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FULL PAPER

Teruyuki Matsumoto · Yasushi Obatake
Yukitaka Fukumasa-Nakai · Eiji Nagasawa

Phylogenetic position of *Pholiota nameko* in the genus *Pholiota* inferred from restriction analysis of ribosomal DNA

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Abstract To estimate the phylogenetic position of *Pholiota nameko* in the genus *Pholiota*, restriction fragment length polymorphisms (RFLPs) for PCR products of 26S ribosomal RNA gene (rDNA), internal transcribed spacers (ITS), and intergenic spacer (IGS) of the rDNA repeat from *P. nameko* and eight of its closely related species were investigated, and a phylogenetic tree was constructed based on data that resulted from RFLP analysis. *P. nameko* was clustered together with *P. adiposa*, *P. limonella*, and *P. aurivella* of the subgenus *Pholiota* (section *Adiposae*). However, *P. nameko* and *P. albocrenulata*, both of which belong to the subgenus *Hemipholiota*, were phylogenetically separated from each other. Our results suggested that *P. nameko* is closely related to the members of the section *Adiposae*. Furthermore, the phylogenetic distance between this section *Adiposae* group including *P. nameko* and *Kuehneromyces mutabillis* was smaller than that between *P. malicola* var. *macropoda* of the subgenus *Flammula* and the members of section *Adiposae*. Our data indicate that molecular information on rDNA will be useful to reconstruct taxa within the genus *Pholiota* in the family Strophariacea that have been classified mostly on the basis of morphological characters.

Key words Intergenic spacer (IGS) · Internal transcribed spacer (ITS) · PCR-RFLP · Phylogeny · 26S rDNA

T. Matsumoto (✉) · Y. Fukumasa-Nakai · E. Nagasawa
The Tottori Mycological Institute, Kokoge 211, Tottori 689-1125, Japan
Tel. +81-857-51-8111; Fax +81-857-53-1986
e-mail: kin-matu@infosakyu.ne.jp

Y. Obatake
Nara Forest Research Institute, Nara, Japan

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Introduction

Pholiota nameko (T. Ito) S. Ito & Imai (Agaricales, Strophariaceae), with the Japanese common name "Nameko," is one of the most popular edible mushrooms in Japan. It has been known only from eastern Asia, being distributed in Japan, China, Korea, and Taiwan (Arita 1978). The morphological character of the "Nameko" mushroom is unique in the genus *Pholiota* (Fr.) P. Kumm. because of the gelatinous nature of the entire surface of pileus, stipe, and annulus, combined with the absence of pleurocystidia and scales in both pileus and stipe. The taxonomic position of *P. nameko* has been revised several times since the first original description was proposed as *Collybia nameko* by Tokutaro Ito in 1929 (Arita 1978). Hongo (1959) and Singer (1962, 1975, 1986) placed this fungus in the subgenus *Hemipholiota* Singer, section *Myxannulatae* Hongo. On the other hand, Ito (1959) treated this fungus as a member of the genus *Kuhneromyces* Singer & A.H. Smith of the same family, Strophariaceae, and proposed the name *K. nameko* (T. Ito) S. Ito. In addition to the taxonomic status of *P. nameko* as already described, the composition of the genus *Pholiota* is also not well established. Furthermore, taxonomic research on *P. nameko* has been based on the biological and the morphological species concepts, and research based on the concept of the phylogeny on the genus *Pholiota* has not been done.

Recently, the molecular approach has been considered more appropriate to confirm the intergenetic relatedness of species of basidiomycetes, as a method for supporting morphological, physiological, and biochemical characteristics. Many different molecular approaches have been developed for genetic analysis of various groups of organisms. The technique of polymerase chain reaction followed by restriction fragment length polymorphism (PCR-RFLP) analyzing ribosomal DNA (rDNA) has become increasingly popular for the identification and phylogenetic studies of genera or species in many groups of fungi (Vilgalys and Gonzalez 1990; Gardes et al. 1990; Henrion et al. 1994). The coding

regions of the rDNA are usually found in multiple copies with regions that are highly conserved. Furthermore, internal transcribed spacer (ITS) regions and intergenic spacer (IGS) regions, which have high genetic variation, have also been utilized (Hintz et al. 1989; Walsh et al. 1990; Bruns et al. 1991; Vilgalys and Sun 1994; Hibbett et al. 1995; Iraçabal et al. 1995).

