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Phylogenetic Classification of *Antrodia* and Related Genera Based on Ribosomal RNA Internal Transcribed Spacer Sequences

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Abstract Sequences of ribosomal internal transcribed spacers (ITS) obtained from two *Antrodia* species and two related species were compared to investigate intrageneric and intergeneric phylogenetic relationships of *Antrodia*. The results showed that *Antrodia* species causing a brown rot in wood did not form a monophyletic clade and were separated into three distinct groups. *Antrodia gossypina* and *A. vaillantii* formed a clade having rhizomorphs as a homologous character. *Antrodia serialis*, *A. sinuosa*, and *A. malicola* formed a group together with *Daedalea*, *Fomitopsis*, and *Postia* species with brown rot habit. *Antrodia xantha* with a trimitic hyphal system and amyloid skeletal hyphae formed another distinct clade from other *Antrodia* species. The *Antrodia* species were separated from white rot genera such as *Antrodiella*, *Diplomitoporus*, *Junghuhnia*, and *Steccherinum*, indicating the phylogenetic importance of the rot type in the classification of the Polyporaceae.

Key words: *Antrodia*, brown rot, polyphyly

Antrodia Karsten is a genus that includes species with a dimitic hyphal system with clamped generative hyphae that cause brown rot [9, 25]. The genus *Antrodia* is accepted in the family Polyporaceae, known as a large and artificial family composed of numerous genera with poroid hymenophores. *Antrodia* was established by Karsten who attempted to rearrange resupinate genera into smaller ones [7]. It was converted from *Trametes* trib. *Resupinati* Fr. with *Trametes serpens* as a type species and with three other species of *Antrodia epilobii*, *Antrodia serena*, and *Antrodia mollis* [5]. Later, *A. mollis* was separated into its own genus, *Datronia*. In America, the generic name *Coriolellus* was used instead of *Antrodia* for a long time [5]. Until 1978, *Antrodia* comprised of both brown rot and white rot species. Then, it was restricted to species causing a brown rot in wood by emphasizing differences in the type of rot [9]. Over twenty species are accepted in the genus *Antrodia* in North America and Europe under the above-mentioned genus specifications [9, 25]. Inclusion of fungal species into *Antrodia* is a continuous process where new species have been added [3, 10]. Several authors have also performed cultural studies on *Antrodia* species [1, 9, 20, 26].

Among many genera in the Polyporaceae, *Antrodia* has long been regarded merely as a pragmatic and polyphyletic group. This was due to many variations in both its macromorphological and micromorphological characters such as the basidiocarp margin, spore morphology, amyloidity of hyphae, and sexuality [6, 9, 24, 25]. The genus *Fibroporia* was once suggested for the species *Antrodia vaillantii* due to conspicuous rhizomorphs along the margin [25]. *Antrodia xantha* and *Antrodia carbonica* were once included in the genus *Amyloporia* because they show amyloid reaction in skeletal hyphae [9, 25]. Recently, Roy and De [23] recommended the transfer of *A. xantha* into *Daedalea* since it has a trimitic hyphal system with true binding hyphae. Among the species whose sexuality is known, most have a heterothallic bipolar mating system. However, *Antrodia odora* and *Antrodia radiculosa* (also classified as *Fibroporia radiculosa*) show heterothallic tetrapolarity, and *A. malicola* homothallic sexuality [9, 20].

Among genera of the Polyporaceae, *Antrodiella* and *Diplomitoporus* have been regarded as being closely related to *Antrodia* [4, 9]. These three genera have similar basidiocarps and similar dimitic hyphal systems with clamped generative hyphae. The main difference is the type of rot. While *Antrodiella* and *Diplomitoporus* show white rot activity, *Antrodia* shows brown rot activity only. In terms of the value of the rot type, many differences exist among polypore taxonomists. Nobles [21. 22] first divided the family Polyporaceae into two main groups of extracellular

