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ORIGINAL ARTICLE

Paraxerula ellipsospora, a new Asian species of Physalacriaceae

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Abstract A new species, *Paraxerula ellipsospora*, is described from southwestern China using both morphological and molecular phylogenetic evidence. This species differs phenotypically from the three known species in the genus by its greyish colored pileus, ellipsoid to elongate basidiospores, and a distribution in pine forests in Yunnan. Geographical divergences of *Paraxerula* in the Holarctic were observed. All species show continental endemisms, yet related species occurring in East Asia and in Europe, or in East Asia and in North America were found.

Keywords Continental endemisms · Fungi · New taxa · *Paraxerula ellipsospora* · Phylogenetic analyses

Introduction

In a recent morphological-systematic treatment of the genus *Oudemansiella* Speg. s. str. (Physalacriaceae), *O. americana* (Dörfelt) Pegler & T.W.K. Young, *O. caussei* (Maire) M.M. Moser and *O. hongoi* (Dörfelt) Zhu L. Yang, previously treated in *O.* sect. *Albotomentosae* Clémençon or *Xerula* sect. *Hyalosetae* Dörfelt, were excluded from *Oudemansiella* because they represent a segregate genus (Yang et al. 2009). Subsequently, the genus *Paraxerula* R.H. Petersen was proposed to accommodate them, with *O. americana* as the generic type (Petersen and Hughes 2010). This genus is characterized by a (1) collybioid, dry pileus, (2) a fertile, lamellar edge, (3) white to whitish, flexuous hairs (pileosetae), and (4) smooth basidiospores.

During our study on the species diversity of agarics in southwestern China, some specimens of *Paraxerula* were collected. Our morphological observations and phylogenetic analyses based on two gene markers showed that these specimens represent a species new to science. This species is described herein. Meanwhile, distribution patterns of and phylogenetic relationships among the four species within *Paraxerula* are discussed.

Materials and methods

Morphology

Macro-morphological descriptions are based on the field notes and images of basidiomata. Color codes of the form “10D7” are from Kornerup and Wanscher (1981). Specimens were deposited in the Herbarium of Cryptogams, Kunming Institute of Botany of the Chinese Academy of Sciences (HKAS). Micromorphological data were obtained from the dried specimens after sectioning and mounting in 5 % KOH solution. In the descriptions of lamellae and basidiospores (hereafter, spores), the abbreviation L=number of entire lamellae; l=number of lamellulae between each pair of entire lamellae; [*n*/*m*/*p*] shall mean *n* spores measured from *m* basidiomata of *p* collections; *Q* is used to mean “length/width ratio” of a spore in side view; and ***Q*** means average *Q* of all spores±sample standard deviation. The descriptive terms of Bas (1969) and Vellinga and Noordeloos (2001) were followed.

DNA extraction, PCR amplification, and sequencing

Genomic DNA was extracted from silica-gel-dried or herbarium materials using the CTAB procedure (Doyle and Doyle

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Table 1 Specimens used in molecular studies and GenBank accession numbers

