the studied specimens and the GenBank accession numbers of ITS, 28S, and *rpb1* are presented in TABLE 1. The final alignments for all four data sets were stored in TreeBASE (<http://www.treebase.org>; accession number 23468).

Phylogenetic analyses.—We conducted maximum likelihood (ML) and Bayesian inference (BI) for all four data sets. ITS and 28S regions and introns and exons of *rpb1* were partitioned separately. For ML analyses, IQ-TREE 1.2.2 (Nguyen et al. 2015) using 1000 bootstrap replicates and the “best-fitted model” was used. Models

and their Bayesian information criterion (BIC) scores are presented in SUPPLEMENTARY TABLE 1. MrBayes 3.2.6 (Ronquist et al. 2012) was used for BI analyses with a GTR and invgamma model for DNA substitution and distribution rate variation across sites at the CIPRES Science Gateway (Miller et al. 2010). Two parallel Markov chain Monte Carlo (MCMC) analyses were run, each consisting of four chains, initiated from random starting trees. The analyses were run for 10 million generations, sampling every thousand generations. The first 25% of the trees were discarded as the burn-in, ensuring the average standard deviation of split frequencies had reached <0.01 for all data sets. Posterior probabilities were calculated from the remaining trees in all cases.

RESULTS

Phylogenetic analyses.—A total of 150 002 trees were used to calculate Bayesian posterior probabilities for each data set. ML and BI analyses generated nearly congruent topologies for all data sets (FIGS. 1 and 2; SUPPLEMENTARY FIGS. 1 and 2) and did not reveal any strongly supported positive topological conflicts.

The analyses of the first three data sets, which represent a wider sample of brown-rot species within the *Antrodia* clade, showed that *Phlebia griseoflavescens*, *A. tenerifensis*, *A. multififormis*, and the species in *Antrodia* s. str. formed a well-supported monophyletic group within Fomitopsidaceae (FIG. 1; SUPPLEMENTARY FIGS. 1 and 2). The earliest diverging species within this clade was the recently described North American *A. multififormis*. The species hitherto known to belong to *Antrodia* s. str. (i.e., species closely related to the type of the genus *Antrodia*, *A. serpens*) formed a separate clade nested within this cluster and also received high posterior probability and bootstrap support values.

Analyses of the taxonomically more restricted fourth data set showed a similar overall topology for *Antrodia* s. str. and closely related species as described above (FIG. 2). Monophyly of *Antrodia* s. str. (sensu Spirin et al. 2013) was highly supported. Sequences of *A. mappa* (Overh. & J. Lowe) Miettinen & Vlasák (a member of *Antrodia* s. str.), *P. griseoflavescens*, and the two recently described species from the southwest United States and Canary Islands, *A. multififormis* and *A. tenerifensis* (earlier not considered members of *Antrodia* s. str.), all formed long distinct branches, but their branching order was well supported and identical with the first three data sets.

Within *Antrodia* s. str., the analyses resolved two new species described below, in addition to those known earlier. *Antrodia peregrina*, sp. nov., appeared to be closely related to *A. heteromorpha* (Fr.) Donk, yet

Table 1. Specimen vouchers, geographic location, and GenBank accession numbers (new sequences in bold) of samples analyzed in this study.

Sample	Specimen voucher or collection	Location	ITS	28S	<i>rpb1</i>
<i>Amylocystis lapponica</i>	FP 105131	USA: Colorado	KY948805	KY948879	KY948973
<i>Amyloporia carbonica</i>	Zabel-40GLN	USA: New York	KC585243	KC585065	KY949013
<i>Amyloporia sinuosa</i>	FP 105386	USA: New Hampshire	KC585244	KC585066	KY949018
<i>Amyloporia xantha</i>	DAOM 16570	Canada: British Columbia	KC585254	KC585076	KY949016
<i>Anthoporia albobrunnea</i>	Spirin 4665	Russia	KY948808	KY948880	KY949020
<i>Antrodia favescens</i>	FP 103723	USA: Virginia	KC585269	KC585092	KY949009
<i>Antrodia favescens</i>	Vlasák 0412/4J	USA	KC543129	ibid.	—
<i>Antrodia griseoflavescens</i>	Spirin 11175	Russia	MK119762	ibid.	MK134850
<i>Antrodia griseoflavescens</i>	Kristiansen 2010	Norway	MK119763	ibid.	MK134849
<i>Antrodia heteromorpha</i>	HHB 14162-T	USA: Alaska	KC585279	KC585102	KY949010
<i>Antrodia heteromorpha</i>	Kosolapov VIII-2003 (H)	Russia	KC543145	ibid.	KY949011
<i>Antrodia heteromorpha</i>	Niemelä 2621	Canada	KC543148	—	—
<i>Antrodia heteromorpha</i>	Niemelä 6348	Finland	JQ700268	ibid.	—
<i>Antrodia hyalina</i>	Spirin 2772	Russia	JQ700283	ibid.	KY949007
<i>Antrodia latebrosa (holotype)</i>	Ryvarden 10031	Tanzania	MK119769	ibid.	—
<i>Antrodia macra</i>	Hottola 2729	Finland	KC543135	ibid.	—
<i>Antrodia macra</i>	Löhmus 1887	Estonia	MK119768	ibid.	MK134851
<i>Antrodia mappa</i>	Spirin 5840	Russia	MK119771	ibid.	MK134843
<i>Antrodia mappa</i>	Spirin 4605	Russia	MK119770	ibid.	MK134844
<i>Antrodia mellita</i>	Spirin 3315	Russia	KC543140	ibid.	KY948994
<i>Antrodia minuta</i>	Spirin 2680	Russia	KC595898	ibid.	KY948993
<i>Antrodia multiformis</i>	Vlasák 1307/9 J (haplotype 1)	USA: Arizona	KT381619	ibid.	MK134845
<i>Antrodia multiformis (holotype)</i>	Vlasák 1209/76	USA: Arizona	KT381618	ibid.	MK134846
<i>Antrodia neotropica</i>	FLOR 0054183	Brazil	KT970443	KT970452	—
<i>Antrodia neotropica (holotype)</i>	FLOR 0054184	Brazil	KT970444	KT970453	—
<i>Antrodia parvula</i>	Miettinen 17750	USA: Florida	MK119765	—	—
<i>Antrodia parvula</i>	Miettinen 18226	Indonesia: Java tengah	MK119764	ibid.	—
<i>Antrodia parvula</i>	Miettinen 11589	Indonesia: Papua Barat	MK119766	ibid.	—
<i>Antrodia parvula</i>	Miettinen 11605	Indonesia: Papua Barat	KC595892	ibid.	—
<i>Antrodia peregrina (holotype)</i>	Dai 3026	China	MK119767	ibid.	—
<i>Antrodia serialis</i>	FP 133692	USA: Oregon	KC585303	KC585127	KY948998
<i>Antrodia serpens</i>	Vampola-X-1989	Slovakia	KC543143	ibid.	KY949012
<i>Antrodia serpens (epitype)</i>	Niemelä 8555	Poland	KC543137	ibid.	—
<i>Antrodia subserpens</i>	Cui 8310	China	KP715310	KP715326	—
<i>Antrodia subserpens (holotype)</i>	Dai 6380	China	KP715308	KP715324	—
<i>Antrodia tanakai</i>	Spirin 3968	Russia	KC543174	—	—
<i>Antrodia tanakai</i>	Haikonen 16285	Finland	KC543142	ibid.	—
<i>Antrodia tenerifensis</i>	Kout 1312/9	Spain: Canary Isl	KY446066	ibid.	MK134848
<i>Antrodia tenerifensis (holotype)</i>	Kout 1412/2	Spain: Canary Isl	KY446065	ibid.	MK134847
<i>Antrodia variiformis</i>	FP 104442	USA: Colorado	KC585309	KC585134	KY948997
<i>Crustoderma corneum</i>	HHB 5685	USA: Montana	KC585318	KC585143	KY949037
<i>Dacryobolus karstenii</i>	Miettinen 18685	USA: Washington	KY948743	KY948900	KY948955
<i>Daedalea quercina</i>	FP 103364	USA: Georgia	KC585335	KC585160	KY948988
<i>Fibroporia gossypium</i>	Rajchenberg 11443	Argentina	KY948811	KY948897	KY949029
<i>Fibroporia vaillantii</i>	FP 90877	USA: New Jersey	KC585345	KC585170	KY949035
<i>Fomitopsis pinicola</i>	AFTOL-ID 770	—	AY854083	AY684164	AY864874
<i>Laetiporus sulphureus</i>	CT1	USA: Connecticut	EU402565	EU402532	KY949025
<i>Oligoporus balsameus</i>	FP 135372	UK: England	KC585358	KC585187	KY948974
<i>Piptoporus betulinus</i>	L-15603-Sp	USA: New York	KC585373	KC585202	KY949005
<i>Postia caesia</i>	Kinnunen 5087	Poland	KY948814	KY948885	KY948978
<i>Pycnoporellus fulgens</i>	CA20	USA: California	KC585385	KC585218	KY949040
<i>Rhodofomes roseus</i>	RLG-6954	USA: Arizona	KC585353	KC585181	KY949003
<i>Rhodonina placenta</i>	Dietz7E	USA: California	KC585390	KC585223	KY949028
<i>Sarcoporia polyspora</i>	L14910	USA: New York	KC585393	KC585226	KY949022
<i>Skeletocutis chrysella</i>	L15957	USA: New York	—	—	KY948982
<i>Skeletocutis chrysella</i>	Miettinen 9472	Finland	FN907916	FN907916	—
<i>Sparassis radicata</i>	OKM4756	USA: Idaho	KC987580	KF053407	KY949023
<i>Wolfiporia cocos</i>	18176	USA: North Carolina	—	KC585233	—
<i>Wolfiporia cocos</i>	MD-104 SS10	—	—	—	genomic
<i>Wolfiporia cocos</i>	Unknown	—	AY728272	—	—