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oxidase-positive and extracellular oxidase-negative groups that correspond to white rot fungi and brown rot fungi, respectively. Ryvarden [24] also put a significant taxonomic value on the wood rot system and defined genera of the Polyporaceae according to the type of rot. His grouping of polyporoid genera into affinity groups also significantly emphasized the type of rot. Therefore, in defining 11 affinity groups, Ryvarden classified *Antrodia* in the *Daedalea* group together with *Amylocystis*, *Daedalea*, *Auriporia*, *Fomitopsis*, *Gloeophyllum*, *Oligoporus*, *Piptoporus*, and *Stiptophyllum* [9]. On the contrary, Corner [4] did not substantially evaluate the type of rot as much as the hyphal system. He classified *Antrodia*, *Antrodiella*, and *Diplomitoporus* into the *Tyromyces* group together with other genera such as *Anomoporia*, *Ceriporiopsis*, *Flaviporus*, *Oligoporus*, and *Postia*, although he acknowledged that assembling into one *Tyromyces* group might be unnatural. Meanwhile, Jülich [13] classified *Antrodia*, *Antrodiella*, and *Cineromyces* (synonym of *Diplomitoporus*) in the same family Coriolaceae, together with other genera such as *Coriolopsis*, *Datronia*, *Dichomitoporus*, *Funalia*, *Lenzites*, *Pycnoporus*, *Trametes*, *Tinctoporellus*, and *Trichaptum*. However, he mistakingly classified *Antrodia* as a white rotter.

Phylogenetic studies using molecular markers have been applied to various taxonomic situations for solving many taxonomic problems [2, 11, 12, 14-17, 19]. Until recently, only a few papers have been dealing with phylogenetic relationships of *Antrodia* and related genera by using nuclear small subunit rDNA, mitochondrial small subunit ribosomal DNA, or ITS region. In Hibbett and Donoghue's analysis using mitochondrial small subunit rDNA [11], *Daedalea*, *Fomitopsis*, and *Piptoporus* that have di- to trimitic hyphal systems with clamped generative hyphae and cause a brown rot were grouped together. However, *Antrodia* was not grouped with *Daedalea*, *Fomitopsis*, and *Piptoporus*, although it has a same dimitic hyphal system with clamped generative hyphae and a brown rot. In the analysis of Boidin *et al.* [2] based on ITS sequences, *Antrodia* was grouped together with *Oligoporus* and *Fomitopsis* in the order Fomitopsidales that has di- to trimitic hyphal systems with generative hyphae and a brown rot. However, two white rot genera, *Skeletocurtis* and *Ischnoderma*, were also included in the order Fomitopsidales. Yao *et al.* [29] performed phylogenetic analysis by using sequences of the ITS region from various species of *Tyromyces s. l.* Their results verified the polyphyly of *Tyromyces s. l.* and identified three groups that were separated mainly by the type of rot. However, even in their analyses, two *Antrodia* species were not grouped together with other genera, thus leaving the phylogenetic position of *Antrodia* undetermined.

This study focuses on the taxonomic and phylogenetic position of the genus *Antrodia*. Phylogenetic relationships of various species in the Polyporaceae were analyzed and compared by using ITS region sequences. Whether or not *Antrodia* is monophyletic and the identification of genera in the Polyporaceae related to *Antrodia* were investigated. This study showed that species in the genus *Antrodia* had significant sequence dissimilarities and that the genus *Antrodia* was not monophyletic. Also, *Antrodia* was phylogenetically more related to the brown rot genera such as *Daedalea*, *Fomitopsis*, and *Postia* than to the white rot genera such as *Antrodiella*, *Diplomitoporus*, *Junghuhnia*, and *Steccherinum*.

