



Taxonomic study of polymorphic basidiomycetous fungi *Sirobasidium* and *Sirotrema*: *Sirobasidium apiculatum* sp. nov., *Phaeotremella translucens* comb. nov. and rediscovery of *Sirobasidium japonicum* in Japan

Muneki Yamada · Rikiya Endoh · Hiroshi Masumoto · Yuma Yoshihashi ·
Moriya Ohkuma · Yousuke Degawa

Received: 17 March 2022 / Accepted: 21 October 2022 / Published online: 3 November 2022
© The Author(s), under exclusive licence to Springer Nature Switzerland AG 2022

Abstract Species in the genera *Sirobasidium* and *Sirotrema* (*Tremellales*, *Tremellomycetes*, *Agaricomycotina*, *Basidiomycota*) have been described based solely on the morphology of teleomorph, and many of them lack both isolates of anamorphic yeast state and nucleotide sequence data. Strains of *Sirotrema translucens* and *Sirobasidium japonicum* were established for the first time from basidiocarps collected in Japan. Also, an undescribed species in the genus *Sirobasidium* was isolated. *Sirobasidium* sp. was characterized by its apiculate epibasidia and 2-celled basidia divided by a longitudinal septum, which is a

unique combination of characteristics in the genus. Although the phylogenetic placement of *Sb. japonicum* within the *Tremellales* was not resolved in our analysis, *Sirobasidium* sp. formed a well-supported monophyletic clade with *Sb. magnum* and *Fibulobasidium* spp., and *Sirotrema translucens* was located in the genus *Phaeotremella*. Mating experiments using single-basidiospore strains showed that *Sb. japonicum* produced basidia, epibasidia, and basidiospores on a nutrient-poor medium, and the life cycle was successfully completed in controlled conditions. In conclusion, we propose *Sirobasidium apiculatum* sp. nov. and *Phaeotremella translucens* comb. nov.

Muneki Yamada Deceased.

Supplementary Information The online version contains supplementary material available at (<https://doi.org/10.1007/s10482-022-01787-9>).

M. Yamada · Y. Yoshihashi · Y. Degawa (✉)
Sugadaira Research Station, Mountain Science Center,
University of Tsukuba, 1278-294 Sugadaira-Kogen,
Ueda, Nagano 386-2204, Japan
e-mail: degawa@sugadaira.tsukuba.ac.jp

R. Endoh · M. Ohkuma
Microbe Division, Collection of Microorganisms (JCM),
RIKEN BioResource Research Center, 3-1-1 Koyadai,
Tsukuba, Ibaraki 305-0074, Japan

H. Masumoto
Graduate School of Global Environmental Studies,
Kyoto University, Yoshida-Honmachi, Sakyo-Ku,
Kyoto 606-8501, Japan

Keywords Basidiomycetous yeasts · Phylogeny ·
Tremellales · *Tremellomycetes* · Taxonomy

Introduction

The genera *Sirobasidium* and *Sirotrema* are basidiocarp-forming fungal taxa belonging to the order *Tremellales* (*Tremellomycetes*, *Agaricomycotina*). The genus *Sirobasidium* is characterized by the morphological characteristics: basidia formed in chains and deciduous primary spores defined as epibasidia (Bandoni 1957). Basidiocarps of *Sirobasidium* spp. usually closely associate with pyrenomycetes, especially *Xylariales*, suggesting that they are mycoparasites (Roberts and Meijer 1997; Chen 1998). A parasitic structure called tremelloid

haustorium (=haustorial branch) is common in the *Tremellales* (Bandoni 1987; Grube and de los Ríos 2001). However, as the structure was reported only one time in the genus *Sirobasidium* (Bandoni 1987; Bandoni et al. 2011), the parasitic nature of *Sirobasidium* species remains unclear. There are around 10 described species in the genus, but only two species have been cultured and few nucleotide sequences data are available. Based on the morphological features, there have been many discussions about the species delimitation or their taxonomic position in higher rank for the species without strains (Dämon and Hausknecht 2002; Roberts and Spooner 1998). For instance, transversally septate basidia of *Sirobasidium japonicum* Kobayasi caused the suspicion that the species is closely related to another order, *Auriculariales* (*Agaricomycetes*; Dämon and Hausknecht 2002).

The other genus, *Sirotrema* is characterized by an occasional formation of basidia in chains and parasitizing rhytismataceous fungi via tremelloid haustoria (Bandoni 1986). Based on its similarity in basidial ontogeny, Bandoni (1986) speculated that *Sirotrema* is a close relative of the genus *Sirobasidium*. Because the genus *Sirotrema* lacks both strains and nucleotide sequence data, the phylogenetic relationship between these two genera has been unknown for years.

In more recent studies, however, the sequences of *Sirobasidium* spp., including those obtained in this study and already published, were added to the dataset of phylogenetic analyses, supporting their attribution to *Tremellales* (Liu et al. 2015; Kachalkin et al. 2019; Li et al. 2020). The sequence of *Sirotrema* obtained in this study has also been included in the above phylogenetic analyses, supporting the attribution to the genus *Phaeotremella* (Kachalkin et al. 2019; Li et al. 2020). On the other hand, information on their morphology, sexual reproduction, and host interactions is not sufficient. In this study, we established strains and intensively observed morphological features of *Sirobasidium japonicum*, one undescribed species of *Sirobasidium*, and *Sirotrema translucens* collected in Japan. Based on the phylogenetic analysis, morphological observations, and physiological characteristics, we discuss the taxonomic status of the species. In addition, mating experiments using single-basidiospore strains were performed for each species, and the results are reported.

Materials and methods

Morphological observations, specimens, and strains

Basidiocarps growing on fallen branches or pine needles were collected in the middle and the southern part of Japan (Table 1). To study microscopic characteristics, handmade sections were mounted in sterile water or 3% (w/v) potassium hydroxide stained with or without phloxine. The sections were observed under a Zeiss Axioskop Microscope (Carl Zeiss, Oberkochen, Germany) or a BX53 upright microscope (Olympus, Tokyo, Japan). For the comparison, a herbarium specimen of *Sirobasidium japonicum* (TNS-F-196751) was observed in the same way. Single-basidiospore isolates of each taxon were established following Wong et al. (1985) using Malt Agar (MA; Nissui, Tokyo, Japan). Morphological features of the anamorphic yeast states were observed according to Kurtzman et al. (2011). Yeast cells for these observations were cultivated on 5% (w/v) malt extract agar (MEA; Kurtzman et al. 2011) at 25 °C for 3 days. Dried specimens of basidiocarps were deposited in the National Museum of Nature and Science, Tokyo (TNS), and strains were in the Japan Collection of Microorganisms (JCM), the Westerdijk Fungal Biodiversity Institute (formerly known as CBS), and the Portuguese Yeast Culture Collection (PYCC) as shown in Table 1.

Physiological tests

Physiological tests of the strains were performed according to Kurtzman et al. (2011). Assimilation of carbon and nitrogen compounds were tested using liquid and solid media, respectively. Growth at various temperatures were tested in YM broth (Difco).