Taxon	Voucher	Locality	GenBank Accession			
			ITS	nrLSU	*β-tubulin*	*tef1-α*
“***Cribbea gloriosa***”	MEL21710	Australia	FJ178110*	FJ178111*	–	–
“*Cribbea turbinispora*”	PIF27162	Australia	FJ178112*	FJ178113*	–	–
“*Dactylosporina glutinosa*”	MCA1775	Guyana	HM005074	HM005137	–	–
“***Dactylosporina steffenii***”	TENN58785	Costa Rica	HM005073*	HM005132*	–	–
Flammulina velutipes	TENN56073 (neotype)	London, England	AF030877*	HM005085*	–	–
Gloiocephala aquatica	CIEFAP50	Argentina	DQ097356*	DQ097343*	–	–
Gloiocephala epiphylla	DED5971 (ITS);DED6353 (nrLSU)	USA	DQ097357*	DQ097344*	–	–
Gloiocephala menieri	DAOM170087	Canada	DQ097358*	DQ097345*	–	–
“***Hydropus mediterraneus***”	MCVE 23445	Tuscany, Italy	JX271809*	JX271809*	–	–
“*Hymenopellis furfuracea*”	PBM 2440 (CUW)	–	DQ494703*	AY691890*	–	–
“*Hymenopellis gigaspora*”	NYBG REH8676	Australia	GQ913357*	HM005121*	–	–
“*Hymenopellis incognita*”	TENN58768	Texas, USA	GQ913425*	HM005105*	–	–
“*Hymenopellis limonispora*”	TENN59438	Tennessee, USA	GQ913406*	HM005133*	–	–
“*Hymenopellis limonispora*”	TENN61379	Tennessee, USA	GQ913403*	HM005134*	–	–
“***Hymenopellis radicata***”	TENN62837	Sweden	GQ913377*	HM005125*	–	–
“*Hymenopellis rubrobrunnescens*”	TENN51262	New York, USA	GQ913373*	HM005113*	–	–
“*Hymenopellis rubrobrunnescens*”	TENN52654	North Carolina, USA	GQ913372*	HM005112*	–	–
“*Hymenopellis rugosoceps*”	TENN57307	Tennessee, USA	GQ913395*	HM005116*	–	–
“*Hymenopellis rugosoceps*”	TENN60604	Tennessee, USA	GQ913394*	HM005117*	–	–
“*Hymenopellis sinapicolor*”	TENN56566	Arkansas, USA	GQ913350*	HM005118*	–	–
“*Hymenopellis superbiens*”	MEL2291946	Australia	GQ913361*	HM005120*	–	–
“*Marasmius micraster*”	DED7647	Malaysia	JN601436*	JN585131*	–	–
“*Marasmius thwaitesii*”	DED5918	Hawaii, USA	JN601437*	JN585132*	–	–
“*Mucidula brunneomarginata*”	TENN53020	Primorsk, Russia	GQ844243*	HM005123*	–	–
“*Mucidula mucida* var. *asiatica*”	TENN49897	Primorsk, Russia	DQ097369*	HM005100*	–	–
“***Mucidula mucida* var. *mucida***”	TENN59324	Lower Austria, Austria	GQ844235*	HM005127*	–	–
Oudemansiella cubensis	TENN51190	Pavones, Costa Rica	GQ892794*	HM005114*	–	–
Oudemansiella platensis	TENN58954 (epitype)	Argentina	GQ892789*	–	–	–
Paraxerula americana	CLO4744	New Mexico, USA	HM005141*	-	–	–
Paraxerula americana	CLO4746	New Mexico, USA	HM005142*	HM005094*	–	–
Paraxerula americana	DBG21746	Colorado, USA	HM005143*	HM005093*	–	–
Paraxerula ellipsospora	HKAS 55404 (B. Feng 293)	Yulong County, Yunnan, China	KF530559	–	–	–
Paraxerula ellipsospora	HKAS 56261 (holotype)	Yulong County, Yunnan, China	KF530557	KF530567	KF530572	KF530577
Paraxerula ellipsospora	HKAS 56283 (Y. C. Li 1443)	Shangri-La County, Yunnan, China	KF530558	–	–	KF530576
Paraxerula hongoi	HKAS 51985 (S. Takehashi No. 17)	Hokkaido, Japan	KF530561	KF530566	–	–
Paraxerula hongoi	HKAS 61794 (X. H. Wang 2593)	Mulan County, Heilongjiang, China	KF530560	KF530565	–	KF530578
Paraxerula hongoi	C 60612	Japan	HM005144*	HM005095*	–	–
“***Ponticulomyces kedrovayae***”	TENN60767	Kedrovaya, Russia	HM005146*	HM005110*	–	–
“***Protoxerula flavo-olivacea***”	NY REH8781	Australia	HM005152*	HM005111*	–	–
Rhizomarasmius epidryas	KH58 (ITS); KRAM F-46706 (nrLSU)	-; Romania	GU234107*	JF297608*	–	–
Rhizomarasmius pyrrocephalus	TENN51091	USA	DQ097369*	DQ097351*	–	–
Rhodotus asperior	HKAS 56754 (holotype)	Yingjiang County, Yunnan, China	KC179737*	KC179745*	–	–
Rhodotus palmatus	HMJAU 6872	Antu County, Jilin, China	KC179742*	KC179752*	–	–

Table 1 (continued)

Taxon	Voucher	Locality	GenBank Accession			
			ITS	nrLSU	*β-tubulin*	*tef1-α*
Strobilurus conigenoides	TENN61318	North Carolina, USA	GQ892821*	HM005091*	–	–
Strobilurus esculentus	HKAS 56525 (Zhu L. Yang 5027)	Botanical Garden, Marburg, Germany	KF530549	KF530564	KF530575	KF530581
"*Xerula caussei*"	C 46662	Denmark	–	AM946473*	–	–
Xerula pudens	TENN59208	Austria	HM005154*	HM005097*	–	–
Xerula sinopudens	HKAS 55377 (B. Feng 266)	Xishuangbanna, Yunnan, China	KF530551	KF530571	–	–
Xerula sinopudens	HKAS 56793 (L. P. Tang 836)	Yingjiang County, Yunnan, China	KF530550	–	KF530573	KF530579
Xerula strigosa	HKAS 48778 (holotype)	Jianchuan County, Yunnan, China	KF530552	–	–	–
Xerula strigosa	HKAS 73323 (J. Qin 337)	Longyang County, Yunnan, China	KF530553	KF530570	KF530574	KF530580
Xerula strigosa	HKAS 73908 (X. T. Zhu 513)	Cheng County, Gansu, China	KF530555	KF530568	–	–

