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Phylogenetic Relationships of the Polyporaceae Based on Gene Sequences of Nuclear Small Subunit Ribosomal RNAs

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The Polyporaceae is a chaotic mass of genera having poroid hymenophores in the Aphyllophorales. To classify the Polyporaceae into more natural groups, phylogenetic analyses were performed using nuclear small subunit ribosomal DNA sequences. Thirty-six species from the families of the Polyporaceae, the Hymenochaetaceae, the Ganodermataceae, the Corticiaceae, the Bondarzewiaceae, the Meruliaceae, the Steccherinaceae and the Lentinaceae were phylogenetically compared. By performing maximum parsimony analysis, seven phylogenetically meaningful groups were identified and discussed. The hyphal system, presence or absence of clamps, and the type of rot were found as important characters in defining the groups. Each group was phylogenetically significant enough to be a core member of each family when the Polyporaceae was split into smaller and more natural families.

KEYWORDS: Polyporaceae, Nuclear small subunit ribosomal RNA, Phylogeny

The Polyporaceae consists of mushrooms of various shapes from resupinate to stipitate basidiocarps with poroid hymenophores in common and belongs to the Aphyllophorales of the Hymenomycetes in the Basidiomycota (Alexopoulos *et al.*, 1996). In the forest system, the Polyporaceae consists of major wood decayers and has attracted many researchers in both basic and applied areas owing to extensive wood rots (Gilbertson, 1980, 1981; Wainwright, 1992). However, in spite of great interests among researchers, the Polyporaceae is still regarded as the most problematic taxonomic group among basidiomycetes (Alexopoulos *et al.*, 1996). The taxonomic problem of the Polyporaceae is that the family is polyphyletic and heterogeneous. Thus, the Polyporaceae needs to be split into small and homogeneous subgroups.

The polyphyly of the Polyporaceae has been suggested by many researchers (Alexopoulos *et al.*, 1996; Donk, 1964, 1971a, 1971b; Hibbett and Donoghue, 1995; Jülich, 1981; Ryvarden, 1991). The Polyporaceae had no common homologous characters and was merely used as a container of remaining genera not properly assigned to more definite and natural families (Donk, 1964, 1971a; Ryvarden, 1991). As a result, diverse types of macroscopic and microscopic characters occur in this family. All types of fruitbody morphology (resupinate, effused-reflexed, pileate and stipitate) are found in the Polyporaceae. All kinds of hyphal systems including monomitic, dimitic with skeletal hyphae or binding hyphae, and trimitic hyphal systems are encountered in the Polyporaceae. The generative hyphae may be clamped or simple-septate. Both brown and white wood-rotting activities are present, and all three types of sexuality including homothallism, heterothallic bipolarity, and heterothallic tetrapolarity exist in the Polyporaceae (Gilbertson and Ryvarden, 1986, 1987; Ryvarden, 1991; Ryvarden and Gilbertson, 1993, 1994).

Throughout the history of taxonomy of polypores, progresses have been continued to make the Polyporaceae more natural. The main trends were to exclude some small homogeneous groups from the Polyporaceae and make them of their own families. The Albatrellaceae, the Bondarzewiaceae, the Ganodermataceae and the Hymenochaetaceae are typical examples of such families segregated from the Polyporaceae. Another method was to transfer some genera from the Polyporaceae into another families that are related with by microscopic characters. For such examples, there are *Anomoporia* (Hjortstam and Ryvarden, 1987), *Boletopsis, Gloeoporus* and *Schizopora* (Donk, 1971a; Ryvarden, 1991). But, in spite of these improvements, the number of residual genera in the Polyporaceae is still great and the family remains still heterogeneous and artificial.

Recently, two authors have made efforts to split the residual Polyporaceae into smaller and putatively more natural families with common evolutionary background. Jülich (1981) was one of the revolutionary mycologists who boldly rearranged higher-level taxonomic relationships among polyporoid taxa and suggested many new orders and families mainly based on hyphal systems and spore morphology. In his system, the Polyporaceae was scattered among four major groups. Ryvarden (1991) was another mycologist who suggested another kind of phylogenetic relationships for polyporoid taxa. The mitic system, presence or absence of clamps, spore morphology, and the type of rot were main characters used in his

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grouping of polypores. According to him, the Polyporaceae was divided into two parts, 11 groups of high affinity (*Polyporus* group, *Daedalea* group, *Trametes* group, *Laetiporus* group, *Rigidoporus* group, *Tyromyces* group, *Junghuhnia* group, *Perenniporia* group, *Fomes* group, *Nigroporus* group, *Grammothele* group) and residual taxa of uncertain affinity.