Previously, we have determined that no intraspecific variation exists in ITS and IGS regions of rDNA in the natural population of *P. nameko* from Japan (Obatake et al. 2002). In this study, we carried out further analysis of polymorphisms in the rDNA from eight closely related species of *P. nameko* by using PCR-RFLP markers to estimate the phylogenetic position of *P. nameko* in the genus *Pholiota*.

Materials and methods

Isolates used

Thirty-six dikaryotic isolates of *P. nameko* (Matsumoto et al. 1999) and 12 dikaryotic isolates of eight closely related species, *Pholiota adiposa* (Batsch: Fr.) P. Kumm., *Pholiota albocrenulata* (Peck) Sacc., *Pholiota aurivella* (Batsch: Fr.) P. Kumm., *Pholiota limonella* (Peck) Sacc., *Pholiota lubrica* (Pers.: Fr.) Singer, *Pholiota malicola* (Kauffman) A.H. Sm. var. *macropoda* A.H.S. & Hesler, *Pholiota squarrosa* (Weigel: Fr.) P. Kumm., and *Kuehneromyces mutabilis* (Schaeff.: Fr.) P. Kumm. (=*Pholiota mutabilis* (Schaeff.: Fr.) P. Kumm.), preserved at the Tottori Mycological Institute Culture Collection (TMIC), were used in this study (Table 1). Voucher specimens (basidiocarps) from which the isolates were obtained are kept in Tottori Mycological Institute Herbarium (TMI), except for those of TMIC-33651 and -34566.

DNA preparation

Fungal isolates were cultured for 2 weeks at 25°C on MYG liquid medium (2% malt extract, 0.2% yeast extract, and 2% glucose). Mycelia were harvested and lyophilized before DNA extraction. The nuclear DNA was purified from lyophilized mycelia according to the procedure of Fukumasa-Nakai et al. (1992) with RNase treatment and fractionation by centrifugation with cesium chloride.

rDNA-RFLP analysis

The 3′- and 5′-halves of the 26S rDNA, the 5.8S rDNA intervening ITS region, and the IGS region of each isolate were amplified by the primer pairs listed in Table 2, respectively. Primer sequences (Table 2) were based on the known sequence of the rDNA repeat from *Saccharomyces cerevisiae* (Georgiev et al. 1981; Walker and Doolittle 1982; White et al. 1990).

The 50-μl reaction mixture for PCR amplification contained the following: 0.1 μg nuclear DNA, 1× amplification buffer for Ex Taq DNA polymerase (Takara, Kusatsu, Japan), 200 μM deoxynucleoside triphosphates (dNTPs), 0.4 μM each primer, and 0.5 U Ex Taq DNA polymerase. Amplifications were performed in a Mp 100 Thermal cycler (Takara), with an initial denaturation step at 94°C for 3 min, followed by 30 amplification cycles of denaturation at 94°C for 30 s, annealing at 55°C for 30 s, and extension at 72°C for 90 s, and a final extension at 72°C for 10 min. Aliquots (4 μl) of amplification products were electrophoresed through 1.5% (w/v) agarose gels in TBE buffer [0.09 M Tris-borate, 2 mM ethylenediaminetetraacetic acid (EDTA), pH 8.3], stained with ethidium bromide (0.5 μg/l), and visualized on a UV transilluminator.