DNA sequencing and phylogenetic analysis

Genomic DNAs were extracted according to Ishida et al. (1999). The D1/D2 region of large subunit ribosomal RNA gene (LSU D1/D2), ITS-5.8S ribosomal RNA gene (ITS), and small subunit ribosomal RNA gene (SSU) were amplified by PCR with Ex Taq (Takara Bio, Otsu, Japan). The LSU D1/D2 was amplified using a primer pair of LR0R (Rehner and Samuels 1994) and LR5 (Vilgalys and Hester 1990), and a pair of ITS1F (Gardes and Bruns 1993) and

Table 1 List of specimens, strains and their sequence depositions

Specimen numbers	Collection site	Collection date	Associated fungus	Strain*	DDBJ/ENA/GenBank accession numbers		
					ITS	LSU D1/D2	SSU
<i>Sirobasidium apiculatum</i>							
TNS-F-66691 ^T	Nishiagina, Amagicho, Oshima-gun, Kagoshima Pref., Japan, 27°46'N 128°57'E	24-Jun-2014	<i>Eutypella scoparia</i>	JCM 32018 ^T (=CBS 14977 ^T)	LC203425	LC203426	LC203427
				JCM 32019 (=CBS 14978)	LC203428	LC203429	LC203430
<i>Sirobasidium japonicum</i>							
TNS-F-66692	Mt. Yonaha, Hiji, Kunigami-son, Kunigami-gun, Okinawa Pref., Japan, 27°46'N 128°57'E	13-Oct-2013	<i>Biscogniauxia capnodes</i>	JCM 32020 (=CBS 14979 =PYCC 6704)	LC203420	LC016573	LC203421
				JCM 32021 (=CBS 14980 =PYCC 6706)	LC203422	LC203423	LC203424
				PYCC 6703	nd [†]	nd	nd
				PYCC 6705	nd	nd	nd
TNS-F-66693	Mt. Nishime, Uka, Kunigami-son, Kunigami-gun, Okinawa Pref., Japan, 26°48'32.364"N 128°16'19.085"E	13-Oct-2013	<i>Biscogniauxia capnodes</i>		nd	nd	nd
TNS-F-66694	Susami, Susami-cho, Nishimuro-gun, Wakayama Pref., Japan, 33°33'36.26"N 135°32'27.99"E	19-Jul-2015	<i>Biscogniauxia</i> sp.		nd	nd	nd
<i>Phaeotremella translucens</i> (= <i>Siro-trema translucens</i>)							
TNS-F-66696	Sugadaira Montane Research Center, University of Tsukuba, Sugadaira-Kogen, Ueda, Nagano Pref., Japan, 36°31'20.7"N 138°21'2.2"E	20-Oct-2014	<i>Lophodermium conigenum</i>	JCM 32022 (=CBS 14981)	LC203431	LC203432	LC203433

Table 1 (continued)

Specimen numbers	Collection site	Collection date	Associated fungus	Strain*	DDBJ/ENA/GenBank accession numbers		
					ITS	LSU D1/D2	SSU
TNS-F-66695	Sugadaira Montane Research Center, University of Tsukuba, Sugadaira-Kogen, Ueda, Nagano Pref., Japan, 36°31'20.7"N 138°21'2.2"E	24-Aug-2014	<i>Lophodermium conigenum</i>	JCM 32023 (=CBS 14982)	LC203434	LC203435	LC203436

*T, holotype or ex-holotype strain; JCM, Japan Collection of Microorganisms, Tsukuba, Japan, CBS, Westerdijk Fungal Biodiversity Institute, Utrecht, the Netherlands, PYCC, Portuguese Yeast Culture Collection, Caparica, Portugal

†nd, not determined

ITS4 (White et al. 1990) was used for the ITS region. For the SSU, a primer pair NS1 (White et al. 1990) and NS8 (White et al. 1990) was used. PCR amplifications were carried out as follows: for the primer pairs LR0R/LR5 and ITS1F/ITS4, initial denaturation at 94 °C for 3 min, followed by 30 cycles of 94 °C for 1 min, 51 °C for 30 s, 72 °C for 1 min, and then final extension at 72 °C for 15 min. For the primer pair NS1/NS8, initial denaturation at 94 °C for 2 min followed by 10 cycles of 98 °C for 10 s, 55 °C for 30 s dropping by 0.5 °C per cycle, and extension at 72 °C for 2 min. Those 10 cycles were followed by 25 cycles of 98 °C for 10 s, 50 °C for 30 s, 72 °C for 2 min. The PCR products were purified by polyethylene glycol precipitation. Sequence reactions containing BigDye terminator v3.1 (Applied Biosystems) and primers, namely LR0R and LR5 for the LSU D1/D2, ITS1F, and ITS4 for the ITS region, and NS1, NS3, NS5, and NS8 for the SSU, were carried out following manufacturer's instructions. DNA sequences were analyzed with ABI PRISM 3130 Genetic Analyzer (Applied Biosystems).

The dataset used for molecular phylogenetic analysis is shown in Table S1. Sequences were aligned using the online version of MAFFT v.7.490 (Kato and Standley 2013; Kato et al. 2019) and ambiguous sites were manually trimmed in SeaView v.5.0.4 (Gouy et al. 2010) after using Gblocks v.0.91b (Castresana 2000), allowing less strict flanking positions. The alignments of three genes (SSU, ITS, and LSU D1/D2) were concatenated in SeaView, and maximum likelihood (ML) analysis was performed using

IQ-TREE v.2.1.2 (Minh et al. 2020). The final alignment comprised of 1480 (SSU), 220 (ITS), and 426 (LSU D1/D2) sites. Among them, 284 (SSU), 89 (ITS), and 173 (LSU D1/D2) sites were parsimony-informative, and 1047 (SSU), 108 (ITS), and 192 (LSU D1/D2) sites were invariable. The concatenated dataset was partitioned by each gene and the best-fit model of nucleotide substitution for each partition based on the Bayesian information criterion (BIC) was estimated by ModelFinder (Kalyaanamoorthy et al. 2017) as implemented in IQ-TREE. The applied substitution models for ML analysis were as follows: TN+I+R3 for SSU, TIM2e+I+I+R3 for ITS, and TIM3e+I+I+R4 for LSU D1/D2. Branch support was assessed using 1,000 replicates of an ultrafast bootstrap approximation approach (Hoang et al. 2018) in combination with a nonparametric Shimodaira–Hasegawa approximate likelihood-ratio test (SH-aLRT). Tree topology was constrained with the well-supported (>85%) bipartitions in the seven-gene-based phylogenetic tree inferred by Li et al. (2020).

Mating experiment of yeast cells

Intraspecific mating experiments were performed to confirm the mating type. In each species, single-basidiospore strains were established from the same basidiocarp. Pairs of the strains were inoculated on conjugation medium (CJM; Flegel 1981) and kept at 25 °C. Method for the inoculation was according to Flegel (1976), and inoculated cells were covered with

flame-sterilized coverslips to reduce yeast cell growth and promote conjugation of yeast cells (Flegel 1981). One month after incubation, mycelia were cut off and inoculated onto weakly nutrient medium (wMY; Spiegel 1990) and kept at 25 °C to promote basidia and basidiocarp production. Those cultivations were directly observed under a light microscope by covering the surface of the media with coverslips, or mounted in phloxine with 3% potassium hydroxide or lacto-cotton blue.

Results and discussion

Isolation and morphological observation

We collected 4 and 2 specimens of *Sirobasidium* and *Sirotrema*, respectively. Their collecting sites, herbarium numbers, and single-basidiospore derived strains are listed in Table 1. According to the morphological

observation, 3 specimens of *Sirobasidium* were identified as *Sb. japonicum* Kobayasi. The other specimen of the genus, however, could not be designated to any previously described species.

In newly collected specimens of *Sirobasidium japonicum*, microscopic features (morphology of basidia, epibasidia, and basidiospores) were fitted with the original description by Kobayasi (1962). Basidiocarps were closely associated with ascomata of *Biscogniauxia* spp. (Table 1; Fig. 1a), which has not been reported before.

