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

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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.

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 data-set 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

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 |         |                                   |
| Sirobasidium apiculatum |          |                 |                   |         |                                   |
| TNS-F-66691 T  | Nishiagina, Amagi-  | 24-Jun-2014     | Eutypella scoparia | JCM 32018 T  | LC203425 LC203426 LC203427       |
|                  | cho, Oshima-gun,  |                 |                   | (=CBS 14977 T) |                                   |
|                  | Kagoshima Pref., |                 |                   | JCM 32019 | LC203428 LC203429 LC203430       |
|                  | Japan, 27°46'N    |                 |                   | (=CBS 14978) |                                   |
|                  | 128°57'E         |                 |                   |         |                                   |
| Sirobasidium japonicum |          |                 |                   |         |                                   |
| TNS-F-66692     | Mt. Yonaha, Hiji, | 13-Oct-2013     | Biscogniauxia capnodes | JCM 32020 | LC203420 LC016573 LC203421       |
|                  | Kunigami-son,    |                 |                   | (=CBS 14979) |                                   |
|                  | Kunigami-gun,    |                 |                   | = PYCC 6704 |                                   |
|                  | Okinawa Pref.,  |                 |                   | JCM 32021 | LC203422 LC203423 LC203424       |
|                  | Japan, 27°46'N   |                 |                   | (=CBS 14980) |                                   |
|                  | 128°57'E         |                 |                   | = PYCC 6706 |                                   |
|                  |                 |                 |                   | PYCC 6703 | nd† nd nd                         |
|                  |                 |                 |                   | PYCC 6705 | nd nd nd                          |
|                  |                 |                 |                   |         |                                   |
| TNS-F-66693     | Mt. Nishime, Uka, | 13-Oct-2013     | Biscogniauxia capnodes | nd | nd nd nd                          |
|                  | Kunigami-son,    |                 |                   |         |                                   |
|                  | Kunigami-gun,    |                 |                   |         |                                   |
|                  | Okinawa Pref.,  |                 |                   |         |                                   |
|                  | Japan, 26°48'32.364"N |                 |                   |         |                                   |
|                  | 128°16'19.085"E |                 |                   |         |                                   |
|                  |                 |                 |                   |         |                                   |
| TNS-F-66694     | Susami, Susami-  | 19-Jul-2015     | Biscogniauxia sp.  | nd | nd nd nd                          |
|                  | cho, Nishimuro- |                 |                   |         |                                   |
|                  | gun, Wakayama   |                 |                   |         |                                   |
|                  | Pref., Japan,   |                 |                   |         |                                   |
|                  | 33°33'36.26"N   |                 |                   |         |                                   |
|                  | 135°32'27.99"E  |                 |                   |         |                                   |
| Phaeotremella translucens (= Sirotrema translucens) |          |                 |                   |         |                                   |
| TNS-F-66696     | Sugadaira Montane | 20-Oct-2014     | Lophodermium conigenum | JCM 32022 | LC203431 LC203432 LC203433       |
|                  | Research Center, |                 |                   | (=CBS 14981) |                                   |
|                  | University of    |                 |                   |         |                                   |
|                  | Tsukuba, Sugada- |                 |                   |         |                                   |
|                  |aira-Kogen, Ueda, |                 |                   |         |                                   |
|                  | Nagano Pref.,   |                 |                   |         |                                   |
|                  | Japan, 36°31'20.7"N |                 |                   |         |                                   |
|                  | 138°21'2.2"E   |                 |                   |         |                                   |
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 (Katoh and Standley 2013; Katoh 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+F+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.
ellipsoid to oblong yeast cells, which are 3.0–5.5(−5.8) × (1.6–)1.7–3.6 µm (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) Hilitzer 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).
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. 3](image-url)
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. magnus 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 Sirotrema 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. magnus and Fibulobasidium spp., Sb. japonicum did not form a monophyletic lineage with other available Sirobasidium sequences (i.e., Sb. intermedium and Sb. magnus). 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.

Sirotrema 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 epibasidium.

