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Original Research

Insights into the molecular taxonomy and phylogeny of *Parengyodontium album*, an uncommon indoor mould from western India

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Abstract

This study represents the first molecular authentication of the medically and industrially relevant fungus, *Parengyodontium album* from Pune, India. The species was identified through an integrative approach that combined detailed morphological assessment with phylogenetic analyses based on three genetic markers, ITS, LSU, and *tef1α*. Based on morphology alone, this taxon can be misidentified as a *Beauveria* species due to its cryptic and comparable microscopic characteristics. Our findings provide the first molecular confirmation and phylogenetic placement of *P. album*, establishing its identity and occurrence as an indoor mould. This species has recently attracted considerable attention due to its dual significance: its emerging role in clinical contexts, particularly in respiratory infections, and its promising potential in plastic biodegradation.

Keywords: *Cordycipitaceae,* medical fungus, phylogeny, taxonomy, Maharashtra.

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1. Introduction

The genus *Parengyodontium* was established by Tsang *et al.* (2016) with *P. album* (Limber) Tsang *et al.* (2016) as the type species, which was formerly classified under the genus *Engyodontium* de Hoog (1978). This fungus was originally introduced by Limber (1940) as *Tritirachium album*, a new genus in the family *Moniliaceae* (Hyde et al., 2024). Later, Saccas (1948) transferred *Tritirachium* to the genus *Beauveria,* opposing the establishment of a new genus to accommodate *Tritirachium,* which possesses phialides ending in a zig-zag filament, alternately bears conidia. Saccas (1948) synonymised *Tritirachium album* with *Beauveria alba* (Limber) Saccas. Later, de Hoog (1978) introduced a new genus, *Engyodontium,* and synonymised *Tritirachium album* as *Engyodontium album* (Limber) de Hoog. Subsequently, Tsang et al. (2016) amended the species description provided by Limber (1940), de Hoog (1972), Matsushima (1975), de Hoog (1978), and de Hoog et al. (2000). They introduced a monotypic genus, *Parengyodontium*, to accommodate *P. album*. *Parengyodontium* represents a distinct phylogenetic lineage within the family *Cordycipitaceae*. *Parengyodontium album,* characterised by conidiogenous cells with zigzag-shaped terminal regions, differs from other species of *Engyodontium* in its phylogenetic and chemotaxonomic features. Tsang et al. (2016) identified three subclades among the *P. album*, which were difficult to differentiate based solely on phenotypic characteristics. Parker et al. (2022) transferred the *P. album* subclade 3 to a new species, *P. torokii*, based on phylogenetic and morphological differences, particularly the distinct shape of the conidia produced by *P. torokii* compared to those of *P. album*. In addition, Teixeira et al. (2020) introduced a new species, *P. americanum,* under the genus, which was isolated from clinical cases of coccidioidomycosis. Currently, the genus *Parengyodontium* comprises three recognised species: *P. album*, *P. americanum* (Teixeira et al., 2020), and *P. torokii* Singh & Venkateswaran (Parker et al., 2022; Index Fungorum, accessed 27 October 2025).

Although *Parengyodontium album* and *P. americanum* have predominantly been described in medical contexts as opportunistic human pathogens (Augustinsky *et al.,* 1990; Macêdo *et al.,* 2007), *P. album* is known to be widely distributed in the environment. It has been recovered from diverse substrates, including plants (Belfiori *et al.,* 2021; Lucero *et al*., 2006; Wu *et al.,* 2013), soil (Kachuei *et al*., 2012; Ma *et al*., 2013), and insects (Chandrashekhar *et al.,* 1981). It is also common in marine environments, occurring on substrates of coastal plants (Liu *et al.,* 2021), marine sediments (Khusnullina *et al*., 2018) and seawater (Pindi, 2012). In addition, *P. album* is frequently reported from cultural heritage environments (Gorbushina and Petersen 2000; Ponizovskaya *et al*., 2019; Leplat *et al*., 2020) and has often been isolated from the air of hypogean sites (Saarela *et al*., 2004), notably in Palaeolithic decorated caves (Dominguez-Moñino *et al*., 2021; Leplat *et al*., 2019; Liñán *et al.,* 2018). Interestingly, the holotype of *P. torokii* was isolated from the Mars 2020 spacecraft assembly facility (Parker *et al.,* 2022).