When fragments of the appropriate size for each target region were obtained, 4-μl aliquots of the PCR products

Table 1. Isolate numbers of *Pholiota nameko* and its related species used in the rDNA PCR-RFLP analysis

Species	TMIC no.[a]	Geographic origin
Kuehneromyces mutabilis	32168	Tottori-shi, Tottori, Japan
Kuehneromyces mutabilis	33651	Vastergotl, Sweden
Pholiota adiposa	31925	Matsumoto-shi, Nagano, Japan
Pholiota adiposa	34566	Hita-shi, Oita, Japan
Pholiota albocrenulata	34031	Saihaku-gun, Tottori, Japan
Pholiota aurivella	30921	Kamikita-gun, Aomori, Japan
Pholiota limonella	30548	Yonago-shi, Tottori, Japan
Pholiota lubrica	30561	Iwami-gun, Tottori, Japan
Pholiota lubrica	30840	Nabari-shi, Mie, Japan
Pholiota nameko	Described previously[b]	Described previously[b]
Pholiota malicola var. *macropoda*	30282	Maniwa-gun, Okayama, Japan
Pholiota malicola var. *macropoda*	30962	Tottori-shi, Tottori, Japan
Pholiota squarrosa	30408	Nakagawa-gun, Hokkaido, Japan

PCR-RFLP, Polymerase chain reaction-restriction fragment length polymorphism
[a] Tottori Mycological Institute Culture Collection number
[b] Matsumoto et al. (1999)

Table 2. Primer name, primer sequence, and location and direction of primer extension used for PCR amplification of rDNA unit of *Pholiota nameko* and its related species

Amplified region	Primer name	Primer sequence (5′ → 3′)	Location and direction of primer extension
ITS	ITS1	TCCGTAGGTGAACCTGCGG	18S rDNA → 3′-end[a]
	ITS4	TCCTCCGCTTATTGATATGC	28S rDNA → 5′-end[a]
5′-half of 26S rDNA	LR0R	ACCCGCTGAACTTAAGC	26–42/25S rDNA → 3′-end[b]
	LR7	TACTACCACCAAGATCT	1448–1432/25S rDNA → 5′-end[b]
3′-half of 26S rDNA	ALR7R	AGATCTTGGTGGTAGGTA	1432–1448/25S rDNA → 3′-end[b]
	LR12	TTCTGACTTAGAGGCGTTCAG	3126–3106/25S rDNA → 5′-end[b]
IGS	LR12R	CTGAACGCCTCTAAGTCAGAA	3106–3126/25S rDNA → 5S rDNA[b]
	M-1	AACCACAGCACCCAGGATTCCC	119–97/5S rDNA → nuclear large rDNA[c]

ITS, internal transcribed spacer; IGS, intergenic spacer
[a] White et al. (1990)
[b] Georgiev et al. (1981)
[c] Walker and Doolittle (1982)

were digested separately with 20 restriction enzymes, *Alu*I, *Ava*II, *Bam*HI, *Bgl*II, *Bsm*I, *Dra*I, *Eco*RI, *Hae*III, *Hha*I, *Hin*cII, *Hin*dIII, *Hin*fI, *Hpa*I, *Msp*I, *Nde*I, *Pst*I, *Rsa*I, *Sac*I, *Taq*I (Nippon Gene, Toyama, Japan), and *Mbo*I (Takara), according to the respective manufacturer's instructions. RFLP analysis of digested DNAs was carried out with a 3% agarose gel.

Phenetic analysis

The presence or absence of reproducible polymorphic bands from PCR-RFLP analysis was scored 1 and 0, respectively. The distance matrix based on a Dice coefficient (Sneath and Sokal 1973) was calculated between pairs of different RFLP phenotypes as $D = 1 - 2(n_{xy})/(n_x + n_y)$ where n_{xy} is the number of shared fragments and n_x and n_y are the number of fragments in the fingerprints of the isolates x and y, respectively. Trees based on this matrix were constructed using the UPGMA (unweighted pair group method algorithm; Sokal and Michener 1958) via the PHYLIP program (Phylogeny Inference Package, version 3.5c; Felsenstein 1994). The tree was drawn with the Treeview (Page 1996) software package.