differing from this species at nine combined ITS and 28S sites. In addition, *Antrodia latebrosa*, sp. nov., belonged to the same subclade as *A. heteromorpha*, together with *A. peregrina*, *A. serpens*, *A. subserpens*, and *A. parvula*, but was more distantly related, differing at 32–36 combined ITS and 28S sites, to other members of this subclade.

Our analyses showed for the first time that *Antrodia parvula* (redescribed below) belongs to *Antrodia* s. str.

This species is represented by three samples from Java, the type locality of *Trametes parvula* Bres., as well as two samples from New Guinea and one from the southeastern United States (FIG. 2). However, this species did not appear monophyletic. Two recently described species, *A. neotropica* and *A. subserpens*, differed from *A. parvula* by 1–4 bases at the ITS locus and showed only negligible morphological differences from *A. parvula*.

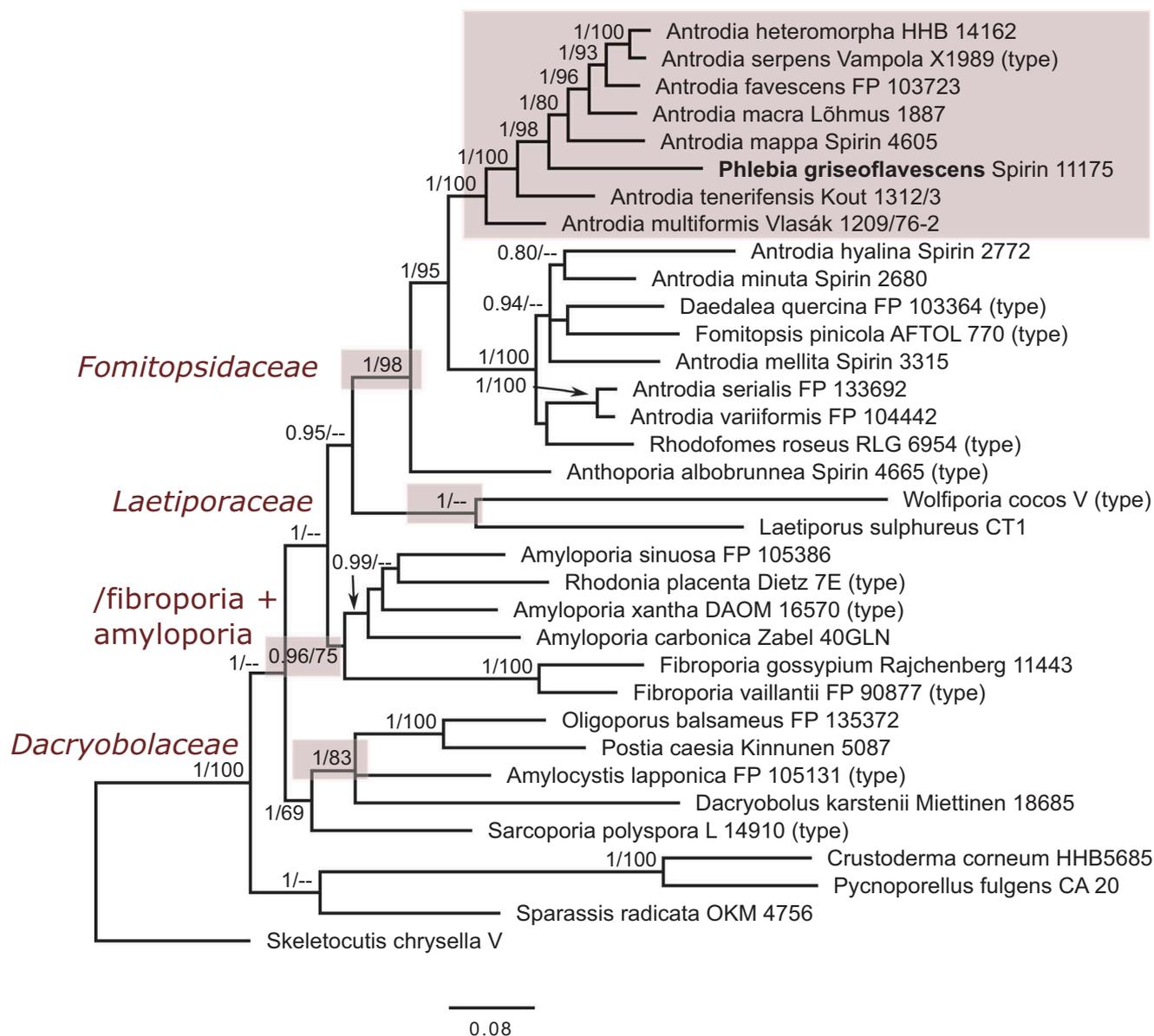


Figure 1. Phylogenetic placement of *Phlebia griseoflavescens* (in bold) and delimitation of redefined *Antrodia* s. str. (box) within the "Antrodia clade" (including all taxa shown other than outgroups) based on Bayesian inference of the ITS+28S+*rpb1* data set. Marked nodes denote larger families within the "Antrodia clade." Generic types are indicated by "type" at the end of tip labels. Numbers on nodes represent posterior probabilities >0.85 and ML bootstrap values >70%. The scale bar indicates the number of expected substitutions per site.