* Sequences were retrieved from GenBank. Boldface in the first column: generic type

1987). Universal primers ITS1/ITS4 or ITS5/ITS4 were used for the amplification of the internal transcribed spacer (ITS) region (White et al. 1990), and primers LROR/LR5 or LROR/LR7 (Vilgalys and Hester 1990) were employed for amplification of the nuclear gene coding for the ribosomal large subunit (nrLSU). Sequences of the translation elongation factor 1-α gene (*tef1-α*) and *β-tubulin* gene of the materials were obtained using universal primers 983 F/1567R (Rehner 2001) and newly designed primer pair TubF/TubR (GGTGCGGGTAACTGGGC/GAGGCAGCCATCATGTTCTT, designed by Guo-Fu Qin, Han-Chen Wang and Jun Zhao). Amplification reactions were performed in an ABI 2720 thermal cycler (Applied Biosystems, Foster City, CA, USA) or an Eppendorf Master Cycler (Eppendorf, Netheler-Hinz, Hamburg, Germany). The PCR program was 95 °C for 3 min; 94 °C for 30 s, 50 °C (ITS, nrLSU and *tef1-α*) or 53 °C (*β-tubulin*) for 50 s, 72 °C for 90 s, 35 cycles; and 72 °C for 8 min. PCR products were purified with the Gel Extraction & PCR Purification Combo Kit (Spin-column, Bioteke, Beijing, China), and then sequenced on an ABI-3730-XL sequence analyzer (Applied Biosystems, Foster City, CA, USA) using the same primers as those used in amplifications.

Sequence alignments and phylogenetic analyses

All ITS and nrLSU sequences of *Paraxerula* in GenBank were retrieved, and combined with those generated in this study (Table 1). *Flammulina velutipes* was selected as an outgroup, and species of other genera within Physalacriaceae, such as *Cryptomarasmius* T.S. Jenkinson & Desjardin, *Gloiocephala* Massee, *Laccariopsis* Vizzini, *Oudemansiella*, *Rhizomarasmius* R.H. Petersen, *Rhodotus* Maire, *Strobilurus* Singer and *Xerula* Maire, were also included in the analyses to confirm the position of the new species that we propose here. *Hydropus mediterraneus*, *Marasmius micraster* and *M. thwaitesii* were recognized as species of *Laccariopsis* or *Cryptomarasmius*, according to recent taxonomic treatments (Vizzini et al. 2012; Jenkinson et al. 2013). The genera *Cribbea* A.H. Sm. & D.A. Reid, *Dactylosporina* (Clémençon) Dörfelt, *Hymenopellis* R.H. Petersen, *Mucidula* Pat., *Ponticulomyces* R.H. Petersen, and *Protoxerula* R.H. Petersen were treated in *Oudemansiella* s.l. in this study (see Fig. 1).

Sequences of *tef1-α* and *β-tubulin* genes that we generated have been deposited in GenBank for reference (Table 1), but were not used for phylogenetic analyses due to limited number of sequences available in GenBank. Two datasets, ITS sequences and nrLSU sequences, were aligned using Opal 0.3.7 (Wheeler and Kececioglu 2007) separately and manually checked on Bioedit v7.0.9 (Hall 1999) or 4SALE v1.5 (Seibel et al. 2006). Sequence lengths of the nrLSU and ITS datasets are 850 and 986 bp, respectively. To test for phylogenetic conflict between the two datasets, the partition homogeneity (PH) test was performed with 1,000 randomized replicates, using heuristic searches with the simple addition of sequences in PAUP* 4.0b10 (Swofford 2002). The result showed that the phylogenetic signals in the two gene markers were not in conflict ($P=0.18$). Consequently, the sequences of the two datasets were concatenated using Phyutility v2.2 (Smith and Dunn 2008) in order to carry out a combined analysis.

For molecular phylogenetic analyses on the combined dataset (nrLSU-ITS), maximum likelihood (ML) and Bayesian inference (BI) were employed by using MrBayes v3.1.2 (Ronquist and Huelsenbeck 2003) and RAxML v7.2.6 (Stamatakis 2006), respectively. The GTR+I+G models were chosen as the best models for nrLSU-ITS, using the Akaike Information Criterion (AIC) implemented in MrModeltest v2.3 (Nylander 2004). Partitioned analyses were conducted for both ML and BI. For ML analysis, all parameters were