The only known Indian-origin strain of *P. album* (CBS 121919), submitted in 2007, isolated from a conjunctivitis case in an uncontrolled diabetic patient by A. J. Kindo (Chennai), is authenticated and preserved in the Westerdijk Institute collection, Netherlands (MycoBank; https://www.mycobank.org accessed on 8 Sept 2025). Most recently, Vaksmaa et al. (2024) reported that *P. album* isolated from the plastic debris in the North Pacific Subtropical Gyre could mineralise UV-treated polyethylene (PE) into CO_2.

This genus holds significant importance, having been reported as an opportunistic pathogen in immunocompromised patients and is also recognised as a potent plastic degrader. Considering

India's immense biodiversity and high population density, comprehensive investigations of *Parengyodontium* are timely and essential, with implications for medical mycology, environmental biotechnology, and fungal biodiversity research. This study aims to authenticate an unusual white fungal colony isolated from lavatory walls in Pune based on morphological characteristics and contemporary multigene phylogenetic analyses. It provides the first molecular confirmation and phylogenetic placement of *Parengyodontium album*, thereby establishing its identity and occurrence as an indoor mould.

2. Materials and Methods

2.1. Isolation and Morphology

Fungal samples were collected from the bathroom wall of a residential house in Pimpri Chinchwad, Pune district of Maharashtra, India. Conidia were isolated directly from the scraped wall material and observed using a binocular stereomicroscope (Olympus SZX16 with Digi-CAM, Japan). Single conidial cultures were established on 2% malt extract agar plates (MEA; Hi-Media, Mumbai, India) following Rajeshkumar *et al.* (2021, 2023). Microscopic observations were made with a Carl Zeiss (AXIO Imager 2, Oberkochen, Germany) compound microscope equipped with Nikon Digital sight DS-Fi1 and AxioCam MRc5 cameras driven by AxioVision Rel 4.8 software (AXIO Imager 2, Oberkochen, Germany). Conidia and conidiophores were mounted in lactophenol cotton blue mixture and measured using an ocular micrometer (confirmed with software available with the Zeiss microscope), with 30 observations per structure. Methods for inoculations, incubation conditions and microscopic slide preparations followed Senanayake et al. (2020). Culture characters were recorded after 2 weeks of incubation on Malt Extract Agar (MEA) and Potato Dextrose Agar (PDA) (HiMedia, Mumbai, India). Colour codes used in descriptions refer to Kornerup and Wanscher (1978). Culture is preserved at the National Fungal Culture Collection of India (NFCCI), MACS Agharkar Research Institute, Pune, India.

2.2. DNA extraction, amplification, and phylogenetic analyses

Genomic DNA was extracted following the protocols of the rapid salt extraction method described by Aljanabi and Martinez (1997), after two weeks of colony growth on MEA plates. The ITS region (ITS1, ITS2, and 5.8S nrRNA) was amplified using ITS5/ITS4 (White *et al*.,1990); the LSU region with LR0R/LR7 (Vilgalys and Hester 1990); and the *tef1α* gene with 983F/2218R primers (Rehner and Buckley 2005). The PCR amplification was performed in a 25 µL reaction volume containing 9.5 µL ddH_2O, 12.5 µL 2 × Taq PCR Master Mix with blue dye (Sangon Biotech, Shanghai, China), 1 µL of DNA template and 1 µL of each primer (10 µM). The amplification conditions for ITS and LSU followed the protocol of White *et al*., (1990), while those for *tef1α* followed the protocol of Rehner and Buckley (2005). The PCR products were purified using the StrataPrep PCR Purification Kit (Agilent Technologies, TX,97, California, USA) and sequenced with the same primers using the BigDye Terminator v. 3.1 Cycle Sequencing Kit (Applied Biosystems, Massachusetts, USA). Sequencing reactions were performed on an ABI PRISM® 3100 Genetic Analyser (Applied Biosystems, Massachusetts, USA).