Morphological comparison of *Antrodia* s. str. and closely related species.—In spite of different macroscopic features, *Phlebia griseoflavescens* shared several anatomical characters with representatives of *Antrodia* s. str., in particular the broadly cylindrical or ellipsoid basidiospores with a tapering distal end and long pedunculate basidia (FIG. 3; SUPPLEMENTARY TABLE 2). In addition, the hymenial cells in senescent basidiocarps

possessed slightly thickened walls, a feature that can be detected in many poroid species formerly addressed to *Antrodia* s.l. *Phlebia griseoflavescens* also had rare and rather poorly differentiated cystidia, the shape and size of which were comparable with cystidioles of poroid species of *Antrodia*. Another feature that *P. griseoflavescens* shared with the poroid relatives of *Antrodia* was the presence of hyphidia.

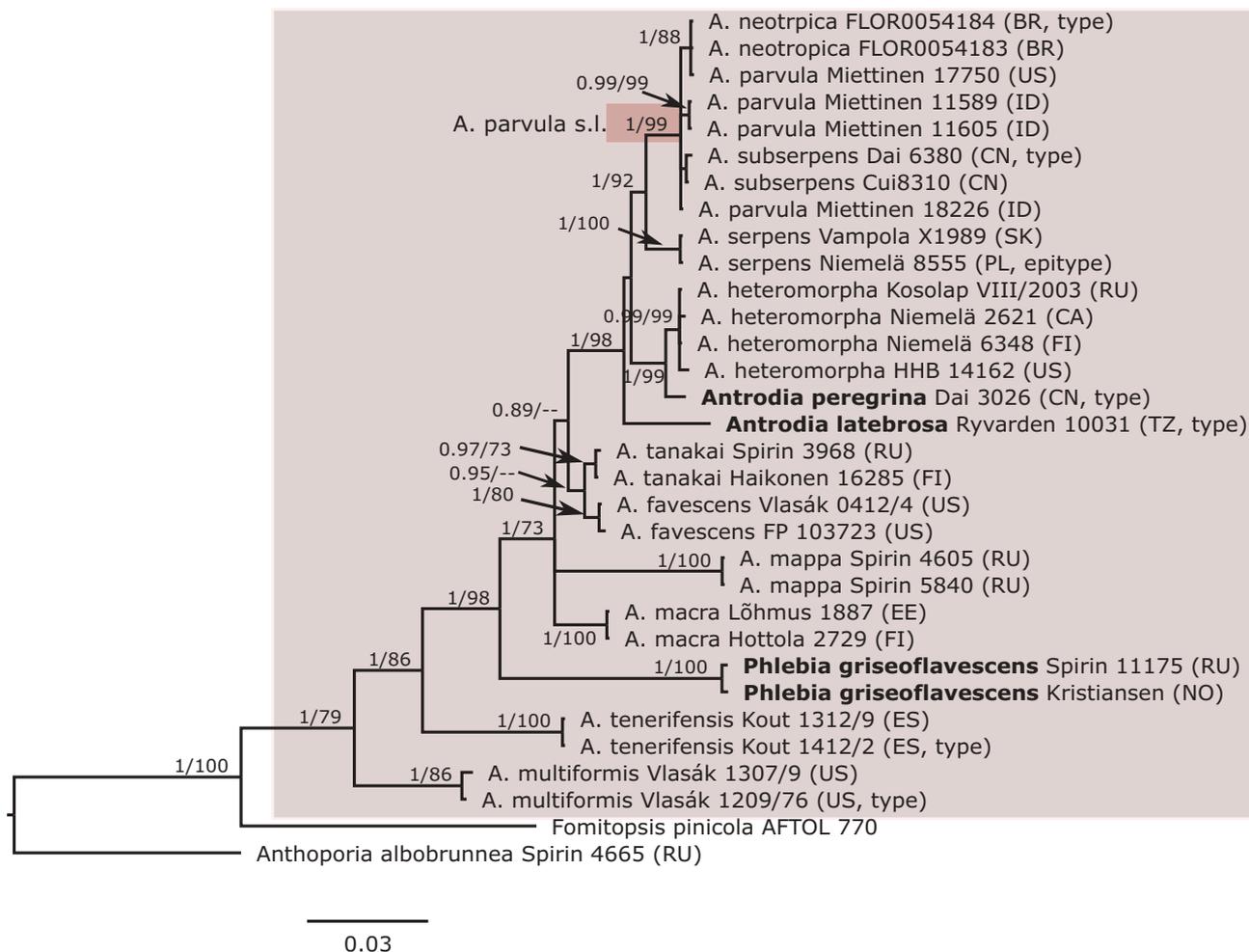


Figure 2. Phylogenetic relationships of species in *Antrodia* s. str. based on Bayesian inference of the ITS+28S data set. Numbers on nodes represent posterior probabilities >0.85 and ML bootstrap values >70%; the scale bar indicates the number of expected substitutions per site. Two-letter codes in the parentheses denote the country of origin. New species and combinations described in this study are in bold.

In contrast to other species of *Antrodia*, the basidiocarps of *P. griseoflavescens* were characterized by their monomitic hyphal system. All species of *Antrodia* are dimorphic, although *A. mappa* develops skeletal hyphae only occasionally (and only in well-developed basidiocarps) and these are located in the subiculum (Spirin et al. 2013). *Antrodia multiformis* and *A. tenerifensis* were morphologically similar to taxa in the “*A. heteromorpha* subclade,” although they produced considerably fewer skeletal hyphae. In this respect, they were similar to the almost monomitic *A. mappa*. In *A. multiformis*, the skeletal hyphae were relatively sparse and located mostly in the subicular layer and uppermost tube trama. In *A. tenerifensis*, skeletal hyphae were extremely rare, occurring as short intercalary fragments of subicular generative hyphae. Another feature that *A. tenerifensis* shared with *A. mappa* was the strongly reduced, small-sized basidiocarps with shallow pores.

TAXONOMY

Antrodia P. Karst., Meddel Soc Fauna Flora Fenn 5:40. 1879.

Type species: Antrodia serpens (Fr.) P. Karst.

Description (emend.): Basidiocarps annual or short-living perennial, pileate, effused-reflexed or resupinate, light-colored, 0.5–5(15) cm in widest dimension. Hymenophore poroid, with angular or irregular pores 0.5–4 per mm, or smooth and ceraceous-waxy to leathery. Hyphal structure monomitic or dimorphic; generative hyphae clamped, skeletal hyphae infrequent (then located mostly in subiculum or context) to dominating throughout. Cystidioles or hymenial cystidia present, clearly tapering to the apex, often slightly thick-walled. Hyphidia present, simple or sparsely branched, generally embedded in hymenial layer. Basidia clavate-pedunculate, 4-spored, normally over 25 µm long;