Sirobasidium sp. is characterized by the combination of the following features: pulvinate to cerebriform and white to grayish-white basidiocarps associated with *Eutypella scoparia* (Schwein.) Ellis et Everh. (Fig. 2a, b), broadly ellipsoid basidia longitudinally divided to 2-cells (Fig. 2c), fusiform to cylindrical epibasidia apiculate at the tip (Fig. 2d), subglobose basidiospores, which are (8.0–)8.5–10.5 × 7.0–8.5(–9.0) μm (Fig. 2e, f), and

Fig. 1 *Sirobasidium japonicum* (TNS-F-66693; JCM 32020; JCM 32021). **a** Basidiocarp on a fallen branch (arrowhead) associated with *Biscogniauxia capnodes* (arrow). **b** Transversally to obliquely septate, 4-celled basidia in chains. **c** Basidia producing epibasidia. **d** Epibasidia forming a sterigma and a basidiospore. **e** Basidiospores. **f** Yeast cells on 5% MEA, 3 days at 25 °C. **g** Yeast cells of JCM 32020 forming true hyphae with a clamp connection (double-arrowhead) on CJM, 3 days at 25 °C. **h** True hyphae with a clamp connection (double-arrowhead) formed after mating between JCM 32020 and JCM 32021 on CJM, 3 days at 25 °C. **i** Basidia on wMY, after transferring the hyphae formed between the mating on CJM. **j** An epibasidium and a basidiospore formed after the basidial formation on wMY. Bars, **a** 1 cm, **b–j**, 10 μm

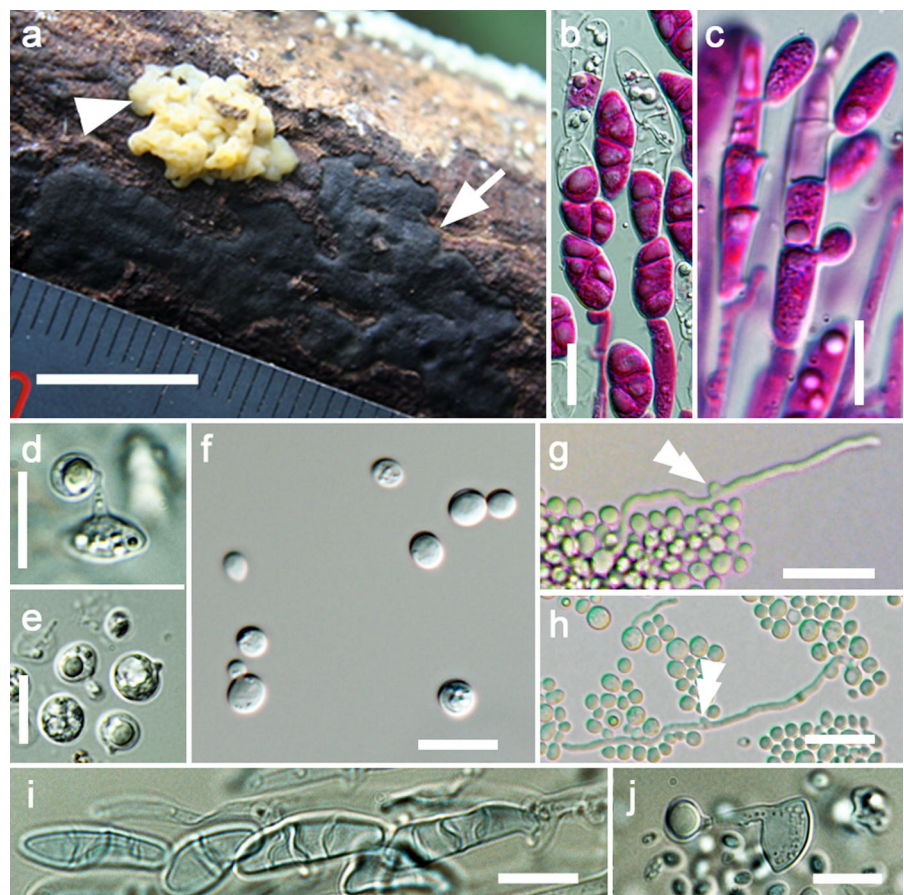
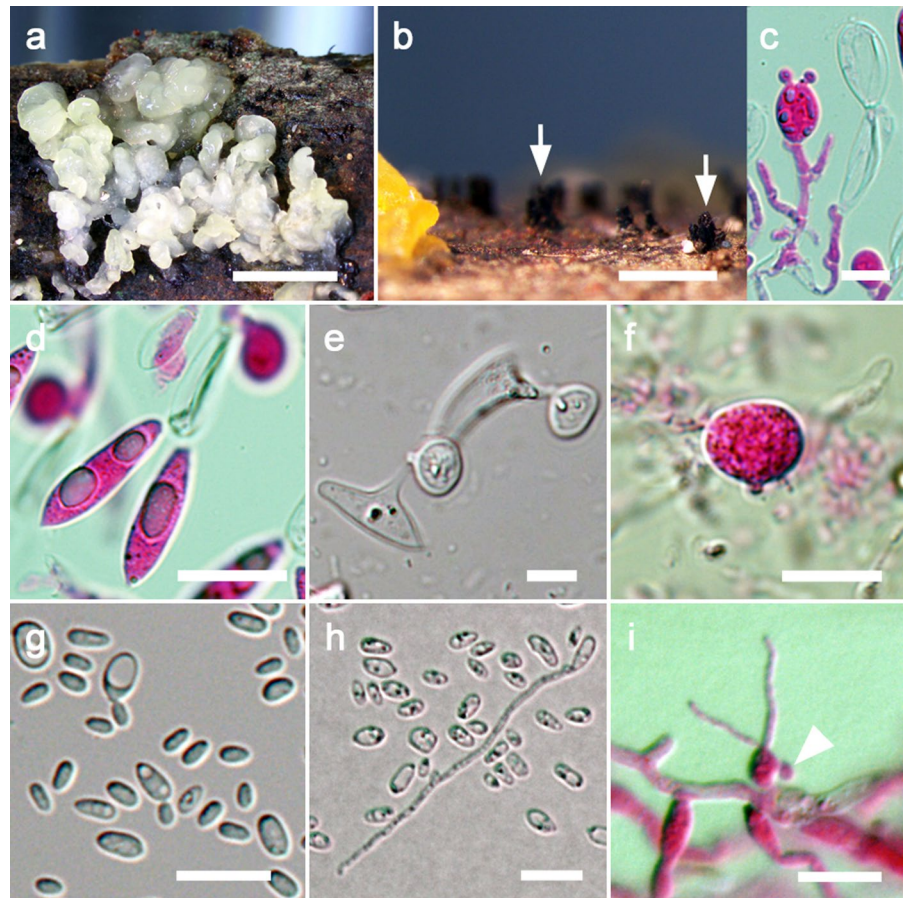


Fig. 2 *Sirobasidium apiculatum* (TNS-F-66691; JCM 32018). **a** Basidiocarp on a fallen branch. **b** Associated fungus, *Eutypella scoparia* (arrows). **c** Two-celled basidia (left) and collapsed basidia in chains (right). **d** Matured epibasidia with apiculate tips. **e** Epibasidia forming sterigmata and basidiospores. **f** Basidiospore. **g** Yeast cells on 5% MEA, 3 days at 25 °C. **h, i** True hyphae with a tremeloid haustorium and basal false clamp (arrowhead) from 3 days cultures on CJM agar. Bars, **a** 5 mm, **b** 1 mm, **c-i** 10 µm



ellipsoid to oblong yeast cells, which are $3.0\text{--}5.5\text{--}(5.8) \times (1.6\text{--})1.7\text{--}3.6\ \mu\text{m}$ (Fig. 2g). The species is similar to *Sb. albidum* Lagerh. et Pat., *Sb. brefeldianum* Möller, *Sb. intermedium* Kundalkar et M.S. Patil, *Sb. minutum* Kisim.-Hor., Oberw. et L.D. Gómez, and *Sb. sandwicense* Gilb. et Adask. (Lagerheim and Patouillard 1892; Möller 1895; Kundalkar and Patil 1986; Gilbertson and Adaskaveg 1993; Van de Put and Antonissen 1995; Kisimova-Horovitz et al. 2000). It can be distinguished from *Sb. albidum* by 2-celled basidia. From the other species, it can be distinguished by apiculate epibasidia and the size of basidia and basidiospores. The last two species (*Sb. minutum* and *Sb. sandwicense*) also resemble *Sb. apiculatum* in having two-celled basidia but differ in that their basidia are divided by an oblique septum, not a longitudinal one.