The NCBI GenBank nucleotide sequence database was searched using MegaBLAST (Morgulis *et al.*, 2008) to identify the closest matching sequences in the database. A sequence dataset was compiled (Table 1) mainly based on sequences published by Leplat et al. (2022). This dataset was aligned with our newly obtained sequences using MAFFT v. 7.453 (Katoh *et al*., 2019) with the G-INS-i option. Species of *Engyodontium* (*Cordycipitaceae*) were chosen as an outgroup (*E. aranearum* CBS 658 80*, E. parvisporum* IHEM 229 10*, E. rectidentatum* CBS

547 82, *E. rectidentatum* CBS 641 74, *E. rectidentatum* CBS 206 74) for the combined ITS-LSU-*tef1α* analyses. Sequence alignments were manually edited where necessary using BioEdit v.7.0.9.0 (Hall 1999), after which the alignments were concatenated using Sequence Matrix v.1.9 (Vaidya et al., 2011). AliView (Larsson, 2014) was used to convert the alignment file into PHYLIP and NEXUS formats for Maximum Likelihood (ML) and Bayesian analyses, respectively. ML analyses were performed using IQ-TREE v.2.1.3 (Nguyen et al., 2015, Kalyaanamoorthy et al. 2017, Minh et al., 2020). Node support was calculated using 1000 non-parametric bootstrap replicates, with IQ-TREE selecting the best model for each data partition through the -m TESTNEW parameter during the analyses. GAMMA Model parameters were estimated with an accuracy of 0.1000000000 log-likelihood units. Every 100th tree was sampled and saved. Bayesian posterior probability (PP) analysis was performed using MrBayes v. 3.2.7a (Ronquist et al., 2012), with two parallel runs of four chains each, run for 100 million generations. The analysis used a stop value of 0.01, a temperature of 0.2 and sampled every 10th generation. The model of evolution was estimated using MrModeltest 2.2 (Nylander, 2004). A 50 % majority rule consensus tree was constructed after discarding the first 25 % of sampled trees as burn-in. The resulting trees were visualised with Figtree v1.3.1 (Rambaut, 2010), and MEGA 7 (Kumar et al., 2016) and tree layout was prepared in Microsoft PowerPoint. DNA sequences newly generated in this study were deposited in GenBank. Species identification was conducted following the guidelines of Chethana et al. (2021) and Pem et al. (2021).

Table 1. Isolates and sequences used in this study (newly generated sequences are indicated in bold).

Species	**Strain**	**ITS**	**LSU**	***tef1α***	**Reference**
Parengyodontium album	IHEM 4198	LC092887	LC092906	LC425561	Tsang *et al.* (2016)
P. album	UAMH 4512	LC092888	LC092907	LC382182	Tsang *et al.* (2016)
P. album	UAMH 11234	LC092890	LC092909	LC425560	Tsang *et al.* (2016)
P. album	UAMH 8313	LC092889	LC092908	—	Tsang *et al.* (2016)
P. album	CBS 504.83	LC092880	LC092899	LC425535	Tsang *et al.* 2016
P. album	CBS 836.71	LC092882	LC092901	LC382178	Tsang *et al.* (2016)
P. album	UAMH 1441	LC092884	LC092903	LC425557	Tsang *et al.* 2016
P. album	UAMH 10043	LC092885	LC092904	LC425537	Tsang *et al.* (2016)
P. album	CBS 121919	LC092883	LC092902	LC425536	Tsang *et al.* (2016)
P. album	CBS 570.71	LC092881	LC092900	LC425551	Tsang *et al.* (2016)
P. album	**NFCCI 6156**	**PX398752**	**PX398979**	**PX406570**	**This study**
Parengyodontium americanum	CA11	KY683771	—	—	Teixeira *et al.* (2020)
P. americanum	CA13	KY683772	—	—	Teixeira *et al.* (2020)
P. americanum	CA19	KY683773	—	—	Teixeira *et al.* (2020)