Results

Amplification of rDNA

A single product 1.4 kb in size resulted from PCR amplification of the 5′-half of 26S rDNA for all isolates examined. Amplification of the 3′-half of 26S rDNA resulted in a single 1.7-kb product for all isolates. As shown in Fig. 1A, slight variation in size of amplification products of the 5.8S rDNA intervening ITS region was observed between species. The fragment sizes varied from 660 to 730 bp. Also, the IGS products, amplified using primers LR12R and M-1, varied from 1.0 to 1.3 kb. Length variations in the IGS amplification products were observed between species but were less frequent within a species (data not shown).

rDNA-RFLP analysis

Of 20 restriction endonucleases, 2 enzymes, *Alu*I and *Nde*II, indicated pertinent restriction sites corresponding to the size of amplification products in every region of rDNA for all isolates examined in this study. In addition, another 2 enzymes, *Hae*III and *Taq*I, also showed recognition sites in all regions of rDNA except for *Hae*III digestions of ITS from two isolates of *K. mutabilis* (TMIC 32168) and *P. squarrosa* (TMIC 30408), and *Taq*I digestions of IGS from 36 isolates of *P. nameko*. Therefore, these 4 enzymes, *Alu*I, *Hae*III, *Nde*II, and *Taq*I, were used for subsequent rDNA-RFLP analysis.

Several RFLPs were observed on the digestion of PCR-amplified DNA from each rDNA region using the four enzymes *Alu*I, *Hae*III, *Nde*II, and *Taq*I as described next. Representative RFLP patterns of the ITS region are shown in Fig. 1B–E. In RFLP analysis for the 5′-half of 26S rDNA of all isolates of nine species by digestion with the endonucleases *Hae*III, *Nde*II, and *Taq*I, 7, 4, and 3 RFLP patterns, respectively, were observed. In analysis for the 3′-half of 26S rDNA, 5 and 2 RFLP patterns were obtained with *Alu*I and *Nde*II, respectively. No RFLPs were shown in restriction digests with *Alu*I for the 5′-half of 26S rDNA and with two enzymes, *Hae*III and *Taq*I, for the 3′-half of 26S rDNA. When RFLPs in each region of 26S rDNA of all the isolates examined were compared by combining the restriction patterns obtained with four enzymes, no RFLP within all 36 isolates of *P. nameko* was shown in both regions of 26S rDNA in addition to the results of ITS and IGS regions described previously (Obatake et al. 2002).

Agreement with the restriction patterns within species was also observed in the 3′-half of 26S rDNA of *P. adiposa*, *P. lubrica*, *P. malicola* var. *macropoda*, and *K. mutabilis*, whereas different restriction patterns within intraspecies were observed in the 5′-half of 26S rDNA of each of these species. The RFLP pattern of *P. nameko* from the 5′-half of 26S rDNA was the same as those of the isolates or species *P. adiposa* TMIC-34566, *P. limonella*, and *K. mutabilis* TMIC-33651. The RFLP pattern of *P. nameko* from the 3′-half of 26S rDNA was also identical with those of the species