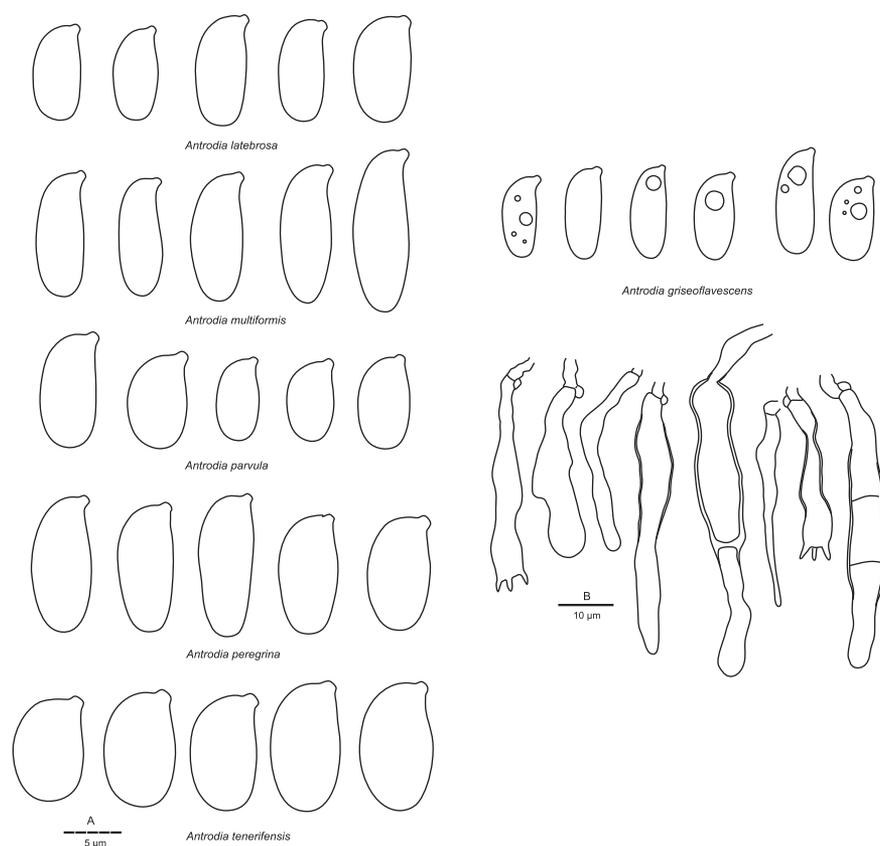


Figure 3. Main morphological characteristics of the species merged with *Antrodia* s. str. and discussed in this paper. A. Spore drawings: *A. latebrosa* (holotype, Ryvarden 10031), *A. multiformis* (isotype, Vlasák 1307/9), *A. parvula* (Mittinen 18226), *A. peregrina* (holotype, Dai 3026), *A. tenerifensis* (paratype, Kout 1312/9), and *A. griseoflavescens* (Spirin 11175). B. Basidia, hyphidia, and cystidia of *A. griseoflavescens* (Spirin 11175).

basidia and basidioles becoming slightly thick-walled in senescent hymenium. Basidiospores $7\text{--}15 \times 3\text{--}7 \mu\text{m}$, often slightly arcuate near apiculus and more or less tapering at the distal end, inamyloid, acyanophilous, hyaline, thin-walled, cylindrical to broadly ellipsoid, content homogeneous or with several small oil drops. Causing bown rot of dead wood of angiosperms and conifers. Belonging to family Fomitopsidaceae.

Antrodia griseoflavescens (Litsch.) Runnel, Spirin & K.H. Larsson, comb. nov. FIGS. 3, 4
Mycobank MB828130

≡ *Corticium griseoflavescens* Litsch. in Pilát & Lindtner, Bull Soc Sci Skopje 18:178. 1938 (basionym). —*Phlebia griseoflavescens* (Litsch.) J. Erikss. & Hjortstam, The Corticiaceae of North Europe 6:1121. 1981.

= *Corticium pallidocremeum* Litsch., Ann Mycol 39:121. 1941.

Description: Basidiocarps annual, resupinate, up to 15 cm wide, very thin (0.1–0.2 mm thick), waxy. Margin rather sharply delimited, pruinose, concolorous with hymenial surface. Hymenium pale cream-colored

to pale ochraceous, smooth at first, but then densely and irregularly cracking.

Hyphal structure monomitic; hyphae hyaline, clamped, inamyloid, acyanophilous. Subicular hyphae $3\text{--}4 \mu\text{m}$ diam, slightly thick-walled, densely interwoven. Subhymenial hyphae $2\text{--}3.5\text{--}(4) \mu\text{m}$ diam, with indistinctly thickened walls, interwoven, twisted, in older basidiocarps rather densely glued together, occasionally incrustated by small crystals of various shape. Basidia $(25\text{--})26\text{--}41\text{--}(45) \times 5.5\text{--}7.5 \mu\text{m}$, with widened apical part and long narrow base (of pedunculate type), 4-spored; senescent basidia slightly thick-walled (walls $0.5\text{--}1 \mu\text{m}$ thick). Hyphidia $2\text{--}4 \mu\text{m}$ diam, normally infrequent, simple or accidentally branched, embedded in hymenial layer, rarely projecting up to $30 \mu\text{m}$ above basidial layer. Cystidia $50\text{--}80 \times 5\text{--}7 \mu\text{m}$, projecting up to $40 \mu\text{m}$ above basidial layer, normally infrequent, thin- to slightly thick-walled, clavate, usually gradually tapering to the apex. Basidiospores $(6\text{--})6.5\text{--}9.5\text{--}(10) \times 3\text{--}4\text{--}(4.5) \mu\text{m}$ ($n = 120/4$), $L = 7.3\text{--}8.3$, $W = 3.3\text{--}3.5$, $Q = 2.22\text{--}2.46$, hyaline, thin-walled, broadly cylindrical to ellipsoid, some clearly arcuate near apiculus, distal end sometimes slightly sharpened, inamyloid.



Figure 4. Basidiocarps in *Antrodia* s. str. A. *Antrodia griseoflavescens* (Spirin 11175). B. *Antrodia mappa* (Spirin 5840). C. *Antrodia parvula* (Miettinen 18226). D. *Antrodia peregrina* (Spirin 5223). Bars = 1 cm.

Ecology and distribution: On thick fallen decorticated aspen (*Populus tremula*) logs in mixed forests in north Europe, mostly on beech (*Fagus sylvatica*) in central Europe, rare in temperate and hemiboreal forests, Jul to Oct.

Other specimens examined: MACEDONIA. JEGUNOVCE: Ljuboten, on *Fagus sylvatica*, Jul 1937, Pilát & Lindtner (isotype of *Corticium griseoflavescens*, GB 0115152). NORWAY. TROMS: Tranøy, Storholtet, 1 Aug 2010, G. Kristiansen (O-F 110331). RUSSIA. LENINGRAD REG.: Boksitogorsk Dist., Vozhani, on *Populus tremula*, 2 Oct 2016, V. Spirin 11175 (H 7009026, TU 128021). SWEDEN. SMÅLAND: Femsjö, Gåshult, *P. tremula*, 11 Oct 1911, L. Romell 2176 (holotype of *Corticium pallidocremeum*, S F11295). SWITZERLAND. TICINO: Rima, on *F. sylvatica*, 23 May 1987, E. Martini 1016 (GB 0181235).