The specimens of the genus *Sirotrema* were identified as *Sirotrema translucens* (H.D. Gordon) Bandoni. Their basidiocarps parasitized *Lophodermium*

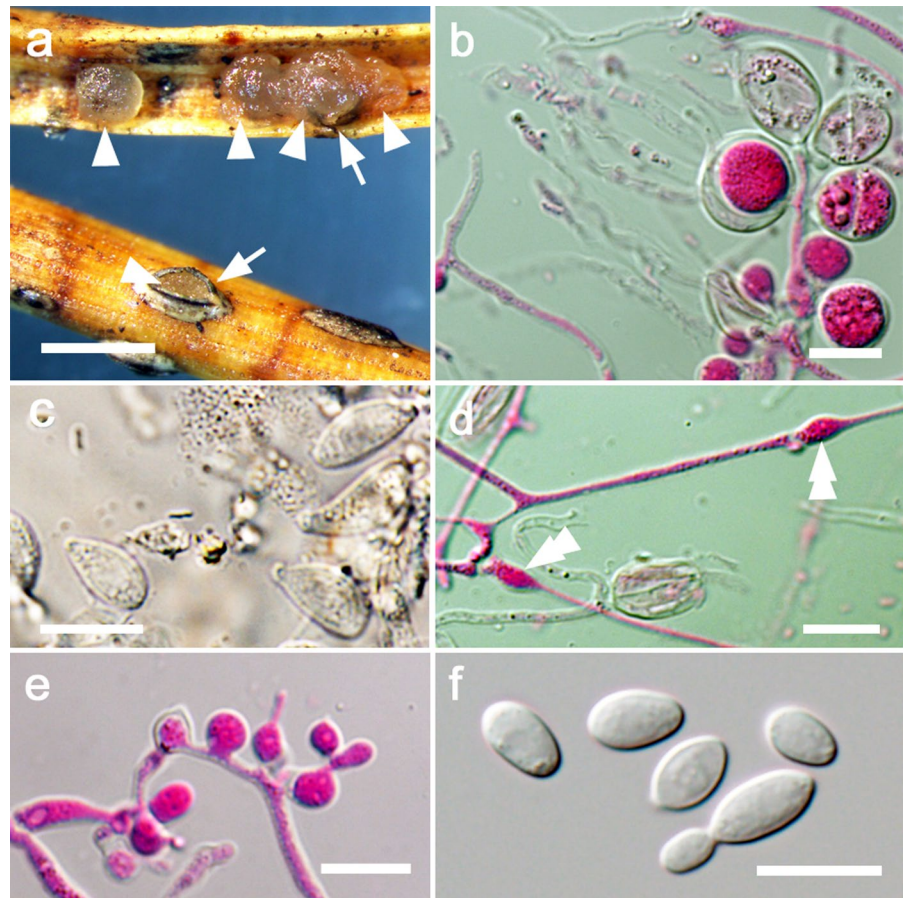
conigenum (Brunaud) Hiltzer growing on fallen needles of Japanese red pine (*Pinus densiflora* Siebold et Zucc.; Fig. 3a). Their microscopic features agreed well with the descriptions by Gordon (1938), Reid and Minter (1979), and Bandoni (1986). Formation of basidia in chains was not detected, which also agreed with observations in the previous studies (Gordon 1938; Reid and Minter 1979).

The descriptions of each species are given in the taxonomy section.

Phylogeny

For the strains of *Sirobasidium japonicum*, *Sirobasidium* sp., and *Sirotrema translucens*, SSU, ITS, and LSU D1/D2 were sequenced (Table. 1). It should be noted that these sequences have already been publicly available for several years and have been added to the dataset of phylogenetic analyses in some studies (e.g., Liu et al. 2015; Kachalkin et al. 2019; Li et al. 2020).

Fig. 3 *Phaeotremella translucens* (TNS-F-66693; JCM 32023). **a** Basidiocarps (arrowheads) growing on *Lophodermium conigenum* (arrows). **b** Basidia. **c** Basidiospores. **d** Swollen nodes near clamp connections (double arrowheads). **e** Tremelloid haustoria. **f** Yeast cells on 5% MEA, 3 days at 25 °C. Bars, **a** 1 mm, **b–f** 10 μ m



In our constrained ML analysis based on a concatenated (SSU-ITS-LSU D1/D2) dataset, *Sirobasidium* sp. (as “*Sb. apiculatum*”) formed a well-supported clade with *Fibulobasidium* spp. (Fig. 4), which is characterized by basidia produced by the expansion of clamp connection and forming cluster (Bandoni 1979), in consistency with previous studies (Kachalkin et al. 2019; Li et al. 2020). In addition, our analysis also agrees with the previous study (Kachalkin et al. 2019) in that *Sb. magnum* was resolved as a monophyletic group with the clade described above (Fig. 4). However, there was no agreement among studies for *Sb. japonicum* and our analysis did not resolve its phylogenetic position within *Tremellales* as in Li et al. (2020), whereas Kachalkin et al. (2019) found *Sb. magnum*, *Sirobasidium* sp., and *Fibulobasidium* spp. formed a moderately supported clade. Further sampling of closely related species and more multiple DNA markers including protein-coding loci will be needed to resolve phylogenetic relationships

of *Sb. japonicum* in *Tremellales*. For *St. translucens* (as “*Phaeotremella translucens*”), there was strong support for its location within the genus *Phaeotremella* (Fig. 4).

Physiological tests

The results of assimilation, fermentation, and other physiological tests were shown in Table 2. All the tested species did not ferment glucose. Two *Sirobasidium* species differed in the assimilation abilities of maltose, raffinose, melezitose, L-arabinose, D-ribose, L-rhamnose, ethanol, methyl- α -D-glucoside, D-glucuronic acid, and *N*-acetyl-D-glucosamine as a sole carbon source.

Mating experiments

As a result of the mating experiments on CJM, 9 tested strains of *Sirobasidium japonicum* formed true

◀**Fig. 4** Maximum-Likelihood (ML) phylogenetic tree of the *Tremellales* and related basidiomycetes, based on the SSU-ITS-LSU (D1/D2) dataset. Tree topology was constrained with the well-supported (>85%) bipartitions in the seven-gene-based phylogenetic tree inferred by Li et al. (2020). Only values of SH-aLRT support $\geq 80\%$ / ultrafast bootstrap support $\geq 95\%$ are shown near by the corresponding node. Sequences obtained in this study are shown in bold. The scale bar represents nucleotide substitution per site

hyphae with clamp connections in all the pairs and single inoculations, but neither basidia nor basidiocarps (Table 3). The hyphae, which germinated from single yeast cells, also had clamp connections (Fig. 1g). Hyphal formation after conjugation of two yeast cells was detected only in some pairs (Table 3; Fig. 1h). After transferring the mycelia to wMY agar plates, basidia (Fig. 1i), epibasidia, and basidiospores (Fig. 1j) were produced from the inoculations in which conjugation of yeast cells was detected on CJM (Table 3). These compatible pairs could be categorized into 4 groups (Table 3), suggesting that the species has a tetrapolar mating system as in *Sb. magnum* and other basidiomycetes (Flegel 1976; Raudaskoski and Kothe 2010).

In *Sirobasidium* sp., we performed a mating experiment using 8 single-basidiospore strains. Conjugation of yeast cells was not detected in all the pairs or single inoculations during one month on CJM or wMY. All the inoculations, however, produced true hyphae with false clamp and tremelloid haustoria (Fig. 2h, i). The results suggest that the true hyphae with false clamps derived from single-cell growth, and the strains would require other conditions to differentiate sexual reproduction.