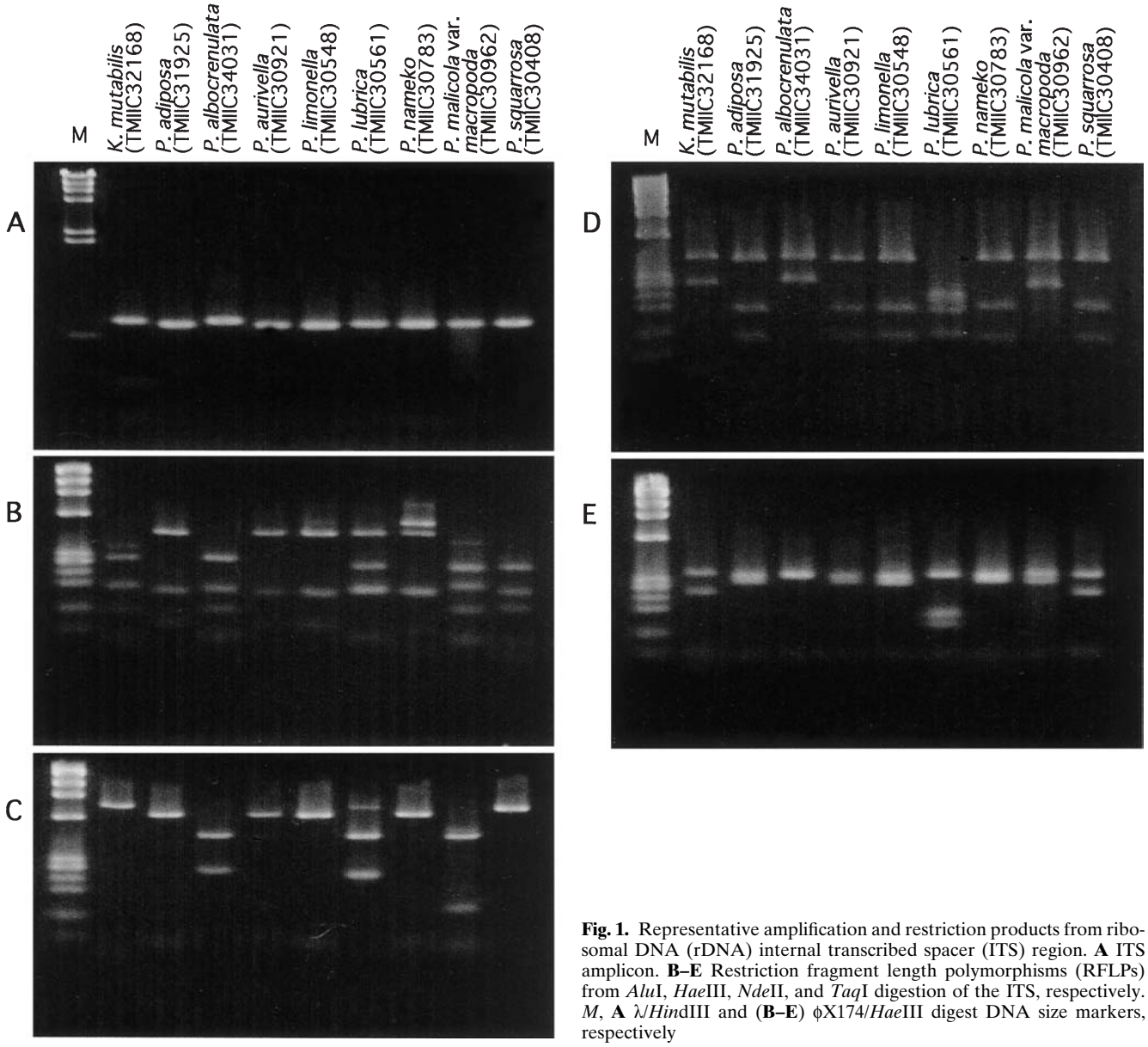

Fig. 1. Representative amplification and restriction products from ribosomal DNA (rDNA) internal transcribed spacer (ITS) region. **A** ITS amplicon. **B–E** Restriction fragment length polymorphisms (RFLPs) from *Alu*I, *Hae*III, *Nde*II, and *Taq*I digestion of the ITS, respectively. *M*, **A** λ/*Hin*dIII and (**B–E**) ϕX174/*Hae*III digest DNA size markers, respectively

P. adiposa, *P. aurivella*, and *P. limonella*. In RFLP analysis of the ITS region of rDNA (Fig. 1B–E) by digestion with the four endonucleases *Alu*I, *Hae*III, *Nde*II, and *Taq*I, 9, 7, 9, and 10 RFLP patterns, respectively, were observed, and in the IGS region of rDNA, 9, 10, 6, and 6 RFLP patterns were obtained by digestion with the four endonucleases *Alu*I, *Hae*III, *Nde*II, and *Taq*I, respectively. These parts of the rDNA allowed resolution of nearly all isolates examined, except for the 36 isolates of *P. nameko*.