MATERIALS AND METHODS

Source of Strains, DNA Extraction, PCR, and Sequencing

The strains chosen for this study are listed in Table 1 with some information on strain sources and GenBank accession numbers. *Antrodia sinuosa* KCTC 6660, *A. xantha* KCTC 6857, *Diplomitoporus crustulinus* KCTC 16121, and *Postia placenta* KCTC 6846 were newly sequenced in this study. The sequences provided by Dr. Jacques Mugnier were once published [2] but are not submitted to a public database yet. DNA extraction from cultures or herbarium specimens was performed as described previously [15]. ITS region was amplified from extracted total genomic DNA with ITS1 and ITS2 primers [28], which were sequenced by using Top cyclic sequencing kits (Bioneer, Korea) according to the manufacturer's instructions.

Data Analysis

Sequences were aligned by using CLUSTAL W and then visually manipulated to assure maximal alignment. Alignment parameters were set at 10.0 for gap opening penalty, 0.05 for gap extension penalty, 40% for delay divergent sequences, and transitions were weighted. To analyze the data set, most parsimonious trees were found by using PAUP 4.02b [27] on a Macintosh computer. Gaps were treated as missing data. Due to the size of taxa, a heuristic search was performed with simple addition sequence, TBR branch swapping, MAXTREES unrestricted, and MULPARS on. The strength to support the branches of trees was evaluated through 500 replicates of the bootstrap resampling (simple addition sequence, TBR swapping, and MAXTREES unrestricted) [8]. The distance-based tree was constructed by using neighbor-joining algorithm in PAUP 4.02b [27]. Likelihood variance test was also performed to compare a hypothetical tree with the most-parsimonious tree [18].

RESULTS AND DISCUSSION

Phylogenetic analysis yielded 28 equally most-parsimonious trees with 1,323 steps and a consistency index of 0.3681. Among them, one most-parsimonious tree with a maximum likelihood value was selected as the best tree (Fig. 1). The

Table 1. Fungal species, sources, and GenBank accession numbers of ITS sequences of studied taxa.

Species	Source	GenBank accession
Agaricus bisporus (J.E. Lange) Imbach	ATCC[1] 62488	AJ 133385
Antrodia albida (Fr.: Fr.) Donk	D[2] 138	
Antrodia albida (Fr.: Fr.) Donk	K[3] 31056	AJ 006680
Antrodia gossypina (Speg.) Ryv.	D 4785	