Notes: Litschauer described this species twice, first as *Corticium griseoflavescens* from Macedonia (Pilát et al. 1938) and then as *C. pallidocremeum* from Sweden (Litschauer 1941). Eriksson et al. (1981) concluded that both were conspecific and combined *C. griseoflavescens* in *Phlebia*, although with some

reservation. Eriksson et al. (1981) described and illustrated cystidia-like elements overlooked by Litschauer. The cystidia of *A. griseoflavescens* are similar to cystidioles occurring in the hymenial layer of poroid representatives of *Antrodia* and differ from them mainly by their length. Moreover, we observed simple or bifurcate hyphidia in the hymenium of *A. griseoflavescens*, characteristic of species in *Antrodia* s. str. too, albeit they are usually uncommon and difficult to find. Unlike other species in *Antrodia* s. str., the hyphal structure of basidiocarps of *A. griseoflavescens* is strictly monomitic: this can be due to its very thin basidiocarps and subtle subiculum. Presence of skeletal hyphae in *Antrodia* seems to correlate with the thickness of basidiocarps, so that also in other thin species in the group (*A. tenerifensis*, *A. multiformis*, and *A. mappa*) the skeletal hyphae are scarce or even absent. Note, however, that Hallenberg (1990) observed skeletal hyphae in cultures of *P. griseoflavescens*. Hallenberg (1990) also described basidiospores of *P. griseoflavescens* as uninucleate, whereas they were characterized as binucleate in the three poroid species of *Antrodia* s.str. (David and

Dequatre 1985). Further studies of *Antrodia* should confirm whether *P. griseoflavescens* is the single representative of the genus having uninucleate basidiospores.

Antrodia latebrosa Spirin, Ryvarden & Miettinen, sp. nov. **FIG. 3**

Mycobank MB828131

Typification: TANZANIA. ARUSHA: Arusha National Park, Mt. Meru, on dead angiosperm wood, 8 Feb 1973, L. Ryvarden 10031 (**holotype** O-F 110332, **isotype** H 7009027). GenBank: ITS+28S = MK119769.

Etymology: *latebrosus* (Latin), hidden, in reference to small morphological differences from other similar-looking species.

Description: Basidiocarps annual, often resupinate and fusing together, rarely with small, fingernail-like pilei; reflexed part 4–5 mm wide, effused part up to 10 × 2.5 cm. Pileal surface uneven, smooth to finely pubescent, azonate, cream-colored. Pileal margin sharp to somewhat blunt, fertile, margin of resupinate parts sterile, 1–3 mm wide, clearly delimited from the substrate, white to cream-colored. Pore surface almost white at first, becoming cream-colored to yellowish or pale ochraceous; pores 1.5–2.5 per mm, rounded to angular, then strongly elongated and split, dissepiments mostly entire. Section: context/subiculum 1–2 mm thick, corky, white to pale cream-colored; tubes 1–2 mm thick, concolorous with context, leathery.

Hyphal structure dimitic; hyphae hyaline, clamped, inamyloid, acyanophilous. Skeletal hyphae in subiculum and context (2.5–)3–4(–4.5) µm diam, interwoven, thick-walled to subsolid; generative hyphae 2.5–3.5 µm diam, relatively infrequent, thin-walled. Tramal hyphae (2.5–)3–4.5 µm diam, interwoven to subparallel; skeletal hyphae dominating, tightly arranged, thick-walled; generative hyphae in trama 2–3.5 µm diam, relatively abundant, thin- to slightly thick-walled. Basidia (18–)19–28(–30) × 6.5–9.5(–10) µm, with widened apical part and long narrow base (pedunculate type), 4-spored; senescent basidia clearly thick-walled (walls 1–2 µm thick). Cystidioles 19–28 × 4.5–6.5 µm, clavate with a narrow apex. Hyphidia 2–3 µm diam, rather infrequent, simple or sparsely branched, embedded in hymenial layer. Skeletocystidia (skeletal hyphae ends, penetrating hymenium) 4.5–5.5 µm diam, infrequent, thick-walled, with slightly widened clavate apices. Crystals variably present in hymenium and trama, 4–10 µm diam. Basidiospores 7–10(–10.5) × 3.5–5(–5.5) µm (n = 90/3), L = 8.4–8.8, W = 4.1–4.3, Q = 2.06–2.08, hyaline, thin-walled, ellipsoid to broadly ellipsoid, clearly arcuate near apiculus, distal end of longest spores sometimes slightly sharpened, inamyloid.

Ecology and distribution: Known only from two localities in Tanzania and Kenya, growing on angiosperm hosts, Feb.

Other specimen examined: KENYA. EAST PROVINCE: Regati Forest Station, 2 Feb 1973, L. Ryvarden 9767 (O-F 915054).

Notes: *Antrodia latebrosa* is introduced here based on small but clear morphological and genetic differences from *A. serpens*, which is the closest relative. *Antrodia latebrosa* differs from *A. serpens* in having smaller pores and distinctly shorter basidia resembling those in *A. macra* (Sommerf.) Niemelä. The spores are shorter and usually more regularly ellipsoid than in *A. serpens* (SUPPLEMENTARY TABLE 2). The North American *A. favescescens* is a superficially similar small-pored species in *A. heteromorpha* group; however, the basidiocarps are darker, ochraceous to brownish, and the basidiospores more narrow than in *A. latebrosa* (SUPPLEMENTARY TABLE 2).

Antrodia parvula (Bres.) Ryvarden, Mycotaxon 33:317. 1988. **FIGS. 3, 4**

≡ *Trametes parvula* Bres., Ann Mycol 10:506. 1912.

= *Trametes similis* Bres., Ann Mycol 10:505. 1912 (fide Ryvarden 1988).

= *Polyporus albojavensis* Lloyd, Mycological Writings 7:1246. 1924.

Description: Basidiocarps annual, often resupinate and fusing together, more rarely with small, fingernail-like pilei; reflexed portions 8–20 mm wide, effused portions up to 10 × 20 mm. Pileal surface uneven, smooth to finely pubescent, azonate, cream-colored. Pileal margin sharp to somewhat blunt, fertile; margin of resupinate parts sterile, 0.5–1 mm wide, clearly delimited from the substrate, white to cream-colored. Pore surface almost white at first, later cream-colored to yellowish or pale ochraceous; pores 3–5 per mm, rounded to angular-elongated, dissepiments mostly entire. Section: context/subiculum 0.5–1.5 mm thick, corky, white to pale cream-colored; tubes 1–1.5 mm thick, concolorous with context, leathery.

Hyphal structure dimitic; hyphae hyaline, clamped, inamyloid, acyanophilous. Skeletal hyphae in subiculum and context (2.5–)3–4.5(–5) µm diam, interwoven or in subparallel bundles, thick-walled to subsolid; generative hyphae 2.5–4 µm diam, relatively infrequent, thin-walled. Tramal hyphae interwoven to subparallel; skeletal hyphae 2–4 µm diam, dominating, tightly arranged, distinctly to very thick-walled; generative hyphae 2–4 µm diam, relatively abundant, thin- to slightly thick-walled. Basidia (19–)22–34(–35) × (6–)6.5–8.5(–9) µm, with widened apical part and long narrow base (pedunculate type), 4-spored; senescent

basidia with thickened walls (up to 1 μm thick). Cystidioles 17–27 \times 4–5.5 μm , clavate with narrowed apex. Hyphidia 2–3.5 μm diam, infrequent, simple or bifurcate, at the apex, embedded in hymenial layer. Skeletocystidia (skeletal hyphae ends penetrating hymenium) very rare, thick-walled, with slightly widened, clavate apices 4–5 μm diam. Basidiospores 7–9.5 \times 3.5–5 μm ($n = 120/4$), $L = 7.6\text{--}8.6$, $W = 3.9\text{--}4.3$, $Q = 1.78\text{--}2.19$, hyaline, thin-walled, ellipsoid to broadly ellipsoid, clearly arcuate near apiculus, distal end of longest spores sometimes slightly sharpened, inamyloid.

Ecology and distribution: On dry but still attached branches, fences, and man-made stumps in Southeast Asia (Indonesia, type), southeast Africa (Malawi), and North America (Florida), throughout the year.