Phenetic analysis

Distance values were calculated between all pairs of the RFLP patterns either from only the 26S rDNA region or from the four regions of rDNA examined in this study (data not shown). Lower distance values were generally obtained within each species than between species in both these distance matrixes. Relationships among the nine species examined were revealed by UPGMA cluster analysis (Sokal and Michener 1958) of genetic distances from only the 26S rDNA region (data not shown) and the four regions examined (Fig. 2), respectively. On the dendrogram obtained by analysis of the 26S rDNA information (data not shown), relationships between *P. nameko* and other species primarily agreed with Fig. 2, although *P. nameko* was not distinguished from *P. adiposa* TMIC-34566 and *P. limonella*. The consensus tree based on the four regions of rDNA examined clustered the isolates of *P. nameko*, *P. adiposa*, *P. limonella*, and *P. aurivella* as a most closely related group. This similarity group was a relatively close phenetic relationship to the isolate of *P. squarosa*. *P. albocrenulata* was shown to be most distantly related to *P. nameko* of the eight other species.

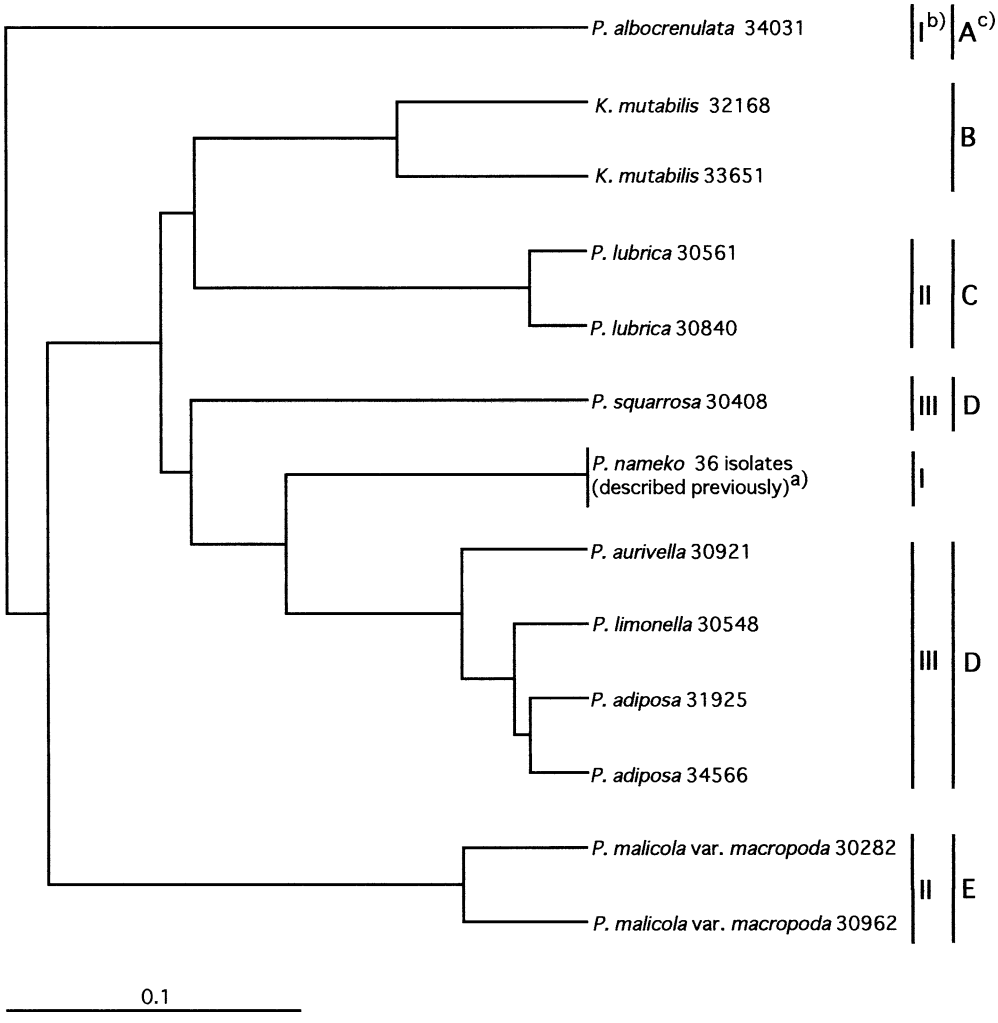

Fig. 2. Unweighted pair group method algorithm (UPGMA) cluster diagram of relationships among all *Pholiota* and *Kuehneromyces* isolates used in this study. The dendrogram is based on genetic dissimilarity coefficients from RFLP patterns for polymerase chain reaction (PCR) products 26S rDNA gene, ITS, and intergenic spacer (IGS) of the rDNA repeat. [a] Matsumoto et al. (1999). [b] Infrageneric position in Singer's (1986) system of the genus *Pholita*: *I*, subgenus *Hemipholiota*; *II*, subgenus *Flammula*; *III*, subgenus *Pholiota*. [c] Infrageneric in Jacobsson's (1990) system of the genus *Pholiota*: *A*, subgenus *Hemipholiota*; *B*, subgenus *Kuehneromyces*; *C*, subgenus *Lubricula*; *D*, subgenus *Pholiota*; *E*, subgenus *Flammula*

Discussion

By the RFLP analysis for 26S rDNA of *P. nameko*, we could confirm that there is no intraspecific variation of this fungus in rDNA following the previous study (Obatake et al. 2002). This result is advantageous in the analysis of the phylogeny target position of *P. nameko* for the rDNA in the genus *Pholiota*.