In *Siotrema translucens*, 8 single-basidiospore strains were crossed. In all the pairs or single inoculations, neither conjugations of yeast cells, formation of basidia nor hyphal growth were detected on both CJM and wMY during one month. As in *Sirobasidium* sp., cultural conditions would not be suitable for the species to induce sexual reproduction.

Taxonomy

The ML analysis demonstrated that *Sirobasidium* sp. is a novel lineage in the order *Tremellales*. Furthermore, as its morphology is different from any species in the genus *Sirobasidium*, a new taxon should

be established. Whereas *Sirobasidium* sp. formed a well-supported monophyletic clade with *Sb. magnum* and *Fibulobasidium* spp., *Sb. japonicum* did not form a monophyletic lineage with other available *Sirobasidium* sequences (i.e., *Sb. intermedium* and *Sb. magnum*). Many studies have shown that *Sb. intermedium* was phylogenetically separated from the other *Sirobasidium* species (e.g., Boekhout et al. 2011; Millanes et al. 2011; Liu et al. 2015; Kachalkin et al. 2019; Li et al. 2020; this study), and thus the genus is polyphyletic. In a phylogenetic tree in Liu et al. (2015), *Sb. intermedium* CBS 7805 formed a clade with another *Sirobasidium* species named *Sb. brefeldianum* AM71. However, since their sequences have the same origin represented by a single isolate (see Millanes et al. 2011), its phylogenetically isolated position needs to be confirmed by new isolates, as pointed out by Boekhout et al. (2011). Unfortunately, the phylogenetic position of the type species of the genus *Sirobasidium*, *Sb. rubrofuscum* (Berk.) P. Roberts (syn. *Sb. sanguineum* Lagerh. et Pat.; Dämon and Hausknecht 2002), is unknown, making it difficult to discuss *Sirobasidium* s. str. Therefore, we here follow the morphological definition of *Sirobasidium* and draw taxonomic conclusions.

Siotrema translucens has been suggested to be related to the genus *Sirobasidium* because its basidia are sometimes formed in chains (Bandoni 1986), but the results of the ML analysis did not support this idea and strongly supported the assignment to the genus *Phaeotremella* (Fig. 4), which was recently emended from the ‘foliacea clade’ recognized in the genus *Tremella* (Liu et al. 2015). In *St. translucens*, both morphological features of teleomorph and physiological traits of anamorph agree with those of the genus *Phaeotremella* (Liu et al. 2015). Therefore, it is reasonable that the species is transferred to the genus *Phaeotremella*.

Description of the species

Sirobasidium apiculatum M. Yamada, Endoh et Degawa sp. nov.

MycoBank No.: MB 821218 (Fig. 2).

Etymology: referring to its apiculate epibasidia.

Basidiocarp gelatinous, pulvinate to cerebriform, 2–4.5 mm in diam., white to grayish-white (Fig. 2a). Basidia basipetally formed in chains, broadly ellipsoid, 13.0–18.0(–21.0) × 8.5–11.5 μ m,

Table 2 Physiological traits of *Sirobasidium japonicum*, *Sirobasidium apiculatum*, and *Phaeotremella translucens*

Physiological test	<i>Sb. japonicum</i>	<i>Sb. apiculatum</i>	<i>P. translucens</i>
<i>Assimilation of carbon source</i>			
Glucose	+	+	+
Galactose	–	w	+
L-Sorbose	w	–	–
Sucrose	+	v	–
Maltose	+	–	s/–
Cellobiose	+	w	–
Trehalose	+	+	+
Lactose	–	–	–
Melibiose	–	–	–
Raffinose	+	–	–
Melezitose	+	–	w/–
Inulin	–	–	–
Soluble starch	–	–	v
D-Xylose	+	+/–	+
L-Arabinose	+	–	–
D-Arabinose	+/s	–/w	+
D-Ribose	+	–	w
L-Rhamnose	+	–	–
Ethanol	+	–	–
Methanol	–	–	–
Glycerol	–	–	–
<i>meso</i> -Erythritol	+/s	–	–
Ribitol	w	s/w	+
Galactitol	w	s	–
D-Mannitol	+	+	+
D-Glucitol	+/w	w	w/–
Methyl- α -D-glucoside	+	–	–
Salicin	w	–	–
Arbutin	+	+	+
Glucono- δ -lactone	+	–/w	+
2-Keto-gluconic acid	+/s	w	w/–
5-Keto-gluconic acid	w/–	w	w/–
DL-Lactic acid	–	–	–
Succinic acid	–	–/w	–
Citric acid	w	–	–
<i>myo</i> -Inositol	–	–	–
D-Glucuronic acid	+	–	+
D-Galacturonic acid	+	–/w	+
D-Gluconic acid	+	w	s/w
D-Glucosamine	w	–	–

Table 2 (continued)

Physiological test	<i>Sb. japonicum</i>	<i>Sb. apiculatum</i>	<i>P. translucens</i>
D-Glucurono lactone	+	+	+ /w
L-Arabinitol	w	–	–
Quinic acid	–	–	–
Saccharic acid	+	+	–
Propyleneglycol	–	–	–
Xylitol	w/–	–	+
<i>N</i> -Acetyl-D-glucosamine	+	–	–
Butane-2,3-diol	–	–	–
Xylo-oligosaccharide	–	–	–
<i>n</i> -Decane	–	–	–
<i>n</i> -Hexadecane	–	–	–
<i>Assimilation of nitrogen source</i>			
Ammonium sulfate	+	+	+
Potassium nitrate	–	–	–
Sodium nitrite	–	–	+
Etylamine hydrochloride	+	+	–
Lysine hydrochloride	+	+	–
Cadaverine dihydrochloride	+	+	–
Creatine	–	–	–
Creatinine	–	–	–
D-glucosamine	+	–	–
Imidazole	–	–	–
<i>Growth at</i>			
25 °C	+	+	+
30 °C	–	+	–
35 °C	–	–	–
<i>Other tests</i>			
Cycloheximide 0.01%	+	–	–
Cycloheximide 0.1%	–	–	–
10% NaCl	–	–	–
Vitamin free	–	–	–
Gelatin liquefaction	–	–	–
Acid production	–	–	–
1% Acetic acid	–	–	–
50% Glucose	–	–	–
Urease	+	+	+
Starch formation	–	–	–
Fermentation (D-Glucose)	–	–	–

Table 2 (continued)

Physiological test	<i>Sb. japonicum</i>	<i>Sb. apiculatum</i>	<i>P. translucens</i>
DBB test	+	+	+

+, Positive; s, slowly positive; w, weakly; –, negative; v, variable

divided 2-cells by a longitudinal septum (Fig. 2c). Epibasidia fusiform to cylindrical, apiculate at the tip, $17.5\text{--}26.0 \times 6.0\text{--}7.0$ μm (Fig. 2d), passively detached from the top of basidia, producing a sterigma from lateral side (Fig. 2e). Basidiospores actively discharged from the tip of sterigmata, subglobose, $(8.0\text{--}) 8.5\text{--}10.5 \times 7.0\text{--}8.5\text{--}(9.0)$ μm (Fig. 2e, f), germinating by budding or repetition. Hyphae with clamp connection, $1.5\text{--}2.5$ μm in diam. in hymenium layer, 3.0 μm in diam. under hymenium layer, anastomoses. After 3 days incubation of the yeast cells on 5% MEA at 25 °C, yeast cells ellipsoid to oblong, $3.0\text{--}5.5$ ($\text{--}5.8$) \times (1.6--) $1.7\text{--}3.6$ μm (Fig. 2g), colony surface shiny, white to cream. Physiological and biochemical characters are shown in Table 2.