Other specimens examined: INDONESIA. JAWA BARAT: Cibodas, no date, *Höhnelt* (isoelectotype of *T. parvula*, S F8035) (selected by Ryvar den 1988:317); on rotten wood, 27 Nov 1921, *van Leeuwen 650* (lectotype of *P. albojavensis*, BPI US0301653, O, H) (selected by Ryvar den 1990:84); JAWA TENGAH: Karanganyar, Mt. Lawu, on fallen branch, 22 May 2014, *O. Miettinen 18226* (BO, H 7008941); PAPUA BARAT: Tambrauw Regency, Anggra, on man-made stump (angiosperm), 4 Feb 2007, *O. Miettinen 11589* (MAN, H 7008935); MALAWI. THYLO: Mulnaje Mts., Lichenya Hut, on angiosperm, 22–24 Jan 1992, *L. Ryvar den 31440* (O). USA. FLORIDA: Alachua County, San Felasco Hammock Preserve, on angiosperm branch, 20 Nov 2013, *O. Miettinen 17750* (H 7009051).

Notes: The authentic material of *T. parvula* is in good condition and corresponds well to recent sequenced collections from Indonesia. Morphologically, *A. parvula* is most similar to the European species *A. macra* (Sommerf.) Niemelä but differs from it mainly by the smaller pores (3–5 per mm vs. 2–3 per mm in *A. macra*). Moreover, *A. parvula* is able to produce well-developed pilei, although their presence is inconstant. Basidiocarps of *A. macra* are resupinate and produce a poorly developed reflexed part only in exceptional cases. Ryvar den (1988) stated that *T. similis* is conspecific to *A. parvula*. The type material of *P. albojavensis* we studied is completely sterile but otherwise identical to all other specimens of *A. parvula*.

ITS sequences of two recently described species, *A. neotropica* from Brazil (Kaipper-Figueiro et al. 2016) and *A. subserpens* from China (Chen and Cui 2016), show very small differences from *A. parvula* (1–4 bases at the ITS locus) and admix with *A. parvula* sequences on the phylogenetic tree (FIG. 2). Morphologically, the samples representing those species differ from *A. parvula* mostly in having larger pores: 1–2 per mm in *A. neotropica* and

1–2.5 per mm in *A. subserpens* (cf. 3–4 per mm in our Florida sample and 2–3.5 per mm in our Malawi sample). In addition, basidiospores of *A. neotropica* are longer than those of *A. parvula* and *A. subserpens*, reaching 14 μm in length. However, these traits are not sufficient for defining species in *Antrodia* s. str. (see also Spirin et al. 2013, 2016); therefore, the taxonomic status of *A. subserpens* and *A. neotropica* should be reevaluated based on further genetic markers. As a preliminary solution, *A. neotropica* and *A. subserpens* should be considered to be *Antrodia parvula* s.l.

Antrodia peregrina Spirin, Y.C. Dai & Vlasák, sp. nov. FIGS. 3, 4

Mycobank MB828133

Typification: CHINA. JILIN: Antu, Changbaishan Nature Reserve, on dead *Quercus* branch, 20 Sep 1998, *Dai 3026* (**holotype** H 7009026, **isotype** BJFC). GenBank: ITS+28S = MK11976.

Etymology: *peregrinus* (Latin), alien, in reference to the unusually soft consistency of the tubes, unlike in similar-looking *Antrodia* species.

Description: Basidiocarps annual, resupinate or effused-reflexed, orbicular; reflexed part 2–5 mm wide, 1–2 mm thick, effused part up to 200 mm in widest dimension. Pileal surface smooth or uneven, occasionally covered by malformed pores, cream-colored to ochraceous. Pileal margin 0.5–1 mm wide, sharp, fertile; margin of resupinate parts sterile, clearly delimited and sometimes detached from substrate, white to cream-coloured or pale ochraceous. Pore surface cream-colored at first, later pale ochraceous or pale gray to brownish; pores (1–)1.5–3 per mm, angular, becoming elongated to daedaleoid or irpicoid, occasionally fused together; dissepiments at first thick, uneven, later becoming lacerate and thinner. Section: context/subiculum very thin (0.1–0.5 mm thick) corky, white to pale cream; tubes 1–3 mm thick, pale ochraceous to pale brownish, papery to soft corky.

Hyphal structure dimitic; hyphae hyaline, clamped, inamyloid, acyanophilous, almost unchanging in KOH. Skeletal hyphae in subiculum and context 3–5(–5.5) μm diam, interwoven, thick-walled to subsolid; generative hyphae 3–5 μm diam, relatively infrequent, thin- or slightly thick-walled. Tramal hyphae (2.5–)3–5 μm diam, interwoven; skeletal hyphae dominating, rather tightly arranged, distinctly to very thick-walled; generative hyphae 3–4 μm diam, thin- to distinctly thick-walled; rhomboid or irregular crystals occasionally present among tramal hyphae. Basidia (25–)26–40(–48) \times (6.5–)7–9.5(–10) μm , pedunculate, 4-spored; senescent basidia with thickened walls (up to 1 μm thick). Cystidioles 18–32 \times 5.5–7 μm , clavate with narrowed apex. Hyphidia 2–4

μm diam, simple or sparsely branched, embedded in hymenial layer. Skeletocystidia 4–6 μm diam, abundant, thick-walled, with slightly widened clavate apices. Basidiospores 8–12.5(–13) \times 4–5.5(–6) μm ($n = 80/3$), $L = 9.2$ – 10.5 , $W = 4.5$ – 4.9 , $Q = 2.01$ – 2.24 , hyaline, thin-walled, narrowly to broadly ellipsoid, often slightly arcuate near apiculus, distal end of longest spores more or less tapered, inamyloid.

Ecology and distribution: On logs and thick fallen (as a rule decorticated) branches of *Quercus*, especially *Q. mongolica*, widely distributed in temperate forests of East Asia.

Other specimens examined: CHINA. LIAONING: Kuandian, Guanshui, on *Quercus*, 25 Sep 1995, Y.-C. Dai 2178 (H 7009055). RUSSIA. KHABAROVSK REG.: Khabarovsk Dist., Malyi Niran, on *Quercus mongolica*, 7 Aug 2012, V. Spirin 5000 (H 7009052); Ulika, on *Q. mongolica*, 13 Aug 2012, V. Spirin 5223 (H 7009053); Voronezhskoe, on *Q. mongolica*, 20 Aug 2013, V. Spirin 6167 (H 7009054); PRIMORIE: Khasan Dist., Ryazanovo, on *Quercus dentata*, 27 Jul 1979, I. Parmasto (TAAM 097826); Partizansky Dist., Sergeevka, on *Q. mongolica*, 28 May 1983, E. Parmasto (TAAM 105368); Shkotovo Dist., Solovaitsev Ruchi, on *Q. mongolica*, 9 Oct 1936, Lyubarsky (LE 31529).

Notes: *Antrodia peregrina* is morphologically similar to *A. heteromorpha* and *A. serpens*, but it differs from them mainly by the smaller pores (0.8–2 per mm in the two latter species). The most distinctive macroscopic feature of *A. peregrina* is the unusually soft, papery consistency of the tubes, which differentiates this species from the leathery or corky basidiocarps of *A. heteromorpha*, *A. serpens*, and *A. tanakai*. Basidiocarps of the latter three species are widely distributed in East Asia and often have well-developed pilei compared with rudimentary caps of *A. peregrina*. In addition, the basidiospores of *A. tanakai* are narrower than in *A. peregrina* (SUPPLEMENTARY TABLE 2).