Antrodia malicola (Berk. & Curt.) Donk	D 363	
Antrodia serialis (Fr.) Donk	D 439	
Antrodia sinuosa (Fr.) P. Karst.	KCTC[4] 6660	**AF 343318**
Antrodia vaillantii (Fr.) Ryv.	D 3653	
Antrodia xantha (Fr.) Ryv.	D 4406	
Antrodia xantha (Fr.) Ryv.	K 31145	AJ 006681
Antrodia xantha (Fr.) Ryv.	CBS[5] 332.29 (= KCTC 6857)	**AF 343319**
Antrodiella semisupina (Berk. & Curt.) Ryv.	D 812	
Antrodiella fissiformis (Pil.) Gilbn. & Ryv.	NS[6]	
Antrodiella hoehnelii (Bres.: Hohn.) Niem.	D 4690	
Antrodiella onychoides (Egeland) Niem.	K 28681	AJ 006674
Bjerkandera adusta (Willd.: Fr.) P. Karst.	K 31061	AJ 006672
Daedalea dickinsii (Berk.: Cooke) Yasuda	IFO[7] 31163	
Daedalea quercina L.: Fr.	CBS 221.62	
Diplomitoporus crustulinus (Bres.) Dom.	CBS 443.48 (= KCTC 16121)	**AF 343320**
Diplomitoporus lindbladii (Berk.) Gilbn. & Ryv.	K 44271	AJ 006682
Fomitopsis officinalis (Vill.: Fr.) Bond. & Sing.	D 543	
Fomitopsis spraguei (Berk. & Curt.) Gilbn. & Ryv.	D 3000	
Galzinia occidentalis D.P. Rogers	B. & L. 14631	
Hyphoderma setigerum (Fr.) Donk	B. & L. 4522	
Hypochnicium bombycinum (Somm.: Fr.) J. Erikss.	B. & L. 1402	
Hypochnicium erikssonii Hallenb. & Hjort.	B. & L. 4574	
Ischnoderma benzoinum (Wahl.: Fr.) P. Karst.	D 4252	
Ischnoderma resinosum (Fr.) P. Karst.	D 4261	
Junghuhnia fimbriatella (Pk.) Ryv.	D 4203	
Meripilus giganteus (Fr.) P. Karst.	D 3650	
Oligoporus caesius (Schrad.: Fr.) Gilbn. & Ryv.	D 592	
Oligoporus leucomallellus (Murr.) Gilbn. & Ryv.	D 3896	
Oligoporus rennyii (Berk. & Br.) Donk	D 449	
Oligoporus sericeomollis (Romell) Bond.	D 897	
Physisporinus sanguinolentum P. Karst.	D 3977	
Postia balsamea (Peck) Jül.	K 31063	
Postia lactea (Fr.) P. Karst.	K 31143	
Postia placenta (Fr.) Gilbn. & Ryv.	KCTC 6671	
Postia placenta (Fr.) Gilbn. & Ryv.	DSM[8] 3088	
Postia placenta (Fr.) Gilbn. & Ryv.	CBS 384.82 (= KCTC 6846)	**AF 343321**
Postia placenta (Fr.) Gilbn. & Ryv.	D 309	
Ptychogaster rubescens Boud.	CBS 425.86	
Rigidoporus lineatus (Pers.) Ryv.	NS	
Skeletocutis amorpha (Fr.) Kotl. & Pouz.	K 31290	AJ 006677
Spongipellis delectans (Pk.) Murr.	CBS 147.40	
Spongipellis pachyodon (Pers.) Kotl. & Pouz.	D 394	
Steccherinum bourdotii Saliva & David	B. & L. 6562	
Steccherinum ochraceum (Pers.) Gray	B. & L. 3660	
Steccherinum rhois (Schw.) Banker	D 3467	
Trametes versicolor (L.: Fr.) Pil.	CBS 292.33	
Tyromyces chioneus (Fr.) P. Karst.	K 31901	AJ 006676