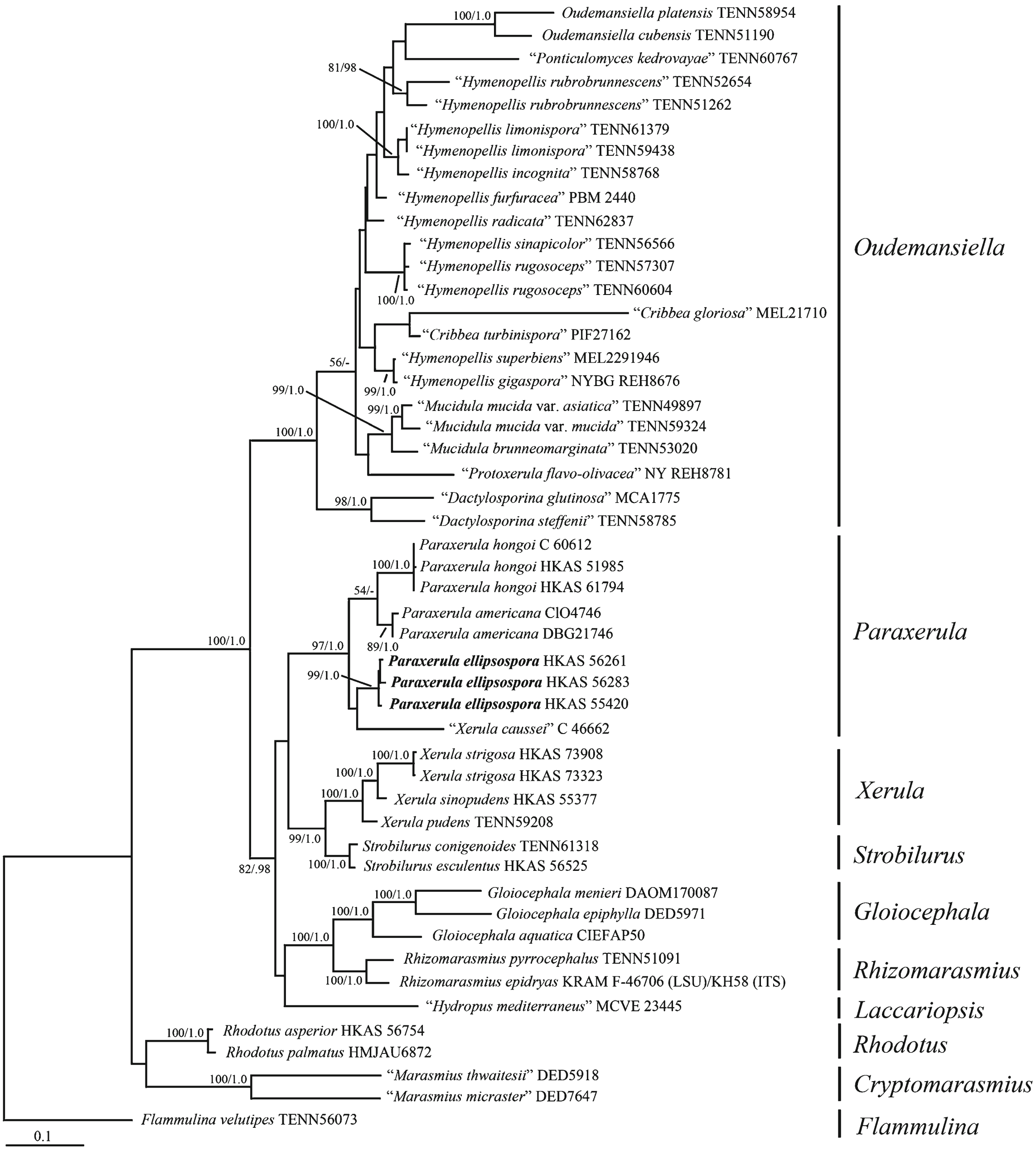

Fig. 1 ML tree of the concatenated nrLSU-ITS alignment. Bootstrap values (> 50 %), together with Bayesian Posterior Probabilities (> 0.90) are indicated along nodes

kept as default except for the model choosing as GTRGAMMAI, and the statistic supports were calculated using nonparametric bootstrapping with 1,000 replicates. BI analysis was carried on MrBayes by using selected models and setting generations to 5 million and using the stoprul command with the value of stopval set to 0.01, while other parameters were kept as default. Subsequently, trees were summarized and statistic supports were obtained by using sumt command complemented in MrBayes by discarding the first 25 % generations as burn-ins.