DISCUSSION

Here, we demonstrate that a corticioid species with a smooth hymenial surface, *Phlebia griseoflavescens*, clusters together with the core polypore group of brown-rot fungi known as *Antrodia* s. str. (Spirin et al. 2013). Hence, this species is placed as the only known corticioid member within a well-resolved, otherwise polypore-comprising genus. This finding highlights the importance of including molecular data on species with different hymenial shapes in phylogenetic analyses in order to make the best taxonomic decisions. In particular, the phylogenetic placement of the brown rot-producing corticioid taxa requires attention. Earlier studies have shown

that such corticioids may belong to the polypore dominated “*Antrodia* clade,” but the taxa explored so far have formed phylogenetic lineages distinct from polypore genera (Binder et al. 2005; Larsson 2007; Ortiz-Santana et al. 2013; Justo et al. 2017).

Based on our phylogenetic and morphological results, we decided to revise *Antrodia* s. str. and accommodate *A. griseoflavescens* and two recently described taxa (*A. multiformis* and *A. tenerifensis*) within this genus. An alternative way for interpreting our results would have been to keep within a narrow concept of *Antrodia* (Spirin et al. 2013) and, additionally, to describe four new monotypic genera (for *A. multiformis*, *A. tenerifensis*, *P. griseoflavescens*, and *A. mappa*). We discounted this option based on the absence of reliable morphological characters to justify these genera. Our solution may be further emended after revising the large, so-called “*Daedalea* clade” neighboring *Antrodia* s. str., which has remained unresolved (Ortiz-Santana et al. 2013; Justo et al. 2017). The question is whether the intergeneric distances in the “*Daedalea* clade” are comparable with those between subclades in *Antrodia* s. str., in which case we would need to reconsider the latter genus concept as well. The current choice also serves the practical use of taxonomy, attempting to refrain from a dual nomenclatural system where most scientists working on the practical aspects of these fungi would likely continue using the old name instead of names of new small genera (see similar discussions for the genera *Amanita* Pers. [Tulloss et al. 2016] and *Fusarium* Link [Geiser et al. 2013]). In addition, society expects stable taxonomy and nomenclature for practical purposes such as for legal acts and other conservation tools (e.g., *A. mappa* is red-listed in Finland; Kotiranta et al. 2019).

This study also showed that there is a high possibility for unaccounted diversity even within the well-studied polypore genera. As expected, new poroid species were found from relatively poorly studied regions, i.e., the tropical Africa and East Asia. In contrast, the new corticioid member in the clade inhabits northern Europe—a relatively well-studied region in terms of wood-inhabiting agaricomycetes. To understand brown-rot evolution, we need to focus on sampling in poorly studied areas, particularly in the tropics, and pay special attention to corticioid taxa.

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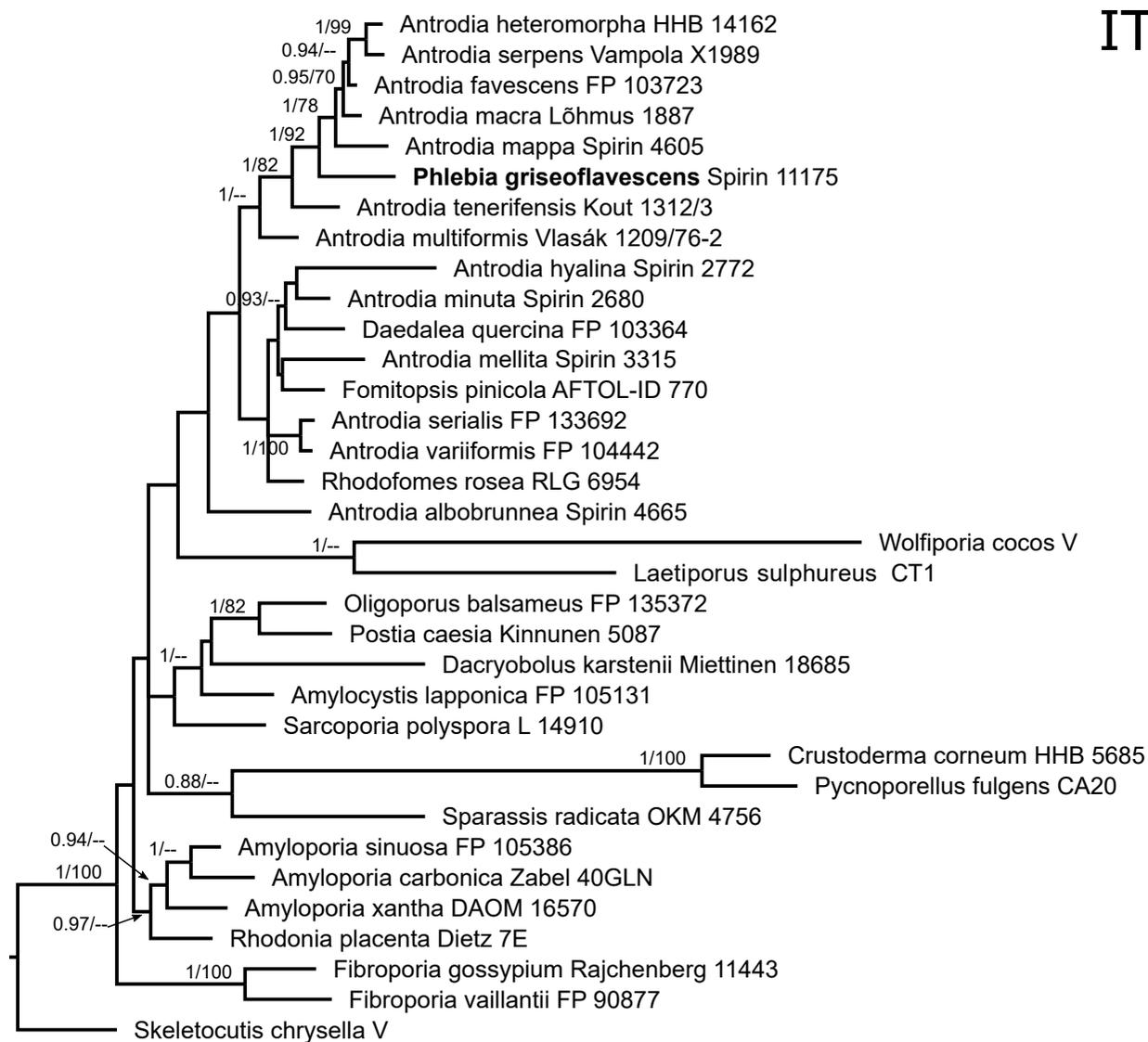
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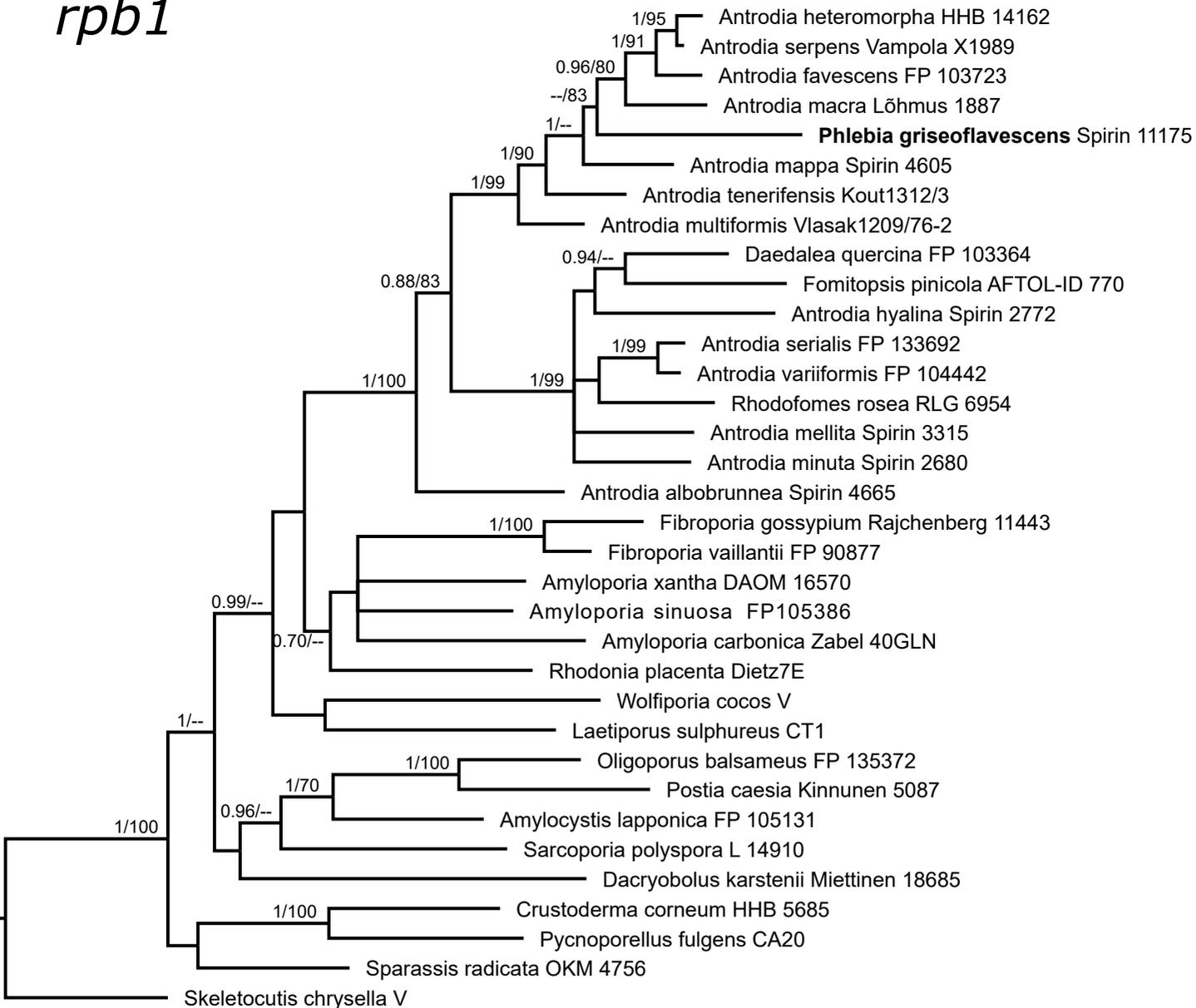
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rpb1