Sequences of strains without GenBank accession numbers were privately donated by Jacques Mugnier. Accession numbers of four strains sequenced for this study were typed in boldface. [1]American Type Culture Collection. [2]David (private collection). [3]Kew Herbarium. [4]Korean Collection for Type Cultures. [5]Centraalbureau voor Schimmelcultures. [6]Not specified. [7]Institute of Fermentation, Osaka. [8]Deutsche Sammlung von Mikroorganismen und Zellkulturen.

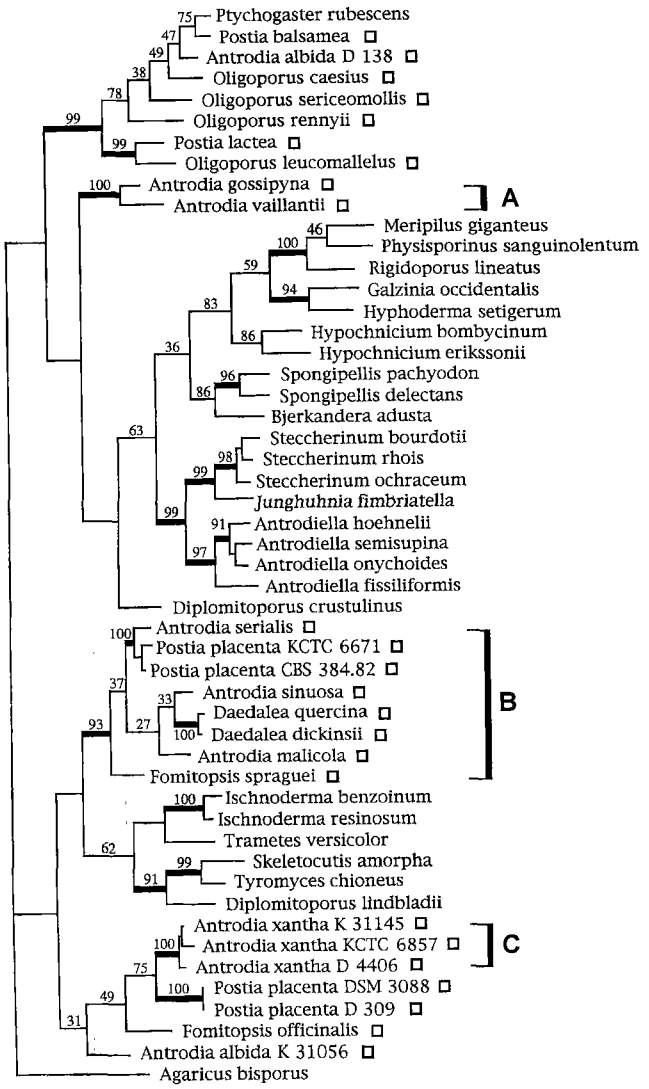

Fig. 1. One of 28 most-parsimonious trees (tree length=1323, CI=0.3681) inferred from nucleotide sequences of ITS regions of *Antrodia* and related genera.
Bootstrap values from 500 replicates are indicated for corresponding branches and bold lines were used for branches supported by more than 90%. Insignificant bootstrap values are not shown. Taxa with squares on the right of species names are all brown rot fungi. *Ptychogaster rubescens* is an anamorph of various species of *Tyromyces s. l.* and is hard to define the type of rot. *Agaricus bisporus* was used as an outgroup taxon for tree rooting.

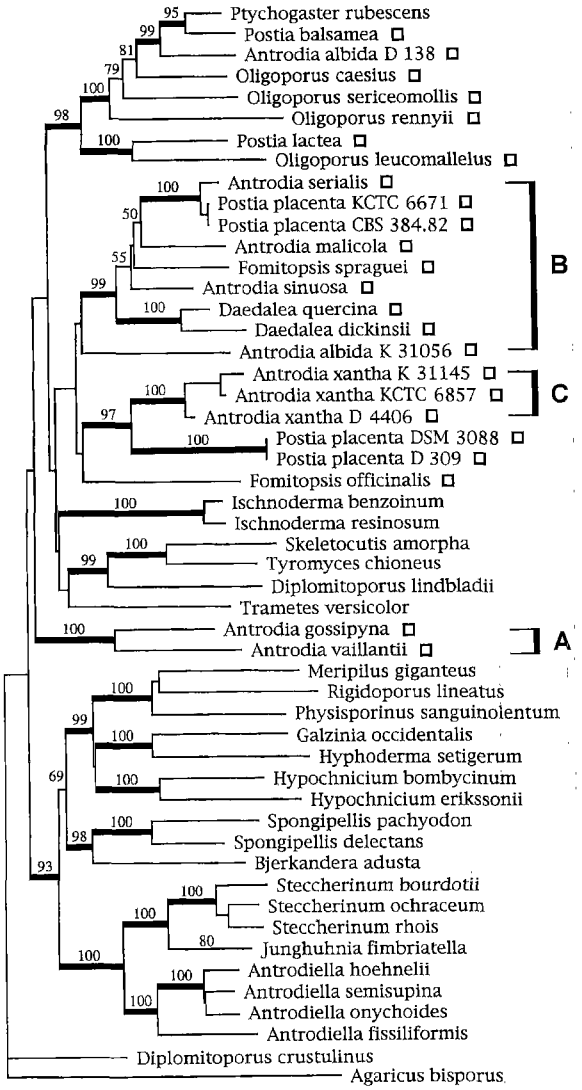

Fig. 2. Neighbor-joining tree based on nucleotide sequences of ITS regions of *Antrodia* and related genera.
Bootstrap values from 500 replicates are indicated for corresponding branches and bold lines were used for branches supported by more than 90%. Insignificant bootstrap values are not shown. Taxa with squares on the right of species names are all brown rot fungi. *Ptychogaster rubescens* is an anamorph of various species of *Tyromyces s. l.* and is hard to define the type of rot. *Agaricus bisporus* was used as an outgroup taxon for tree rooting.