Results

Molecular phylogeny

The phylogenetic tree of most genera of Physalacriaceae (Fig. 1) inferred from the nrLSU-ITS dataset using ML and BI analyses indicates the monophyly of *Paraxerula*. The materials collected from the Yunnan Province of China cluster in *Paraxerula* clade, but are distinct from the three known species, *P. americana*, *P. hongoi* and *P. caussei*. Therefore, a new species, *P. ellipsospora*, is recognized to accommodate these collections. Our analyses indicate that *Oudemansiella* s.l. (including *Cribbea*, *Dactylosporina*, *Hymenopellis*, *Mucidula*, *Ponticulomyces* and *Protoxerula*) is monophyletic (Fig. 1), which is consistent with the suggestion of Vellinga (2010). The treatment of Yang et al. (2009) is the same as that of Vellinga (2010), yet without including the secotioid genus *Cribbea*.

Taxonomy

Paraxerula ellipsospora Zhu L. Yang & J. Qin, **sp. nov.** (Figs. 2a–c; 3; 4a-b)

MycoBank: MB 804929

Etymology: referring to the ellipsoid spores.

Holotypus: China, Yunnan Province, Yulong County, Yulong Snow Mountain, Heibaishui, at 100°13.910′ E, 26°53.075′N, alt. 2373 m, 10 Aug 2008, Y.C. Li 1421 (HKAS 56261).

Pileus (Fig. 2a–c) convex to applanate, 2–7 cm in diam, dry to slightly viscid, brownish grey to greyish (5B1–2, 6B1–2), slightly darker at center, with white to whitish, flexuous hairs; context white, unchanging. Lamellae distant, adnexed to sinuate, up to 6 mm in height, white to cream, L=21–27, l=1–3, edge concolorous with lamellar surface. Stipe (Fig. 2a–c) 5–7× 0. 2–0.5 cm, subcylindrical, enlarged at ground line (0.6–1 cm), surface gray with very pale-brownish tinge, but nearly white at apex, covered with whitish, flexuous hairs. Pseudorhiza dark grey to blackish. Taste mild; odor indistinct.

Spores (Figs. 3a; 4a) [160/6/6] (9) 10–13 (15)×5.5–7 (8) µm, Q=(1.43) 1.54–2.0 (2.30), $\boldsymbol{Q}$=1.76±0.16, ellipsoid to elongate, thin-walled, colorless hyaline, smooth, inamyloid. Basidia (Figs. 3b; 4b) 45–85×7.5–11 µm, 4-spored. Pleurocystidia (Figs. 3c; 4b) fairly abundant, 65–93×11–18 µm, nearly subventricose, subcapitate, or attenuate towards apex, thin- to slightly thick-walled (walls≤0.5 µm thick). Lamellar edge fertile, cheilocystidia scattered, similar to pleurocystidia in size and form. Pileipellis (Fig. 3d) 40–60 µm thick, a hymenoderm composed of clavate to broadly clavate cells (20–60×10–25 µm), with grey-brown to yellow-brown vacuolar pigment. Pileocystidia (hairs, Fig. 3d–e) very abundant, lanceolate, (60) 120–400 (420)×10–15 (18) µm, thick-walled (walls≤3 µm thick), nearly colorless or with yellowish to light brown cell walls; base usually enlarged; apex narrowly rounded, rarely acute. Caulocystidia (hairs, Fig. 3c) numerous, lanceolate, 100–500×10–20 µm, nearly colorless and hyaline, sometimes with brownish cell wall, thin- to thick-walled (walls≤2 µm thick); apex narrow and rounded; basal part often enlarged. Clamp connections common in all parts of basidioma.

Habitat and known distribution: fruiting in forests dominated by *Pinus* spp. (e.g., *Pinus densata* and *P. armandii*); in summer at alt. 2,700–3,200 m in southwestern China.

Additional specimens examined: China, Yunnan Province: Shangri-La County, Haba Snow Mountain, 12 Aug 2008, Y. C. Li 1443 (HKAS 56283); Shangri-La County, Haba Snow Mountain, Mianshaba, alt. 3,200 m, 13