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 µm,
| Physiological test | *S. japonicum* | *S. apiculatum* | *P. translucens* |
|--------------------|---------------|----------------|-----------------|
| **Assimilation of carbon source** |               |               |                 |
| Glucose            | +             | +             | +               |
| Galactose          | −             | w             | +               |
| L-Sorbose          | w             | −             | −               |
| Sucrose            | +             | v             | −               |
| Maltose            | +             | −             | s/ −            |
| Galactose          | +             | 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           | −             | −             | −               |
| *meso*-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             | −             | −               |
| *myo*-Inositol     | −             | −             | −               |
| D-Glucuronic acid  | +             | −             | +               |
| D-Galacturonic acid | +           | −/w           | +               |
| D-Gluconic acid    | +             | w             | s/w             |
| D-Glucosamine      | w             | −             | −               |
### Table 2 (continued)

| Physiological test                              | **Sb. japonicum** | **Sb. apiculatum** | **P. translucens** |
|------------------------------------------------|-------------------|--------------------|-------------------|
| D-Glucurono lactone                            | +                 | +                  | +/w               |
| L-Arabinitol                                    | w                 | −                  | −                 |
| Quinic acid                                     | −                 | −                  | −                 |
| Saccharic acid                                  | +                 | +                  | −                 |
| Propyleneglycol                                 | −                 | −                  | −                 |
| Xylitol                                         | w/ −              | −                  | +                 |
| N-Acetyl-D-glucosamine                          | +                 | −                  | −                 |
| Butane-2,3-diol                                 | −                 | −                  | −                 |
| Xylo-oligosaccharide                            | −                 | −                  | −                 |
| n-Decane                                        | −                 | −                  | −                 |
| n-Hexadecane                                    | −                 | −                  | −                 |
| **Assimilation of nitrogen source**             |                   |                    |                   |
| Ammonium sulfate                                | +                 | +                  | +                 |
| Potassium nitrate                               | −                 | −                  | −                 |
| Sodium nitrite                                  | −                 | −                  | +                 |
| Ethylamine hydrochloride                        | +                 | +                  | −                 |
| Lysine hydrochloride                            | +                 | +                  | −                 |
| Cadaverine dihydrochloride                      | +                 | +                  | −                 |
| Creatine                                        | −                 | −                  | −                 |
| Creatinine                                      | −                 | −                  | −                 |
| D-glucosamine                                   | +                 | −                  | −                 |
| Imidazole                                       | −                 | −                  | −                 |
| **Growth at**                                   |                   |                    |                   |
| 25 °C                                           | +                 | +                  | +                 |
| 30 °C                                           | −                 | +                  | −                 |
| 35 °C                                           | −                 | −                  | −                 |
| **Other tests**                                 |                   |                    |                   |
| 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)                        | −                 | −                  | −                 |
divided 2-cells by a longitudinal septum (Fig. 2c). Epibasidia fusiform to cylindrical, apiculate at the tip, 17.5–26.0 × 6.0–7.0 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–) 8.5–26.0 × 6.0–7.0 (–9.0) µm (Fig. 2e, f), germinating by budding or repetition. Hyphae with clamp connection, 1.5–2.5 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, 3.0–5.5 (–5.8) × (1.6–) 1.7–3.6 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°46’ N 128°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 sirobasidiaceous 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. magnam*. 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 apllanate-cerebriform, white to pale yellow (Fig. 1a). Basidia basipetally formed in chains, cylindrical to ellipsoid, (15.0–)17.5–32.5 × 5.0–8.0 µm, divided to 4-cells by transverse to oblique septa (Fig. 1b, c). Epibasidia fusiformis, (7.5–)9.0–15.0 (–20.5) × 4.0–7.0 µm, producing a sterigma from lateral side (Fig. 1c, d). Basidiospores globose to subglobose, 4.0–7.0 (–7.5) × 3.5–6.5 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–)3.0–5.0 × (2.1–)2.5–4.2 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, Kumage-cho, Kagoshima Pref., 24 Oct 1961, col. H. Indoh, TNS-F-196751 (holotype); JAPAN, Mt. Yonaha, Hiji, Kunigami-son, Kunigami-gun, Okinawa Pref., 26°43′19.5″ N 128°12′54″ E, alt. 360 m, on a fallen branch of *Alnus japonica* (Thunb.) Steud. var. *formosana* (Burkitt) Callier, associated with *Biscogniauxia capnodes* (Berk.) Y.M. Ju et J.D. Rogers, 13 Oct 2013, col. M. Yamada, TNS-F-66694; JAPAN, Susami, Susami-cho, Nishimuro-gun, Wakayama Pref., 33°33′36.2″ N 135°32′27.9″ E, alt. 85 m, on a fallen branch of broadleaf tree, associated with *Biscogniauxia* sp., 19 Jul 2015, col. K. Yamamoto, TNS-F-66694.
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) Hilitzer, 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) Hilitzer, 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 *Sirotremata*, *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.

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**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; YY and MO supervised the study. All authors approved the final manuscript.

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