distance-based tree using neighbor-joining algorithm (Fig. 2) produced a generally similar phylogenetic tree to Fig. 1 but developed some differences in order of tree branching. For instance, the group B in the most-parsimonious tree clustered with the *Ischnoderma-Skeletocutis* group (Fig. 1) but was linked to the *A. xantha-Postia-Fomitopsis* group in the neighbor-joining tree (Fig. 2). The position of the group A was significantly different between the most-parsimonious and the neighbor-joining trees. These results partly illustrate that the phylogenetic position of *Antrodia* is quite ambiguous. *Antrodia* species were scattered into three distinct groups that were defined as groups A, B, and, C in this paper. *Antrodia gossypina* and *A. vaillantii* formed the group A, *Antrodia serialis*, *A. sinuosa*, and *Antrodia malicola* formed the group B, and *A. xantha* formed the group C. Two *Antrodia albida* species were separated into two different clades, and four *P. placenta* species were also divided into two different groups.

To discover whether *Antrodia* is monophyletic and whether *Antrodia* is phylogenetically close to the *Antrodiella-Junghuhnia-Steccherinum* group, a hypothetical tree was

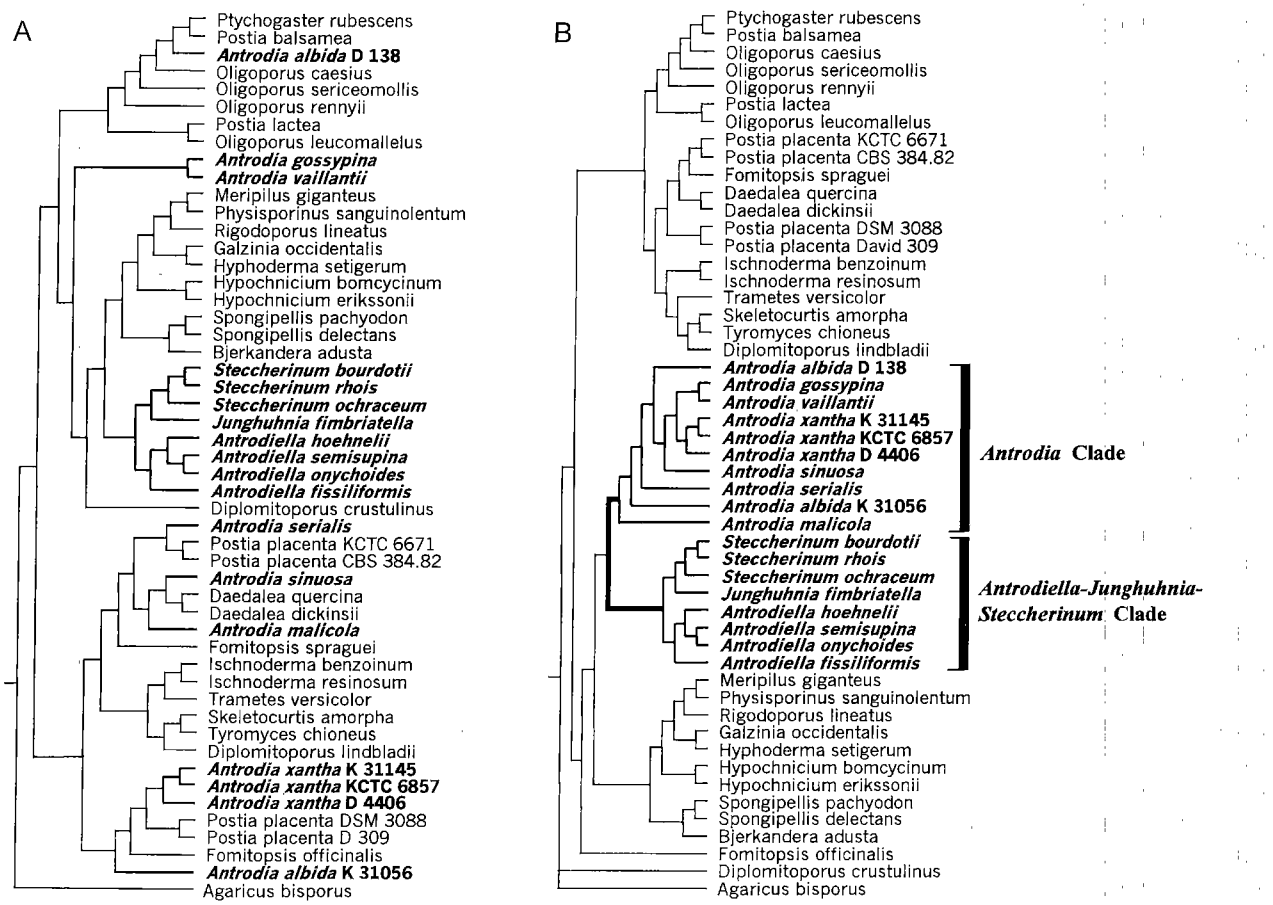

Fig. 3. Hypothetical tree based on the maximum likelihood analysis to test a hypothesis on the phylogenetic relationships of *Antrodia* with *Antrodiella*, *Junghuhnia*, and *Steccherinum*.

Taxa of *Antrodia*, *Antrodiella*, *Junghuhnia*, and *Steccherinum* were typed in bold italics and their branches were made in bold lines. (A) One of 28 equally most-parsimonious trees produced by the heuristic search option of PAUP 4.02b. (B) A constrained tree compelling the *Antrodia* clade to be grouped with the *Antrodiella-Junghuhnia-Steccherinum* clade.