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SUPPLEMENTARY TABLE 2. Identification characters of all known poroid species in Antrodia

s str. For basidia average measurements are given.

Species	Distribution	Hosts	Habit / pores per mm	Skeletal hyphae	Basidia, µm	Basidiospores, µm
<i>A. favesces</i>	North	almost	effused-	dominating	21–26 ×	(6.1–) 6.4–9.4 (–11.4) ×
	America, temperate	exclusively angiosperms	reflexed / 1–2	throughout	6–7	(2.5–) 2.8–4.1 (–4.4), L = 7.25–8.51, W = 3.14–3.68, Q = 2.24– 2.53
<i>A. griseoflavescens</i>	Europe, temperate	angiosperms	effused, hymenophore smooth	absent	26–41 × 5.5–7.5	(6.1–) 6.3–9.6 (–10.0) × (2.8–) 2.9–4.0 (–4.3), L = 7.33–8.28, W = 3.30–3.52, Q = 2.22– 2.46
	<i>A. heteromorpha</i>	holarctic	mostly gymnosperms	effused- reflexed / 0.5–1.5	dominating throughout	27–36 × 6–8.5
<i>A. latebrosa</i>	East Africa, tropical montane	angiosperms	effused- reflexed / 1.5–2.5	dominating throughout	19–28 × 6.5–9.5	(7.0–) 7.2–10.2 (–10.3) × (3.4–) 3.6–5.2 (–5.4), L = 8.44–8.85, W = 4.11–4.27, Q = 2.06– 2.08
	<i>A. neotropica</i> ¹	neotropical	angiosperms (<i>Baccharis</i> spp.)	resupinate or effused- reflexed / 1-2	dominating in trama	35–50 × 8.5–10

						4.41, Q = 1.92– 2.74
<i>A. macra</i>	holarctic	angiosperms, most often <i>Salicaceae</i>	resupinate / 2–3	dominating throughout	20–45 × 6.5–9.5	(6.5–) 7.1–11.2 (–11.8) × (2.8–) 2.9–4.6 (–4.7), L = 8.13–9.78, W = 3.19–4.16, Q = 2.03– 2.86
<i>A. mappa</i>	holarctic	gymnosperms (North America), <i>Salicaceae</i> (Europe)	resupinate / 2–4	absent or occasionally present in subiculum	21–27 × 7–7.5	(7.4–) 8.5–10.8 (–12.1) × (2.0–) 2.5–3.5 (–3.6), L = 9.30–10.18, W = 2.77–3.30, Q = 3.09– 3.62
<i>A. multiformis</i>	North American South-West, continental	gymnosperms	effused- reflexed / 2–3	sparse	21–31 × 8.5–10	(9.0–) 9.1–13.8 (–14.2) × (3.7–) 3.8–5.0 (–5.2), L = 10.43–12.16, W = 4.14–4.46, Q = 2.53– 2.73
<i>A. parvula</i>	pantropical – warm temperate	angiosperms	effused- reflexed / 3–5	dominating throughout	22–34 × 6.5–8.5	(6.8–) 6.9–9.4 (–9.5) × (3.3–) 3.4–5.0 (–5.1), L = 7.63–8.57, W = 3.92–4.29, Q = 1.78– 2.19
<i>A. peregrina</i>	East Asia, temperate	angiosperms (<i>Quercus</i> spp.)	effused- reflexed / 1.5–3	dominating throughout	26–40 × 7–9.5	(8.0–) 8.1–12.4 (–12.8) × (4.0–) 4.2–5.7 (–6.1), L = 9.18–10.58, W = 4.60–4.87, Q = 2.01– 2.24
<i>A. serpens</i>	Europe, temperate	angiosperms	effused- reflexed / 1–2	dominating throughout	29–38 × 7–9.5	(6.3–) 8.0–12.6 (–14.4) × (2.9–) 3.6–5.3 (–6.0), L = 9.03–11.70, W =

						3.88–4.76, Q = 2.02– 2.58
<i>A. subserpens</i> ²	China	angiosperms	resupinate or effused- reflexed / 1– 2.5	frequent throughout	23–32 × 6.5–8	(6–)6.5–9(–11) × (3.5–) 3.7–4.8(–5.1), L = 7.7, W = 4.2, Q = 1.75–1.94
<i>A. tenerifensis</i>	Macaronesia, subtropical	angiosperms	resupinate, 3–4	occasionally present in subiculum	28–62 × 9–12	(8.2–) 8.3–11.1 (–11.2) × (5.2–) 5.3–7.0, L = 9.84, W = 6.10, Q = 1.62

¹ Based on Kaipper-Figueiro et al. 2016

² Based on Chen and Cui 2016