Modern taxonomic studies have been greatly influenced by molecular systematics, which have helped in solving many taxonomic problems (Hillis *et al.*, 1996). Fungal systematics also experienced major revolutions through recent molecular studies, and the changes are still in progress (Barr, 1992; Bruns and Szaro, 1992; Swann and Taylor, 1993). Recently, some molecular studies have been performed on the Polyporaceae. Hibbett and Vilgalys (1993) determined partial sequences of nuclear large subunit ribosomal DNA genes from 34 taxa and revealed that *Lentinus sensu stricto* among three monophyletic groups of *Lentinus sensu* Pegler was phylogenetically related to the Polyporaceae. Hibbett and Donoghue (1995) also tried

Table 1. Source of fungal taxa used in the analysis of nuc-ssu RNA gene sequences

Species	Family	Source	GenBank accession
Anomoporia albolutescens (Rom.) Pouz.	Polyporaceae	CBS[a] 337.63 = KCTC[b] 6867	**AF082675**
Antrodia carbonica (Overh.) Ryv. & Gilbn.	Polyporaceae		U59059
Antrodiella americana Ryv.	Polyporaceae	CBS 386.51 = KCTC 6877	**AF082677**
Bjerkandera adusta (Willd. : Fr.) P. Karst.	Polyporaceae		U59061
Bondarzewia berkeleyi (Fr.) Bond. & Sing.	Bondarzewiaceae		U59062
Ceriporia purpurea (Fr.) Donk	Polyporaceae		U59065
Ceriporiopsis subvermispora (Pil.) Gilbn. & Ryv.	Polyporaceae	CBS 525.92	**AF082678**
Coltricia perennis (L. : Fr.) Murr.	Hymenochaetaceae		U59064
Daedalea quercina L : Fr.	Polyporaceae		U59067
Datronia mollis (Sommerf. : Fr.) Donk	Polyporaceae	SFC[c] 941028-38	**AF082669**
Diplomitoporus crustulinus (Bres.) Dom.	Polyporaceae	CBS 443.48 = KCTC 16021	p. c.[d]
Donkiporia expansa (Desm.) Kotl. & Pouz.	Polyporaceae	CBS 299.93 = KCTC 6999	**AF082679**
Fomes fomentarius (L. : Fr.) Kickx.	Polyporaceae		U59069
Fomitopsis pinicola (Swartz : Fr.) P. Karst.	Polyporaceae		U59071
Ganoderma australe (Fr.) Pat.	Ganodermataceae		AF026629
Gloeophyllum sepiarium (Wulf. : Fr.) P. Karst.	Polyporaceae		AF026608
Gloeoporus taxicola (Pers. : Fr.) Gilbn. & Ryv.	Meruliaceae	SFC 950815-16	**AF082682**
Junghuhnia nitida (Pers. : Fr.) Ryv.	Polyporaceae	SFC 949030-7	**AF082685**
Laetiporus sulphureus (Bull. : Fr.) Murr.	Polyporaceae		U59079
Lentinus tigrinus (Bull. : Fr.) Fr.	Lentinaceae		U59098
Melanoporia nigra (Berk.) Murr.	Polyporaceae	CBS 341.63 = KCTC 6848	**AF082684**
Meripilus giganteus (Fr.) P. Karst.	Polyporaceae		U59082
Oligoporus balsameus (Pk.) Gilbn. & Ryv.	Polyporaceae	SFC 910803-6	**AF082684**
Oxyporus latemarginatus (E. J. Durand & Mont.) Dom.	Polyporaceae	ATCC[e] 9408 = KCTC 6661	**AF082670**
Oxyporus sp.	Polyporaceae		AF026616
Perenniporia subacida (Peck) Donk 1	Polyporaceae	ATCC 12241	p. c.
Perenniporia subacida (Peck) Donk 2	Polyporaceae	SFC 941028-8	p. c.
Phaeolus schweinitzii (Fr.) Pat.	Hymenochaetaceae		U59087
Phellinus igniarius (L. : Fr.) Quél.	Hymenochaetaceae		AF026614
Phlebia radiata Fr.	Corticiaceae		AF026649
Polyporus squamosus Hud. : Fr.	Polyporaceae		U59089
Rigidoporus vinctus (Berk.) Ryv.	Polyporaceae	ATCC 32575	**AF082673**
Schizopora paradoxa (Schrad. : Fr.) Donk	Corticiaceae		AF026612
Steccherinum rhois (Schw.) Banker	Steccherinaceae	SFC 941015-47	**AF082680**
Tremella foliacea Fr.	Tremellaceae		L22262
Trichaptum abietinum (Dicks. : Fr.) Ryv.	Polyporaceae		U59097
Wolfiporia cocos (Schw.) Ryv. & Gilbn.	Polyporaceae	ATCC 13490	**AF082671**