constructed and a maximum likelihood test was performed. The tree was a constrained one in which *Antrodia* species were compelled to be monophyletic and to be grouped with the *Antrodiella-Junghuhnia-Steccherinum* clade (Fig. 3B). The result showed that the *Antrodia* monophyly tree and the *Antrodia-Antrodiella-Junghuhnia-Steccherinum* monophyly tree were worse than the best parsimonious tree by 3.3235 and 8.1557 T values, respectively (Table 2). This result strongly suggests that the genus *Antrodia* with brown rot habit is not related to the *Antrodiella-Junghuhnia-Steccherinum* group with white rot habit and the difference in the type of rot is an important generic character for *Antrodia*. In the phylogenetic trees, genera with a brown rot type such as *Antrodia*, *Daedalea*, *Fomitopsis*, *Oligoporus*, and *Postia* (indicated by squares on the right of species names in Figs. 1 and 2) were divided into four monophyletic groups. Genera with a white rot type such as *Antrodiella*, *Bjerkandera*, *Diplomitoporus*, *Galzinia*, *Hyphoderma*, *Hypochnicium*, *Ischnoderma*, *Junghuhnia*, *Meripilus*, *Physisporinus*, *Skeletocutis*, *Spongipellis*, *Steccherinum*,

Table 2. Results of the maximum likelihood analysis of *Antrodia* and related genera.

Tree	Ln L	Differences	SD[2]	T value[3]	Significantly worse?[4]
Most-parsimony tree	−10691.56235	best	–	–	–
Antrodia monophyly tree	−10770.16119	78.57721	23.64921	3.3235	Yes
Antrodia-Antrodiella-Junghuhnia-Steccherinum monophyly tree	10956.54143	264.91434	32.48211	8.1557	Yes

[1]Difference in log likelihood compared to that of the best tree. [2]The standard deviation of log likelihood. [3]The different value divided by SD. [4]The difference is considered significantly worse if the T value is more than 1.96.

Trametes, and *Tyromyces* were divided into two monophyletic groups. Such a tree topology suggested that both brown rot fungi and white rot fungi might have convergently developed their nutrition mode four times and two times, respectively, during the history of evolution.