Type materials: **holotype** TNS-F-66691 (deposited to the National Museum of Nature and Science, Ibaraki, Japan), JAPAN, Nishiagina, Amagi-cho, Oshima-gun, Kagoshima Pref., $27^{\circ}46'$ N $128^{\circ}57'$ E, 24 Jun 2014, col. M. Yamada. Ex-holotype culture JCM 32018 (=CBS 14977) was established from a basidiospore obtained from a basidiocarp (TNS-F-66691) on a fallen branch of broadleaf tree, associated with *Eutypella scoparia* (Schwein.) Ellis et Everh. A single-basidiospore isolate JCM 32019 (=CBS 14978) was also established from the same basidiocarp.

Notes: Although *Sb. apiculatum* was associated with *Eutypella scoparia*, we could not observe tremelloid haustoria in a basidiocarp. Nevertheless, there are many reports of co-occurrence of sirobasi-diaceous fungus with *Xylariales* (e.g., Chen 1998; Gilbertson and Adaskaveg 1993), but no reports of tremelloid haustoria were there until Bandoni et al. (2011) mentioned the rare formation of them at the interface with associated ascomycetous stroma in *Sb. magnum*. Although tremelloid haustoria were not detected during the observation of the basidiocarp in *Sb. apiculatum*, their formation under the cultural conditions suggests the mycoparasitic nature of the species.

Sirobasidium japonicum Kobayasi, Trans. Mycol. Soc. Japan 4: 29 (1962).

MycoBank No.: MB 339295 (Fig. 1).

Basidiocarps pulvinate to appanate-cerebri-form, white to pale yellow (Fig. 1a). Basidia basipetally formed in chains, cylindrical to ellipsoid, $(15.0\text{--})17.5\text{--}32.5 \times 5.0\text{--}8.0$ μm , divided to 4-cells by transverse to oblique septa (Fig. 1b, c). Epibasidia fusiformis, $(7.5\text{--})9.0\text{--}15.0\text{--}(20.5) \times 4.0\text{--}7.0$ μm , producing a sterigma from lateral side (Fig. 1c, d). Basidiospores globose to subglobose, $4.0\text{--}7.0\text{--}(7.5) \times 3.5\text{--}6.5$ μm , actively discharged from the tip of sterigmata (Fig. 1d, e), germinating by budding or repetition. After 3 days incubation of the yeast cells on 5% MEA at 25 °C, yeast cells globose to subglobose, $(2.5\text{--})3.0\text{--}5.0 \times (2.1\text{--})2.5\text{--}4.2$ μm (Fig. 1f), colony surface shiny, white to cream colour. Physiological and biochemical characters are shown in Table 2.

Materials examined: JAPAN, Nagata, Kumage-gun, Yakushima-cho, Kagoshima Pref., 24 Oct 1961, col. H. Indoh, TNS-F-196751 (holotype); JAPAN, Mt. Yonaha, Hiji, Kunigami-son, Kunigami-gun, Okinawa Pref., $26^{\circ}43'19.3''$ N $128^{\circ}12'54''$ E, alt. 360 m, on a fallen branch of *Alnus japonica* (Thunb.) Steud. var. *formosana* (Burkill) Callier, associated with *Biscogniauxia capnodes* (Berk.) Y.M. Ju et J.D. Rogers, 13 Oct 2013, col. M. Yamada, TNS-F-66692, its compatible single-basidiospore isolates deposited as JCM 32020 (=CBS 14979=PYCC 6704), JCM 32021 (=CBS 14980=PYCC 6706), PYCC 6703, and PYCC 6705; JAPAN, Mt. Nishime, Uka, Kunigami-son, Kunigami-gun, Okinawa Pref., $26^{\circ}48'32.364''$ N $128^{\circ}16'19.085''$ E, alt. 350 m, on a fallen branch of *Styrax japonica* Siebold et Zucc., associated with *Biscogniauxia capnodes* (Berk.) Y.M. Ju et J.D. Rogers, 13 Oct 2013, col. M. Yamada, TNS-F-66693; JAPAN, Susami, Susami-cho, Nishimuro-gun, Wakayama Pref., $33^{\circ}33'36.26''$ N $135^{\circ}32'27.99''$ E, alt. 85 m, on a fallen branch of broadleaf tree, associated with *Biscogniauxia* sp., 19 Jul 2015, col. K. Yamamoto, TNS-F-66694.

Table 3 Reactions in the paired or single inoculations of *Sirobasidium japonicum* on CJM, and those after transferring the mycelium from CJM onto wMY

Strains		Type 1		Type 2		Type 3		Type 4		
		MY1111-02	MY1111-03	MY1111-04	JCM 32020	PYCC 6703	MY1111-06	JCM 32021	MY1111-07	PYCC 6705
Type 1	MY1111-02		+/+	+/+	+/+	+/+	*B	*B	+/+	+/+
	MY1111-03		+/+	+/+	+/+	+/+	*B	*B	+/+	+/+
	MY1111-04			+/+	+/+	+/+	*B	*B	+/+	+/+
Type 2	JCM 32020						*B	*B	+/+	+/+
Type 3	PYCC 6703						+/+	+/+	*B	*B
Type 4	MY1111-06						+/+	+/+	+/+	+/+
	JCM 32021								+/+	+/+
	MY1111-07								+/+	+/+
	PYCC 6705								+/+	+/+
Single inoculations		+/+	+/+	+/+	+/+	+/+	+/+	+/+	+/+	+/+

Left, reactions of inoculated yeast cells on CJM; right, reactions of the mycelium transferred from CJM onto wMY. +, true hyphae with clamp connections; *, true hyphae from conjugated yeast cells; B, formation of basidia and basidiospores. All the strains were derived from a single basidiocarp (TNS-F-66692)

Notes: Sirobasidium japonicum had been reported only from Yakushima, Kagoshima, Japan and Jianfengling, Hainan, China (Kobayasi 1962; Peng and Liu 1992), and this is the first report of the isolates and their nucleotide sequence data. The type material was deposited in the TNS herbarium, but its number was not mentioned in the original description (Kobayasi 1962). We found one specimen of *Sb. japonicum* numbered TNS-F-196751. Although the collection date (24. Oct. 1961) was one day earlier than that of the description (Kobayasi 1962), the other data (locality and collector) were identical. In the specimen, any basidiospores were not found, however, basidia (22–32 × (3.0–)5.0–7.0 μm) and epibasidia (10.5–13.0 × 4.0–6.0 μm) were observed and corresponded to those in the original description (Kobayasi 1962). As a result, it is reasonable to regard the specimen (TNS-F-196751) as the type material.

Phaeotremella translucens (H.D. Gordon) M. Yamada, Endoh et Degawa *comb. nov.*

Mycobank No.: MB 821219 (Fig. 3).

Basionym: *Tremella translucens* H.D. Gordon, Transactions of the British Mycological Society 22 (1–2): 111 (1938); MB 280499.

≡ *Pseudostypella translucens* (H.D. Gordon) D.A. Reid et Minter, Transactions of the British Mycological Society 72 (2): 345 (1979); MB 321880.

≡ *Sirotrema translucens* (H.D. Gordon) Bandoni, Canadian Journal of Botany 64 (3): 674 (1986); MB 103818.

Basidiocarps pulvinate, translucent, 0.5–1.0 mm in diam., 0.5 mm high (Fig. 3a). Basidia spherical, 4-celled with longitudinal septa (tremelloid), 9.0–11.0(–13.0) × 8.0–10.0 μm, formed singly or in cluster at the tip of hyphae (Fig. 3b). Basidiospores ovoid, (3.5–)4.0–5.5 × (7.0–)8.0–11.0 μm (Fig. 3c), germinating by budding. Hyphae 1.0 μm in diam., lack vesicles and swollen cells (sensu Chen 1998), with clamp connections, bearing tremelloid haustoria (Fig. 3e). In some cases, hyphae swollen up to 4.5 μm beside clamp connections (Fig. 3d). After 3 days on 5% MEA at 25 °C, yeast cells ellipsoid to oblong, 4.9–8.3(–9.2) × (2.8–)3.0–5.0(–5.3) μm (Fig. 3f), colony surface dull, pale orange. Physiological and biochemical characters are shown in Table 2.