Accession numbers of strains previously sequenced and reported by authors (Kim and Jung, 2000) were typed in boldface. The other numbers typed in lightface were those retrieved from GenBank. Strains from CBS and ATCC were mycelial cultures and those from SFC were dried herbarium specimens.

[a]Centraalbureau voor Schimmelcultures.

[b]Korean Collection for Type Cultures.

[c]Seoul National University Fungus Collection.

[d]Personal communication with Mycology Laboratory, School of Biological Sciences, where sequences were obtained.

[e]American Type Culture Collection.

to classify the polyporoid taxa into more natural taxa and investigated 62 species including 28 species belonging to the Polyporaceae *sensu stricto* using mitochondrial small subunit ribosomal DNA (mt-ssu rDNA) sequences. With some limitations, they figured out seven groups, six of which belonged to the Polyporaceae. Hibbett (1996) performed phylogenetic analyses of nuclear small subunit ribosomal DNA (nuc-ssu rDNA) sequences of many genera in the Aphyllophorales. However, his interests were centered on the evolution of group I introns existing in the nuc-ssu rDNA gene without any taxonomic discussion on the Polyporaceae. Hibbett *et al.* (1997) again reported the evolution of basidiocarp morphology using both nuc-ssu and mt-ssu rDNA sequences. Ko *et al.* (1997) carried out molecular phylogenetic studies on eight strains belonging to the genus *Trichaptum* using nuc-ssu rRNA gene sequences. They reported the monophyly of the genus *Trichaptum* and emphasized the relatedness of *Trichaptum* with the Hymenochaetaceae sharing imperforate parenthosomes. Recently, Boidin *et al.* (1998) performed extensive molecular phylogenetic studies on the Aphyllophorales using internal transcribed spacers (ITSs) and suggested many new orders and families based on molecular data. Kim and Jung (2000) also analyzed nuc-ssu rDNA sequences of 81 species from the Aphyllophorales and investigated the phylogenetic relationships between them, but because of the large samplings, their study on the Polyporaceae was limited in phylogenetic analyses and taxonomic discussions.

Although many achievements have been made through recent molecular works, the Polyporaceae remains as a chaotic mass of polyporoid fungi. The main purpose of this study was to settle down taxonomic problems of the Polyporaceae at the family level and split the artificial polyphyletic Polyporaceae into more natural and related small groups. For this purpose, the nuc-ssu rDNA region was chosen. Such a choice for this molecular taxonomic study was based on the report of Hibbett and Donoghue (1995) that the variation of the mt-ssu rDNA region was too great to be utilized at the family level.

Materials and Methods

Sequences and data analysis. Strains chosen for the study are listed in Table 1. All sequences used here were originally reported by Kim and Jung (2000). Among the strains used in the work of Kim and Jung (2000), 36 strains from the Polyporaceae, the Ganodermataceae, the Hymenochaetaceae, the Corticiaceae, the Bondarzewiaceae, the Meruliaceae, the Steccherinaceae and the Lentinaceae were selected to restrict the taxonomic discussions on the Polyporaceae *sensu lato*. Based on the study of Swann and Taylor (1993) who showed that *Tremella foliacea* was a nearby outgroup to homobasidiomycetes, *Tremella foliacea* of the Tremellaceae was used as an outgroup taxon to root the tree. Sequences were initially aligned using CLUSTALW program, manually checked, and relocated to allow maximal alignment. The alignment parameters were 10.0 for gap-opening penalty, 0.05 for gap extension penalty, 40% for delay divergent sequences, and weighted for transitions. To analyze data, most parsimonious trees were sought using PAUP 4.0 (Swofford, 1999) running on a Macintosh computer. Gaps were treated as missing data. Due to the size of taxa, searching was limited to the heuristic search with simple addition sequence, TBR branch swapping, MAXTREES unrestricted, and MULPARS on. To evaluate the strength of support for branches in the parsimonious trees, 100 replicates of bootstrap resamplings (simple addition sequence, TBR swapping, MAXTREES 10) were performed (Felsenstein, 1985).