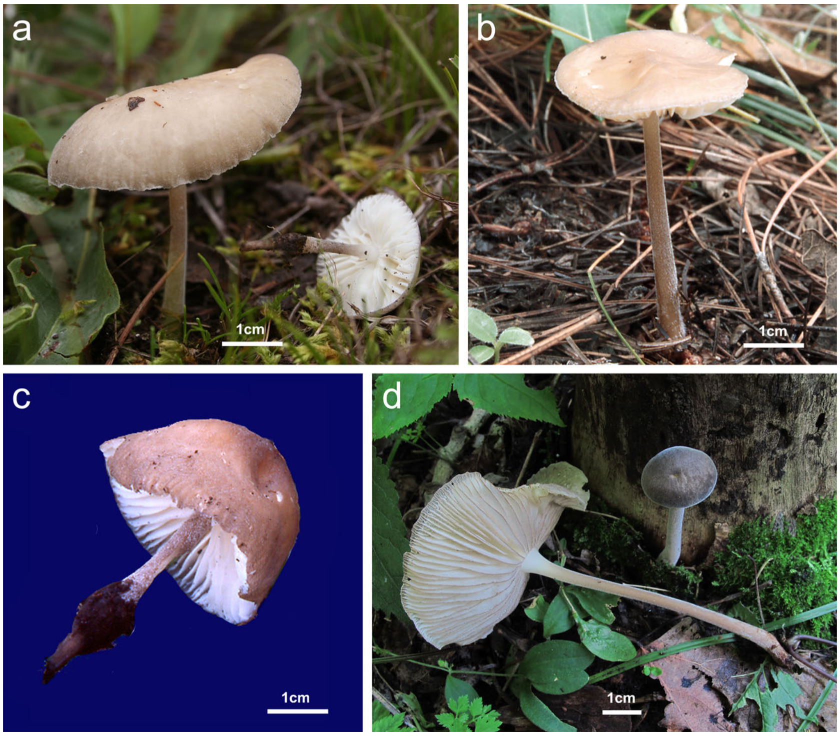

Fig. 2 Basidiomata of *Paraxerula ellipsospora* and *P. hongoi*. **a** *P. ellipsospora* (holotype); **b**, **c** *P. ellipsospora* (HKAS 48467); **d** *P. hongoi* (HKAS 61794, by courtesy of X.H. Wang)

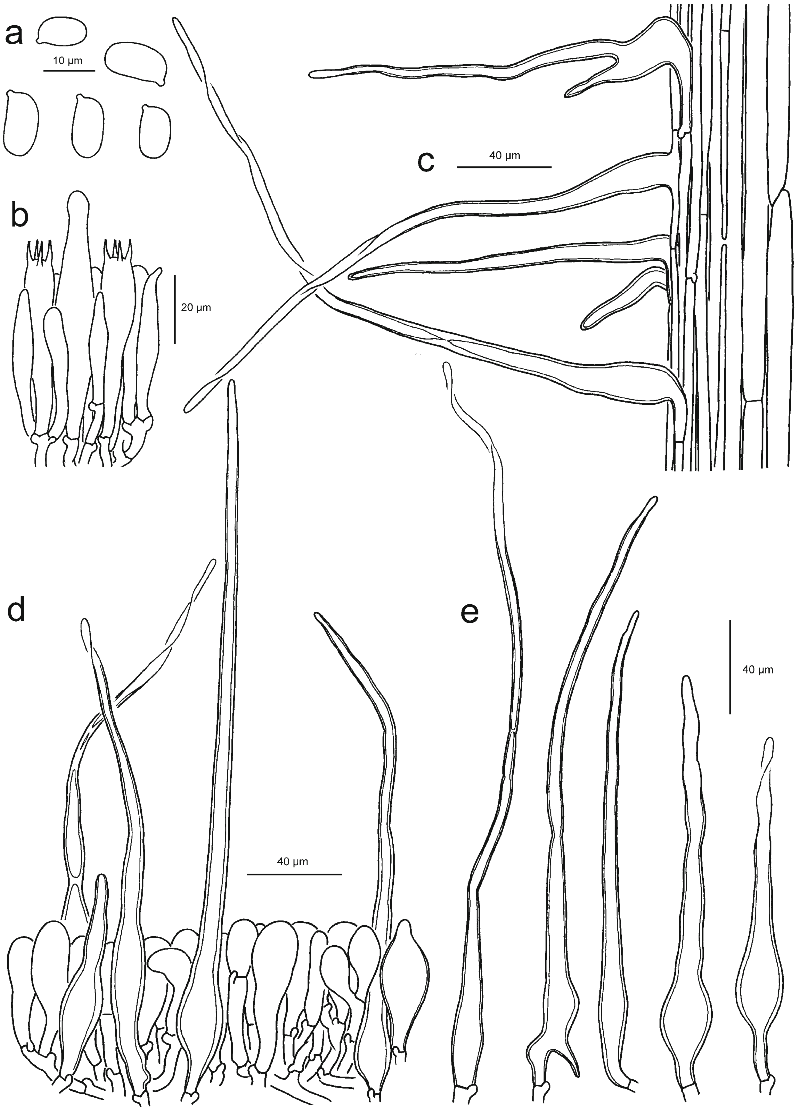

Fig. 3 Microscopic features of *Paraxerula ellipsospora.* **a** Basidiospores (holotype); **b** Hymenium (holotype); **c** Stipipellis (HKAS48467); **d** Radial-vertical section of pileipellis (HKAS 48467); **e** Pileosetae (hairs on pileus, HKAS48467)

Aug 2008, B. Feng 309 (HKAS 55420); Yulong County, Xiangshan, alt. 2,700 m, 1 Aug 1985, E. Horak 2890 (HKAS 15134, as *O. caussei* by Yang and Zang 1993); Yulong County, Yulong Snow Mountain, Ganhaizi, 4 Aug 1995, M. Zang 12550 (HKAS 30116); Yulong County, Yulong Snow Mountain, Heibaishui, alt. 2,900 m, 30 Jul 2001, Zhu L. Yang 3111 (HKAS 38288); Yulong County, Yulong Snow Mountain, alt. 3,100 m, 4 Aug 2005, Zhu L. Yang 4524 (HKAS 48467); Yulong County, Yulong Snow Mountain, Ganhaizi, alt. 3,200 m, 10 Aug 2008, B. Feng 293 (HKAS 55404).