P. americanum	CA21	KY683774	—	—	Teixeira *et al*. (2020)
P. americanum	AZ2	KY683770	—	—	Teixeira *et al*. (2020)
Parengyodontium torokii	CBS 368.72	LC092891	LC092910	LC382183	Tsang *et al.* (2016)
P. torokii	NRLL 64203	MT704894	—	—	Parker *et al*. (2022)
P. torokii	UAMH 9836	LC092892	LC092911	LC382184	Tsang *et al.* (2016)
P. torokii	CBS 658.80	LC092897	LC092916	—	Tsang *et al.* (2016)
P. torokii	IHEM 22910	LC092896	LC092915	LC425558	Tsang *et al.* (2016)
P. torokii	CBS 547.82	LC092894	LC092913	LC425544	Tsang *et al.* (2016)
P. torokii	CBS 641.74	LC092895	LC092914	LC425540	Tsang *et al.* (2016)
P. torokii	CBS 206.74	LC092893	LC092912	LC425553	Tsang *et al.* (2016)

3. Results

3.1. Phylogeny

Based on a MegaBLAST search of the strain in NCBI's GenBank nucleotide database, the closest matches using ITS were; *P. album* KNUE 24S046 [GenBank PQ357218; Identities = 560/560(100%), Gaps = 0/560(0%)], *P. album* OUCMDZ-5353 [GenBank OR978341; Identities = 560/560(100%), Gaps = 0/560(0%)] and *P. album* S2_9_2 [GenBank LR782548; Identities = 560/560(100%), Gaps = 0/560(0%)]. The closest hits using LSU were *P. album* LRMH C327 [GenBank OL981481; Identities = 861/861(100%)), Gaps = 0/861(0%)], *P. album* LRMH C267 [GenBank OL981478; Identities = 861/861(100%), Gaps = 0/861(0%)], *P. album* LRMH C343 [GenBank OL981482; Identities = 860/860(100%), Gaps = 0/860(0%)]. The closest hits using *tef1α*-were *P. album* CBS 570.71 [GenBank LC425551; Identities = 589/589(100%), Gaps = 0/589(0%)], *P. album* CBS 121919 [GenBank LC382179; Identities = 589/589(100%), Gaps = 0/589(0%)], *P. album* UAMH 1441 [GenBank LC425557; Identities = 587/589(99%), Gaps = 0/589(0%)].

The final combined ITS-LSU-*tef1α* dataset consisted of 1731 characters, including all alignment gaps for 24 strains, including the outgroups. A maximum likelihood (ML) tree was obtained from the concatenated alignment using IQ-TREE with a log-likelihood of -4052.322. The matrix contained 208 distinct alignment patterns, including 180 parsimony-informative sites, 51 singleton sites, and 1500 constant sites. Parameters for the TN+F+I model of the combined ITS-LSU-*tef1α* dataset were estimated as follows: base frequencies A = 0.230, C = 0.289, G = 0.273, T = 0.209; substitution rates AC = 1.00000, AG = 1.05576, AT = 1.00000, CG = 1.00000, CT = 5.00777, GT = 1.00000. The final ML tree derived from sequence analyses of a concatenated dataset with posterior probability PP values superimposed is shown in Figure 2. Phylogenetic analyses of both the concatenated datasets and individual gene datasets confirmed the placement of the *Parengyodontium album* NFCCI 6156 within *P. album* Clade 1 with statistical support (ML-BS/BY-PP: 100/1.00)

4. Taxonomy

Parengyodontium album (Limber) C.C.C. Tsang, J.F.W. Chan, W.M. Pong, J.H.K. Chen, A.H.Y. Ngan, M. Cheung, C.K.C. Lai, D.N.C. Tsang, S.K.P. Lau & P.C.Y. Woo, *Medical Mycol.* 54(7): 709, 2016 (Fig.1).