Results and Discussion

The heuristic search using the stepwise addition option of

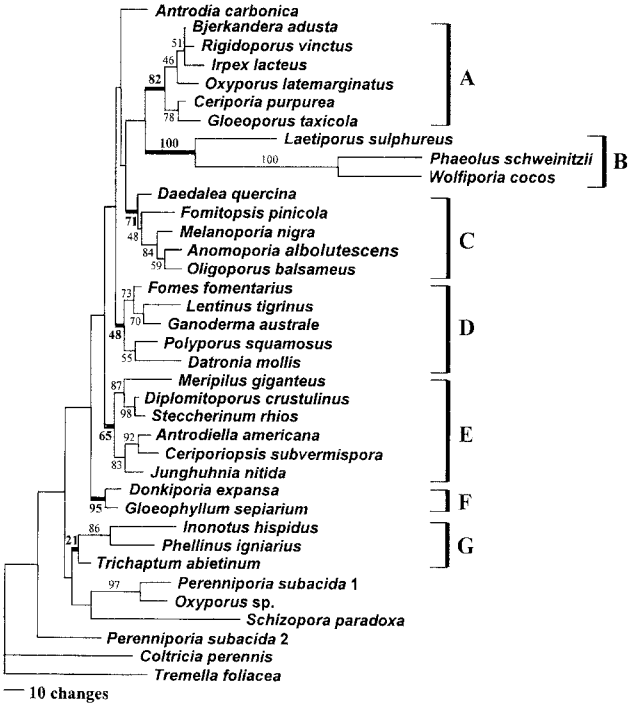

Fig. 1. Most parsimonious tree inferred from the analysis of nuclear small subunit ribosomal RNA gene sequences of 37 taxa. Twenty most parsimonious trees were generated using stepwise addition option of the heuristic method of PAUP 4.0 (Swofford, 1999). *Tremella foliacea* was used as an outgroup to root the tree. This tree is one of most parsimonious trees (tree length = 1050, CI = 0.613). Percentages from 100 bootstrap resamplings are shown at significantly supported or phylogenetically meaningful branches. Bootstrap values for the branches of seven recognized groups were typed in boldface.

PAUP 4.0 yielded 20 most parsimonious trees (tree length = 1050, consistency index = 0.613). Fig. 1 is one of 20 most parsimonious trees with statistical supports for branches from 100 bootstrap resamplings. In the most parsimonious tree, seven distinct groups were identified (A to G in Fig. 1). Among them, *Antrodia carbonica* of the Polyporaceae and *Coltricia perennis* of the Hymenochaetaceae were not assigned to any group.

Group A (bootstrap support 82%) was composed of five species of the Polyporaceae (*Bjerkandera adusta, Ceriporia purpurea, Irpex lacteus, Oxyporus latemarginatus, Rigidoporus vinctus*) and one species of the Meruliaceae (*Gloeoporus taxicola*). In Group B, two species of the Polyporaceae (*Laetiporus sulphureus, Wolfiporia cocos*) and one species of the Hymenochaetaceae (*Phaeolus schweinitzii*) were included by 100% bootstrap support. In Group C, five species of the Polyporaceae (*Anomoporia bombycina, Daedalea quercina, Fomitopsis pinicola, Melanoporia nigra, Oligoporus balsameus*) were included by 71% bootstrap support. Group D (bootstrap support 48%) was composed of three species of the Polyporaceae (*Datronia mollis, Fomes fomentarius, Polyporus squamosus*), one species of the Ganodermataceae (*Ganoderma australe*) and one species of the Lentinaceae (*Lentinus tigrinus*). In Group E (bootstrap support 65%), five species of the Polyporaceae (*Meripilus giganteus, Diplomitoporus crustulinus, Antrodiella americana, Ceriporiopsis subvermispora, Junghuhnia nitida*) and one species of the Steccherinaceae (*Steccherinum rhois*) were included. Group F (bootstrap support 95%) included two species of the Polyporaceae (*Donkiporia expansa, Gloeophyllum sepiarium*) and Group G (bootstrap support 21%) one species of the Polyporaceae (*Trichaptum abietinum*) and two species of the Hymenochaetaceae (*Phellinus igniarius, Inonotus hispidus*).