Materials examined: JAPAN, Sugadaira Montane Research Center (now as Sugadaira Research Station), University of Tsukuba, Sugadaira-Kogen, Ueda, Nagano Pref., 36°31'20.7"N 138°21'2.2"E, alt.

1327 m, on fallen leaves of *Pinus densiflora* Siebold et Zucc., associated with *Lophodermium conigenum* (Brunaud) Hiltzer, 24 Aug 2014, col. M. Yamada, TNS-F-66695; JAPAN, Sugadaira Montane Research Center, University of Tsukuba, Sugadaira-Kogen, Ueda, Nagano Pref., 36°31'20.7"N 138°21'2.2"E, alt. 1327 m, on fallen leaves of *Pinus densiflora* Siebold et Zucc., associated with *Lophodermium conigenum* (Brunaud) Hiltzer, 20 Oct 2014, col. M. Yamada, TNS-F-66696, its single-basidiospore isolates deposited as JCM 32022 (=CBS 14981) and JCM 32023 (=CBS 14982).

Notes: The formation of basidia in chains was not detected in the specimen examined, which is consistent with some previous reports (Gordon 1938; Reid and Minter 1979). Bandoni (1986) indicated the different frequencies of basidia in chains among collections. These inconsistent observations suggest that the formation of basidia in chains is an unstable characteristic. In the genus *Sirotrema*, *St. parvula* Bandoni and the type species *St. pusilla* Bandoni have been described in addition to this species (Bandoni 1986). It is necessary to establish these cultures in the future to determine if these two species are also placed in the genus *Phaeotremella*, as is the case with the here examined species.

In the genus *Phaeotremella*, many species are known to be parasitic on *Stereaceae* (*Russulales*, *Agaricomycotina*, *Basidiomycota*), and *P. mycetophiloides* (Kobayasi) Millanes et Wedin, *P. mycophaga* (G.W. Martin) Millanes et Wedin, and *P. simplex* (H.S. Jacks. et G.W. Martin) Millanes et Wedin are also known as mycoparasites other than *P. translucens*. They parasitize basidiomycetous hosts, *Aleurodiscus* spp. (Kobayasi 1939; Martin 1940; Bandoni and Ginns 1993) and have hyphal swellings near clamp connections similar to *P. translucens* (Bandoni and Ginns 1993). This analysis revealed that the genus includes *S. translucens*, with an ascomycete host (*Lophodermium*) for the first time. While phylogenetic relationships of the mycoparasitic species in the genus are still not clear, this character appears to be common to the mycoparasitic taxa in the genus.

Acknowledgements This manuscript was almost drafted by Muneki Yamada, a young talented and personable postgraduate student who had an enthusiasm for the study of fungi, especially *Tremellomycetes*, although he sadly passed away at the age of 25 by an unexpected accident on 20 May 2017. We are very grateful to the members of the Laboratory of Mycology,

Sugadaira, Dr. Takamichi Orihara (KPM), Dr. Kyohei Watanabe (KPM), Dr. Mitsuru Moriguchi of Okinawa University, Dr. Yusuke Takashima, and Dr. Kohei Yamamoto for providing specimens and support in sampling. We would like to thank Dr. Tsuyoshi Hosoya (TNS) for his kind support by loaning a specimen.

Authors' contribution MY and YD designed the study; MY performed field sampling, isolation of the fungi, morphological observation, molecular characterization, and wrote the original draft; HM and YY performed phylogenetic analysis; MY and RE performed phenotypic characterization; YD, RE, MO, and HM edited the original draft; YD and MO supervised the study. All authors approved the final manuscript.

Funding This study was partially funded by JSPS KAKENHI Grant Number 15K18720 to RE and 19H03281 to YD.

Ethical approval This article does not contain any studies with human and animals.

Competing interests The authors declare no competing interests.

References

- Bandoni RJ (1957) The spores and basidia of *Sirobasidium*. *Mycologia* 49:250–255. <https://doi.org/10.2307/3755633>
- Bandoni RJ (1979) *Fibulobasidium*: a new genus in the Sirobasidiaceae. *Can J Bot* 57:264–268. <https://doi.org/10.1139/b79-036>
- Bandoni RJ (1986) *Sirotrema*: a new genus in the Tremellaceae. *Can J Bot* 64:668–676. <https://doi.org/10.1139/b86-085>
- Bandoni RJ (1987) Taxonomic overview of the Tremellales. *Stud Mycol* 30:87–110
- Bandoni RJ, Ginns J (1993) On some species of *Tremella* associated with Corticiaceae. *Trans Mycol Soc Japan* 34:21–36
- Bandoni RJ, Sampaio JP, Boekhout T (2011) *Sirobasidium* de Lagerheim and Patouillard (1892). In: Kurtzman C, Fell JW, Boekhout T (eds) *The Yeasts, a Taxonomic Study*, 5th edn. Elsevier Science, Amsterdam, pp 1545–1548. <https://doi.org/10.1016/B978-0-444-52149-1.00129-4>
- Boekhout T, Fonseca Á, Sampaio JP, Bandoni RJ, Fell JW, Kwon-Chung KJ (2011) Discussion of teleomorphic and anamorphic basidiomycetous yeasts. In: Kurtzman C, Fell JW, Boekhout T (eds) *The Yeasts, a Taxonomic Study*, 5th edn. Elsevier, Amsterdam, pp 1339–1372. <https://doi.org/10.1016/B978-0-444-52149-1.00100-2>
- Castresana J (2000) Selection of conserved blocks from multiple alignments for their use in phylogenetic analysis. *Mol Biol Evol* 17:540–552. <https://doi.org/10.1093/oxfordjournals.molbev.a026334>
- Chen CJ (1998) *Morphological and molecular studies in the genus Tremella*. Schweizerbart Science Publishers, Stuttgart, Germany. ISBN 9783443590765