Antrodia species were not clustered into one monophyletic group. *Antrodia gossypina* and *A. vaillantii* formed the group A, fully supported by the bootstrap support of 100%. An important common character of the two species is the presence of rhizomorphs in the basidiocarp. Present data support Parmasto's taxonomic viewpoint that separated the genus *Fibroporia* comprising of *A. vaillantii* and *A. gossypina* from *Antrodia*, and phylogenetically contradict Ryvarden's viewpoint that considered the presence of rhizomorphs insufficient for a generic character [24].

Antrodia serialis, *A. malicola*, and *A. sinuosa* formed the group B together with *Postia placenta*, *Daedalea quercina*, *Daedalea dickinsii*, and *Fomitopsis spraguei* that were all brown rotters. Macro- and microscopically, the three *Antrodia* species have some similarities and differences. *Antrodia serialis*, *A. malicola*, and *A. sinuosa* have similar small pore sizes (1–3/mm). However, the spore sizes of *A. malicola* and *A. serialis* (7–10 μm) are larger than those of *A. sinuosa* (4-5.5 μm). *Antrodia malicola* is distinct from other *Antrodia* species by the pale brown color of the basidiocarp and its homothallic sexuality. *A. malicola* is found on dead angiosperms, while *A. serialis* and *A. sinuosa* are found mainly on dead conifers [9, 25].

Three *A. xantha* species did not cluster with other *Antrodia* species and formed its own group C. Previously, *A. xantha* together with *A. carbonica* was elected as a separate genus called *Amyloporia* due to the amyloidity of skeletal hyphae, but Ryvarden insisted that the amyloidity of the spore does not warrant generic separation [24]. It will be quite interesting to investigate by the ITS sequence whether *A. carbonica* is close to *A. xantha*. Roy *et al.* [23], based on an extensive investigation on the hyphal structure, concluded that *A. xantha* had a true trimitic hyphal system and suggested *A. xantha* to be included in the genus *Daedalea*. However, current phylogenetic analysis did not combine *A. xantha* in the *Daedalea* group.

In the phylogenetic tree, two strains of *A. albida*, one strain sequenced by Boidin *et al.* [2] and the other sequenced by Yao *et al.* [29], were distantly separated from each other. *Antrodia albida* K 31056 was placed near the group C by weak bootstrap support (31%), while *A. albida* D 138 belonged to the *Postia-Oligoporus* group by strong bootstrap support (99%). At the present time, we do not know exactly what causes this phenomenon. It might possibly be due to misidentification, mislabeling, genetic heterogeneity of strains, or DNA polymorphism unique to the species. *Antrodia albida* is also conspicuous among *Antrodia* species by having unusually large basidiospores (10–14 μm).

Through the phylogenetic analysis of sequences of the ITS region, genus *Antrodia* was found not to be monophyletic. In conclusion, *Antrodia* was split into three distinct groups. One group was comprised of *A. gossypina* and *A. vaillantii* with rhizomorphs as a common character. *Antrodia serialis*, *A. sinuosa*, and *A. malicola* were included in the second group together with the species of *Daedalea*, *Fomitopsis*, and *Postia*. The third group was *A. xantha* with a trimitic hyphal system as a distinguishing character. *Antrodia albida* was not assigned to any group due to an inconsistency between two studied strains. This study clearly showed that *Antrodia* species were heterogeneous and had to be split into more natural genera. However, it should be mentioned that the current study had many limitations due to the small number of *Antrodia* species investigated. Currently, over 20 species are known in the genus *Antrodia* and only 7 species were included in this study. Better taxonomic classification of *Antrodia* would be possible when the remaining species are sequenced and analyzed together. This study also showed that *Antrodia* was not related to the *Antrodiella-Junghuhnia-Steccherinum* group and enabled to understand the phylogenetic position of *Antrodia* in the family Polyporaceae. However, the closest relative of *Antrodia* could not be identified in the present study, and a further study is needed.

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