Six species in Group A have inamyloid, smooth, and hyaline spores and cause white rot in attacked wood. In hyphal systems, *Bjerkandera adusta* has a monomitic hyphal system with clamped generative hyphae, *Ceriporia purpurea, Gloeoporus taxicola* and *Oxyporus latemarginatus* a monomitic hyphal system with simple-septate generative hyphae, but *Irpex lacteus* and *Rigidoporus vinctus* a dimitic hyphal system with skeletal hyphae. Of the species included in Group A, the relatedness among *Ceriporia, Rigidoporus* and *Oxyporus* has been pointed out by several authors (Jülich, 1981; Kim and Jung, 2000; Pouzar, 1966; Ryvarden, 1991). These three genera have the same type of generative hyphae without clamps and cause white rot. *Ceriporia* differs from *Rigidoporus* with tramal cystidia and *Oxyporus* with hymenial cystidia in lacking cystidia. In the phylogenetic analysis of Boidin *et al.* (1998) based on ITS sequences, *Ceriporia* and *Bjerkandera* were grouped together in the order Phanérochaetales. But, in their analysis, *Oxyporus latemarginatus* was grouped in another order Phlébiales contrary to our analysis based on nuc-ssu rDNA sequences. In another analysis using mt-ssu rDNA sequence data, *Oxyporus latemarginatus* was grouped with *Ceriporia* species (Kim and Jung, 1999).

Group B is composed of 3 species with a brown rot activity and simple-septate generative hyphae. Among them, *Phaeolus schweinitzii* has a monomitic hyphal system, while *Laetiporus sulphureus* and *Wolfiporia cocos* have a dimitic hyphal system with skeletal hyphae. The relatedness of *Phaeolus* and *Laetiporus* was already reported and discussed at length by Hibbett and Donoghue (1995) in their analysis using mt-ssu rDNA sequences. According to the classification of Ryvarden (1991), *Laetiporus, Phaeolus* and *Wolfiporia* were grouped together having mono- to dimitic hyphal systems, simple-septate generative hyphae, and brown rot. And current nuc-ssu rDNA data support their monophyletic relationship, although Boidin *et al.* (1998) reported that the position of *Phaeolus* was unstable to be formalized yet.

Group C is composed of *Melanoporia nigra, Fomitopsis pinicola, Anomoporia albolutescens, Oligoporus balsameus* and *Daedalea quercina*. The relatedness of *Fomitopsis, Daedalea* and *Piptoporus* has been suggested by Ryvarden (1991) and was again verified by analysis using mt-ssu rDNA sequence data by Hibbett and Donoghue (1995). In the analysis of (Kim and Jung, 1999) based on mt-ssu rDNA sequence data, *Melanoporia nigra* was connected to the clade of *Fomitopsis pinicola, Daedalea quercina* and *Piptoporus betulina* by a strong bootstrap support. Thus, four species are phylogenetically related by sharing dimitic to trimitic hyphal systems with clamped generative hyphae, perennial or persistent basidiocarps, inamyloid, hyaline, and smooth spores of a thin wall, heterothallic bipolar mating system (unknown for *Melanoporia nigra*) and brown rot activity (Gilbertson and Ryvarden, 1986, 1987). The black and resupinate basidiocarp of *Melanoporia nigra* seems to be a recently acquired autapomorphy useful only in the identification of the species. The inclusion of *Oligoporus balsameus* in Group C is also consistent with the previous taxonomic view based on morphological data (Ryvarden, 1991). *Oligoporus balsameus* treated within the *Daedalea* group by Ryvarden (1991) has a monomitic hyphal system with clamps and causes brown rot. In the analysis of Boidin *et al.* (1998) using ITS sequences, *Oligoporus* species were grouped together with *Antrodia, Fomitopsis, Ischnoderma, Ptychogaster*, and *Skeletocutis*.