Specimen of P. americana *examined*: USA: New Mexico, 29 Aug 1995, R. Halling 7504 (NY, and HKAS 43810).

Specimen of P. caussei *examined*: Denmark: Sjaelland, Køge, Lellinge Skevhusvaenge, in *Fagus* forest,19 Sep 1999, T. Læssøe 5589 (UTM, and HKAS 45056).

Specimens of P. hongoi *examined*: Japan: Hokkaido, 18 Sep 2005, S. Takehashi 19 (HKAS 51969). China: Heilongjiang Province, Mulan County, Dagui Town, 11 Aug 2010, X. H. Wang 2593 (HKAS 61794).

Discussion

Paraxerula ellipsospora was misidentified as *O. caussei* by Yang and Zang (1993). Both *P. caussei* and *P. ellipsospora* share similar slender pleurocystidia (Fig. 4b; d). However, our study showed that the spores of *P. caussei* are [20/1/1] (7) 7.5–9.5 (10)×6–7 µm; *Q*=(1.14) 1.16–1.47 (1.50); ***Q***=1.32±0.10 (Fig. 4c), which is generally consistent with other reports, viz., 8.5–12×7–8.5 µm, ***Q***=1.4 in Pegler and Young (1987), and 10–12×7–8 µm, ***Q***=1.47 in type studies of Petersen and Hughes (2010).

Additionally, *P. hongoi* (Fig. 2d) and *P. americana* were also arranged in the genus (Petersen and Hughes 2010). The two species have much longer and broader distinctly capitate