Cluster analysis (see Fig. 2) based on the RFLPs in the three rDNA regions, 26S rDNA, ITS, and IGS, clearly separated *P. nameko* from other species examined in the genus *Pholiota* and grouped it with *P. adiposa*, *P. aurivilla*, and *P. limonella*, all belonging to the subgenus *Pholiota* (Singer 1962, 1975, 1986; Jacobsson 1990), but not with *P. albocrenulata* of the subgenus *Hemipholiota* (Singer 1986; Jacobsson 1990). Therefore, the results based on molecular information from the rDNA of *P. nameko* suggest that this fungus is phylogenetically more closely related to members of the subgenus *Pholiota* than the subgenus *Hemipholiota*, although it has long been treated as a member of the latter subgenus *Hemipholiota* (Hongo 1959; Singer 1962, 1975, 1986). Ito (1959) proposed transferring *P. nameko* to the genus *Kuehneromyces*, but our result does not support his opinion on the basis of the molecular data presented here (Fig. 2).

The different opinions for an infrageneric classification of the genus *Pholiota* have been discussed. For example, Singer (1951, 1975, 1986) has set the genus *Kuehneromyces* for *K. mutabilis* and some of its allies. On the other hand, Jacobsson (1990), Kuhner (1980), and Noordeloos (1999) proposed that *Kuehneromyces* should be reunited with *Pholiota*. In this study, our results (Fig. 2) showed that the isolates of *K. mutabilis* were grouped with *P. lubrica* of the subgenus *Pholiota*, supporting the opinion proposed by Jacobsson (1990), Kuhner (1980), and Noordeloos (1999).

These results indicate that the previous taxonomic scheme, based mostly on morphological characters, is in need of revision by introducing molecular genetic information. Furthermore, we suppose that PCR-RFLP markers of multiple rDNA regions, such as ITS or IGS and highly conserved regions of 26S or 18S genes, will provide useful information to reevaluate the relationships between taxa in the genus *Pholiota* using species and isolates obtained from many parts of the world.

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