- Dämon W, Hausknecht A (2002) First report of a *Sirobasidium* species in Austria, and a survey of the Sirobasidiaceae. *Osterr Z Pilzkd* 11:133–151
- Flegel TW (1976) Conjugation and growth of *Sirobasidium magnum* in laboratory culture. *Can J Bot* 54:411–418. <https://doi.org/10.1139/b76-040>
- Flegel TW (1981) The conjugation process in the jelly fungus *Sirobasidium magnum*. *Can J Bot* 59:929–938. <https://doi.org/10.1139/b81-127>
- Gardes M, Bruns TD (1993) ITS primers with enhanced specificity for basidiomycetes-application to the identification of mycorrhizae and rusts. *Mol Ecol* 2:113–118. <https://doi.org/10.1111/J.1365-294x.1993.Tb00005.X>
- Gilbertson R, Adaskaveg J (1993) Studies on wood-rotting basidiomycetes of Hawaii. *Mycotaxon* 49:369–397
- Gordon HD (1938) *Tremella translucens*, a new species on dead pine needles. *Trans Br Mycol Soc* 22:107–112. [https://doi.org/10.1016/S0007-1536\(38\)80009-7](https://doi.org/10.1016/S0007-1536(38)80009-7)
- Gouy M, Guindon S, Gascuel O (2010) SeaView Version 4: A multiplatform graphical user interface for sequence alignment and phylogenetic tree building. *Mol Biol Evol* 27:221–224. <https://doi.org/10.1093/molbev/msp259>
- Grube M, de los Ríos A (2001) Observations on *Biatoropsis usnearum*, a lichenicolous heterobasidiomycete, and other gall-forming lichenicolous fungi, using different microscopical techniques. *Mycol Res* 105:1116–1122. <https://doi.org/10.1017/S0953756201004610>
- Hoang DT, Chernomor O, Von Haeseler A, Minh BQ, Vinh LS (2018) UFBoot2: improving the ultrafast bootstrap approximation. *Mol Biology Evol* 35:518–522. <https://doi.org/10.1093/molbev/msx281>
- Ishida K, Green BR, Cavalier-Smith T (1999) Diversification of a chimaeric algal group, the Chlorarachniophytes: phylogeny of nuclear and nucleomorph small-subunit rRNA genes. *Mol Biol Evol* 16:321–331. <https://doi.org/10.1093/oxfordjournals.molbev.a026113>
- Kachalkin AV, Turchetti B, Inácio J, Carvalho C, Mašínová T, Pontes A, Röhl O, Glushakova AM, Akulov A, Baldrian P, Begerow D, Buzzini P, Sampaio JP, Yurkov AM (2019) Rare and undersampled dimorphic basidiomycetes. *Mycol Prog* 18:945–971. <https://doi.org/10.1007/s11557-019-01491-5>
- Kalyaanamoorthy S, Minh BQ, Wong TK, Von Haeseler A, Jermiin LS (2017) ModelFinder: fast model selection for accurate phylogenetic estimates. *Nat Methods* 14:587–589. <https://doi.org/10.1038/nmeth.4285>
- Katoh K, Standley DM (2013) MAFFT multiple sequence alignment software version 7: improvements in performance and usability. *Mol Biol Evol* 30:772–780. <https://doi.org/10.1093/molbev/mst010>
- Katoh K, Rozewicki J, Yamada KD (2019) MAFFT online service: multiple sequence alignment, interactive sequence choice and visualization. *Brief Bioinform* 20:1160–1166. <https://doi.org/10.1093/bib/bbx108>
- Kisimova-Horovitz L, Oberwinkler F, Gómez LD (2000) Basidiomycetes resupinados de Costa Rica. Especies nuevas o raras de Atractiellales (Auriculariales s.l.), Exidiaceae, Sirobasidiaceae y Tremellaceae *Rev Biol Trop* 48:539–554. <https://doi.org/10.15517/rbt.v48i2-3.18823>
- Kobayasi Y (1939) On the genus *Tremella* and its allies from Japan. *Sci Rep Tokyo Bunrika Daigaku Sect B* 4:1–26
- Kobayasi Y (1962) Revision of *Sirobasidium*, with description of a new species found in Japan. *Trans Mycol Soc Japan* 4:29–34
- Kundalkar B, Patil M (1986) Study of sirobasidiaceous fungi from India. *Indian Phytopathol* 39:356–360
- Kurtzman CP, Fell JW, Boekhout T, Robert V (2011) Methods for isolation, phenotypic characterization and maintenance of yeasts. In: Kurtzman CP, Fell JW, Boekhout T (eds) *The Yeasts, a Taxonomic Study*, 5th ed. Elsevier Science, Amsterdam, pp 87–110. <https://doi.org/10.1016/B978-0-444-52149-1.00007-0>
- Lagerheim MM, Patoouillard N (1892) *Sirobasidium*, nouveau genre d'hyménomycètes Hétérobasidiés. *J De Botanique* 6:465–469
- Li AH, Yuan FX, Groenewald M, Bensch K, Yurkov AM, Li K, Han PJ, Guo LD, Aime MC, Sampaio JP, Jindamorakot S, Turchetti B, Inacio J, Fungsin B, Wang QM, Bai FY (2020) Diversity and phylogeny of basidiomycetous yeasts from plant leaves and soil: Proposal of two new orders, three new families, eight new genera and one hundred and seven new species. *Stud Mycol* 96:17–140. <https://doi.org/10.1016/j.simyco.2020.01.002>
- Liu XZ, Wang QM, Göker M, Groenewald M, Kachalkin AV, Lumbsch HT, Millanes AM, Wedin M, Yurkov AM, Boekhout T, Bai FY (2015) Towards an integrated phylogenetic classification of the Tremellomycetes. *Stud Mycol* 81:85–147. <https://doi.org/10.1016/j.simyco.2015.12.001>
- Martin GW (1940) Some Heterobasidiomycetes from Eastern Canada. *Mycologia* 32:683–695. <https://doi.org/10.2307/3754653>
- Millanes AM, Diederich P, Ekman S, Wedin M (2011) Phylogeny and character evolution in the jelly fungi (Tremellomycetes, Basidiomycota, Fungi). *Mol Phylogenet Evol* 61:12–28. <https://doi.org/10.1016/j.ympev.2011.05.014>
- Minh BQ, Schmidt HA, Chernomor O, Schrempf D, Woodhams MD, Von Haeseler A, Lanfear R (2020) IQ-TREE 2: new models and efficient methods for phylogenetic inference in the genomic era. *Mol Biol Evol* 37:1530–1534. <https://doi.org/10.1093/molbev/msaa015>
- Möller A (1895) Protobasidiomyceten. Untersuchungen aus Brasilien. In: Schimper AFW (ed) *Botanische Mittheilungen aus den Tropen* 8. Verlag von Gustav Fischer, Jena, pp 1–179
- Peng YB, Liu BFL (1992) *Flora fungorum sinicorum*, vol 2. Tremellales et Dacrymycetales. Science Press, Beijing
- Raudaskoski M, Kothe E (2010) Basidiomycete mating type genes and pheromone signaling. *Eukaryot Cell* 9:847–859. <https://doi.org/10.1128/EC.00319-09>
- Rehner SA, Samuels GJ (1994) Taxonomy and phylogeny of *Gliocladium* analysed from nuclear large subunit ribosomal DNA sequences. *Mycol Res* 98:625–634. [https://doi.org/10.1016/S0953-7562\(09\)80409-7](https://doi.org/10.1016/S0953-7562(09)80409-7)
- Reid DA, Minter DW (1979) *Pseudostypella translucens* (Gordon) Reid and Minter comb.nov., a hyperparasite on *Lophodermium conigenum*. *Trans Br Mycol Soc* 72:345–347. [https://doi.org/10.1016/S0007-1536\(79\)80059-5](https://doi.org/10.1016/S0007-1536(79)80059-5)
- Roberts P, de Meijer AAR (1997) Macromycetes from the state of Parana, Brazil. 6 Sirobasidiaceae and Tremellaceae. *Mycotaxon* 64:261–283

- Roberts P, Spooner B (1998) Heterobasidiomycetes from Brunei Darussalam. *Kew Bull* 53:631–650. <https://doi.org/10.2307/4110483>
- Spiegel FW (1990) Phylum Plasmodial Slime Molds Class Protostelida. In: Margulis L (ed) *Handbook of protoctista*. Jones and Bartlett Publishers, Boston, pp 484–497. ISBN 0867200529
- Van de Put K, Antonissen I (1995) *Sirobasidium albidum* Lagerh. and Pat., een Zuidamerikaanse nieuwkomer of een verborgen cosmopoliet? *Medel Antwerpse Mycol Kring* 95:31–34
- Vilgalys R, Hester M (1990) Rapid genetic identification and mapping of enzymatically amplified ribosomal DNA from several *Cryptococcus* species. *J Bacteriol* 172:4238–4246. <https://doi.org/10.1128/jb.172.8.4238-4246.1990>
- White TJ, Bruns T, Lee S, Taylor JW (1990) Amplification and direct sequencing of fungal ribosomal RNA genes for phylogenetics. In: Innis MA, Gelfand DH, Sninsky JJWT (eds) *PCR protocols: A guide to methods and applications*. Academic Press, San Diego, California, pp 315–322
- Wong GJ, Wells K, Bandoni RJ (1985) Interfertility and comparative morphological studies of *Tremella mesenterica*. *Mycologia* 77:36–49. <https://doi.org/10.2307/3793246>

Publisher's Note Springer Nature remains neutral with regard to jurisdictional claims in published maps and institutional affiliations.

Springer Nature or its licensor (e.g. a society or other partner) holds exclusive rights to this article under a publishing agreement with the author(s) or other rightsholder(s); author self-archiving of the accepted manuscript version of this article is solely governed by the terms of such publishing agreement and applicable law.