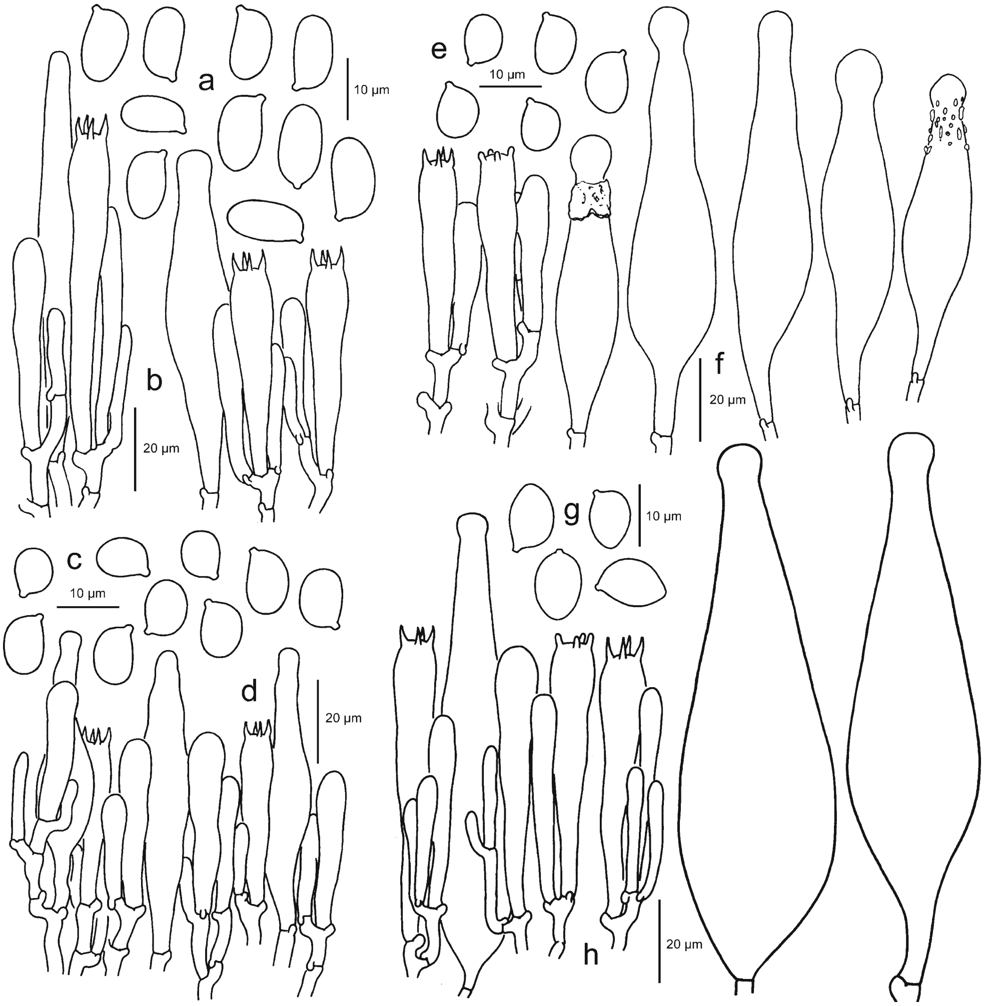

Fig. 4 Basidiospores and hymenium (including basidia and pleurocystidia) of *Paraxerula*. **a** Spores of *P. ellipsospora* (HKAS 48467); **b** Hymenium of *P. ellipsospora* (HKAS 48467); **c** Spores of *P. caussei* (HKAS 45056); **d** Hymenium of *P. caussei* (HKAS 45056); **e** Spores of *P. hongoi* (HKAS 51969); **f** Hymenium of *P. hongoi* (HKAS 51969); **g** Spores of *P. americana* (HKAS 43810); **h** Hymenium of *P. americana* (HKAS 43810)

pleurocystidia (Fig. 4f; h) than *P. caussei* and *P. ellipsospora. Paraxerula hongoi* is characterized by its rudimental pseudorhiza, encrusted pleurocystidia and the subglobose to broadly ovate spores (Fig. 4e; Yang 2000; Mizuta 2005; Petersen and Hughes 2010). For *P. americana*, we found the spores to be [10/1/1] 9–10 (11.5)×(6.5) 7–8 (8.5) μm, Q=(1.22) 1.26–1.35 (1.46), $\boldsymbol{Q}$ =1.32±0.10 (Fig. 4g). Pegler and Young (1987) reported the spores of *P. americana* as 9–12.5×7–8.5 μm, while Petersen and Hughes (2010) stated the spores of the holotype of *P. americana* as 9–11.5×7–8.5 μm, $\boldsymbol{Q}$ =1.36. Both reports are consistent with our observations.

The color of the basidioma of *P. ellipsospora* (brownish grey to greyish) also makes it distinct from *P. americana*, *P. caussei* and *P. hongoi*. The colors of the later three species are usually darker (from nearly black to brown series, “snuff brown”, “olive brown”, “greyish brown”, “nut brown”, “tobacco brown” or “sayal brown”) (Fig. 2; Ridgway 1912; Petersen and Hughes 2010).

The four species also differ in ecology: *Paraxerula ellipsospora* was only found in *Pinus densata* and *P. armandii* forests (Fig. 2a–c), while *P. americana* is usually associated with *Populus* spp. (Petersen and Hughes 2010); *Paraxerula hongoi* was reported from *Abies* and *Rhododendron* (Yang 2000) or mixed hardwoods of *Castanopsis*, *Celtis*, *Ilex*, *Quercus*, *Pinus densifolia* and *Alnus* (Petersen and Hughes 2010); and *Paraxerula caussei* grows in *Fagus sylvatica* forests (Petersen and Hughes 2010).

Three additional names, viz. *Oudemansiella nigra* Dörfelt, *O. renati* Clémençon and *O. xeruloides* Bon, may be mentioned in connection to *Paraxerula*. The former two names were treated as synonyms of *P. caussei* (under the name of *O. caussei* by Boekhout and Bas 1986; Pegler and Young 1987; Boekhout 1999; Contu 2000; Ronikier 2003; Petersen and Hughes 2010). The last one, *O. xeruloides*, originally described from France, differs from *P. ellipsospora* by its larger, broadly amygdaliform or ovate spores (Bon 1975; Clémençon 1979; Dörfelt 1983; Reid 1985). Although *O. xeruloides* was transferred to *Hymenopellis* by Petersen and Hughes (2010), its systematic position is still unsettled.

It’s worth noting that the four species within *Paraxerula* show strong geographical divergences in the Northern

Hemisphere. On one hand, *P. ellipsospora* has so far only been found in southwestern China of East Asia, while its sister taxon *P. caussei* was only reported in Europe. On the other hand, *P. americana* occurs in the Rocky Mountains of North America, while its closest relative, *P. hongoi*, is distributed in East Asia (Japan, far-eastern Russia and China). The related species or species pairs observed in East Asia-Europe and East Asia-North America may indicate broad historical exchange of *Paraxerula*, as documented in many other saprophytic, and ectomycorrhizal fungi (Redhead 1989; Mueller et al. 2001; Geml et al. 2006; 2008; Li et al. 2009; Feng et al. 2012; Zhao et al. 2012).

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