Anomoporia albolutescens also has a monomitic hyphal system of clamped generative hyphae and causes brown rot. But, for the assignment of *Anomoporia* in a family, there have been some controversies among taxonomists. Originally, *Anomoporia* was segregated from *Polyporus* due to its amyloid spores but retained in the Polypora-

ceae (Pouzar, 1966). Recently, *Anomoporia* was transferred to the Hericiaceae because of the monomitic hyphal system and amyloid spores (Hjortstam and Ryvarden, 1987; Ryvarden, 1991). On the contrary, *Anomoporia* was grouped to *Tyromyces* by Corner who gave less weight on the significance of the amyloidity of spores (Corner, 1989). Meanwhile, *Anomoporia* was speculated to be related to *Oligoporus* sharing the same types of basidiocarps, mitic systems and wood rot (Gilbertson and Ryvarden, 1986) and also to be a relative of *Gloeocystidiellum* or *Amylonotus* (Gilbertson and Ryvarden, 1986). Current data based on 18S rDNA sequences show that the closest relative of *Anomoporia* is *Oligoporus* differing only in the amyloidity of spores. Although spore amyloidity is a very important and significant character in the classification of Aphyllophorales (Donk, 1964; Hibbett and Donoghue, 1995; Lee and Jung, 1997; Ryvarden, 1991), it has arisen several times independently among many unrelated taxonomic groups (Donk, 1964; Ryvarden, 1991). So, the assignment of *Anomoporia* to the Hericiaceae just because of the spore amyloidity seems to be inappropriate for the present.

Group D is composed of four species of the Polyporaceae and *Ganoderma australe* of the Ganodermataceae. Group D is a quite homogeneous one having dimitic to trimitic hyphal systems, cylindrical spores and a tetrapolar mating system, and causing white rot. This group is comparable to the *Polyporus s. s.* defined and discussed by Hibbett and Donoghue (1995) and corresponds to *Polyporus* and *Trametes* groups defined by Ryvarden (Ryvarden, 1991).

Group E consists of six species, *Diplomitoporus crustulinus*, *Steccherinum rhois*, *Meripilus giganteus*, *Antrodiella americana*, *Ceriporiopsis subvermispora* and *Junghuhnia nitida*. The relatedness among *Diplomitoporus*, *Antrodiella*, *Junghuhnia* and *Steccherinum* has been mentioned by many taxonomists (Donk, 1971a; Jülich, 1981; Ryvarden, 1991; Yu and Niemelä, 1997). *Steccherinum* and related genera share a dimitic hyphal system, smooth, inamyloid, thin-walled, hyaline spores, identical cystidia in most genera, and white rot. In that series were included *Steccherinum* (hydnoid and resupinate), *Irpex* (hydnoid and pileate), *Mycorrhapium* (hydnoid and stipitate), *Junghuhnia* (resupinate and poroid) and *Antrodiella* (pileate and poroid). *Steccherinum* and related genera are one of examples to which taxonomic significance is given on microscopic similarities regardless of macroscopic characters like basidiocarps and hymenophores. However, current data prove that emphases on microscopic characters are phylogenetically adequate.

Ceriporiopsis subvermispora differs from *Junghuhnia nitida* and *Antrodiella americana* by having a monomitic hyphal system and no cystidia, instead of a dimitic one and cystidia of the latter species. But, in other taxa like Group A, the difference in the presence or absence of skeletal hyphae or cystidia is rather common between phylogenetically related species. For this reason, Corner (1989) treated above three genera together with *Anomoporia*, *Antrodia*, *Diplomitoporus*, *Flaviporus* and *Oligoporus* in the same *Tyromyces* group, although he acknowledged that *Tyromyces* in his sense might be polyphyletic. The phylogenetic relatedness of *Ceriporiopsis* to *Antrodiella* has also been shown in a phylogenetic study using mt-ssu rDNA sequences (Kim and Jung, 1999).

Meripilus giganteus has a monomitic hyphal system with simple-septate generative hyphae and was treated in the *Rigidoporus* group along with *Ceriporia*, *Oxyporus* and *Rigidoporus* by Ryvarden (1991). The inclusion of *Meripilus giganteus* in Group E was unexpected and poses some difficulties to explain with appropriate taxonomic criteria. However, Boidin *et al.* (1998) also showed that *Meripilus giganteus* was grouped together with *Antrodiella*, *Junghuhnia* and *Steccherinum*.

The grouping of *Irpex lacteus* in Group A rather than in Group E was an unpredicted result. Many authors pointed out that *Irpex* is related to *Antrodiella*, *Junghuhnia* and *Steccherinum* having a dimitic hyphal system with skeletal hyphae, encrusted cystidia, and causing brown rot (Donk, 1971b; Ryvarden, 1991; Yu and Niemelä, 1997). However, current data did not support this viewpoint but *Irpex lacteus* of Group A was connected to *Rigidoporus*, *Ceriporia* and *Oxyporus* sharing simple-septate generative hyphae and white rot in common.

Group F is composed of two species, *Donkiporia expansa* and *Gloeophyllum sepiarium* of the Polyporaceae. *Donkiporia expansa* and *Gloeophyllum sepiarium* have a trimitic hyphal system with clamped generative hyphae (Gilbertson and Ryvarden, 1986) and brown-colored skeletal hyphae. Main difference is the type of rot. While *D. expansa* develops white rot in attacked wood, *G. sepiarium* causes brown rot. Ryvarden (1991) commented that resupinate *Phellinus* species and *Gloeophyllum* species might be possible relatives as both have brown basidiocarps and brown hyphae in common. But, at the same time, he emphasized the differences between *Phellinus* (with simple-septate generative hyphae) and *Gloeophyllum* (with cylindrical spores, cystidia and brown rot) as contrasted to *D. expansa*. On the taxonomic position of *Gloeophyllum*, Ryvarden (1991) related *Gloeophyllum* to the *Daedalea* group since it has dimitic to trimitic hyphal systems with clamped generative hyphae and brown rot. No molecular data have supported Ryvarden's viewpoint yet (Biodin *et al.*, 1998; Hibbett and Donoghue, 1995). However, molecular data could not tell the phylogenetic position of *Gloeophyllum* affirmatively yet. Although current nuc-ssu rDNA sequence data related *Gloeophyllum* with *Donkiporia*, it is necessary to compare more taxa before coming to a conclusion on the taxonomic position

of *Gloeophyllum*.

Group G is composed of *Inonotus hispidus*, *Phellinus igniarius* and *Trichaptum abietinum*. *Trichaptum* has drawn attention of many taxonomists as a sole genus in the Polyporaceae by having an imperforate parenthosome that used to be found only in the Hymenochaetaceae and in the heterobasidiomycetes (Moore, 1985; Ryvarden, 1991). And this similarity between *Trichaptum* and the Hymenochaetaceae turned out to be an important autapomorphy that was verified by both mt-ssu rDNA (Hibbett and Donoghue, 1995) and nuc-ssu rDNA sequence data (Ko *et al.*, 1997). Recently, fungal ultrastructures such as parenthosomes and spindle pole bodies have been proven to be phylogenetically important characters (Berbee and Taylor, 1995; McLaughlin *et al.*, 1995; Wells, 1994), and more ultrastructural data on various species are being accumulated. So Group G is characterized by species having imperforate parenthosomes in common. The microstructures of the included genera are quite different. *Trichaptum abietinum* has a dimitic hyphal system with clamped generative hyphae, and non-amyloid spores. In the type of rot, *Trichaptum* causes white rot. *Inonotus hispidus* and *P. igniarius* have characters such as setae, xanthochroic reaction and lack of clamps characteristic of the Hymenochaetaceae, and white rot.

Among remaining taxa, Jülich postulated that *Perenniporia* was derived from the *Polyporus* group and commented that it might be related to the Ganodermataceae due to its truncated spore (Jülich, 1981). Other authors (Donk, 1964; Ryvarden, 1991) also suggested relatedness of *Perenniporia* to the Ganodermataceae. However, Donk (1964) pointed out detailed differences between *Perenniporia* and the Ganodermataceae with a conclusion that the two might be unrelated to each other. Recent molecular works have been helpful in distinguishing homologies from homoplasies. Current sequence data also support Donk's concept, suggesting that the proposed relatedness due to truncated spores is regarded as homoplasy that was acquired independently during evolution. In the present study, seven meaningful groups were identified through phylogenetic analyses using nuc-ssu rRNA gene sequences. Micromorphological characters such as hyphal systems, presence or absence of clamps and type of rot were proved to be phylogenetically significant and important.

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