Index Fungorum Registration Identifier: 815050.

Hyphae, hyaline, septate, 0.90-1.80µm wide. *Conidiophores* erect to procumbent, mononematous, septate, smooth-walled, occasionally biverticillate, with one to five whorls of conidiogenous cells borne at wide or right angles. *Conidiogenous cells* elongated, tapering, 22–26 (up to 35µm × 1.6–1.8 µm, and the terminal fertile region is zigzag in shape. *Conidia* smooth, hyaline, globose to sub-globose, 2.1–2.7 × 1.6–2.0 µm, apiculate, and produced at each bent point of the zigzag rachides.

Culture characteristics: — Colonies on MEA at 25 ± 2 ºC after 7 d, 14–16 mm diam., white (5A1), cobweb-like, floccose, velvety, umbonate at centre, colonies reverse white (5A1) to orangish white (5A2). Margin irregular, lobate.

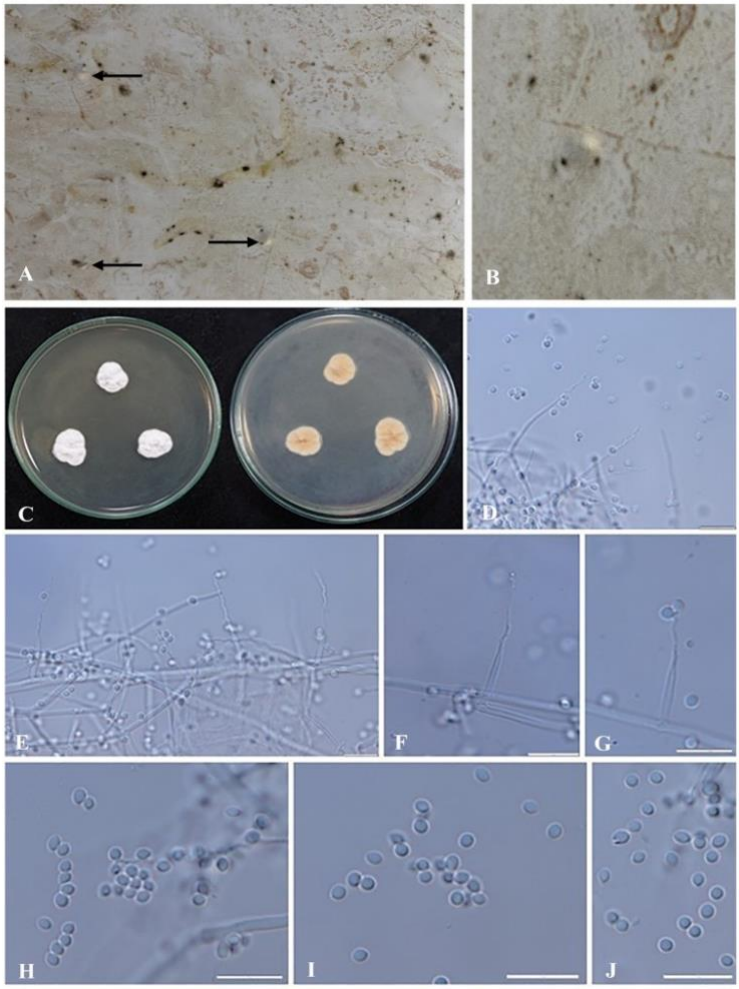

Figure 1. A. Colonies on substrate, B. Enlarged image of colony, C. Colonies on MEA (obverse and reverse) at 25±2 °C after 7 days. D, E. Elongated rachis with attached and dispersed conidia. F, G. Lateral rachis with sympodial narrow tip. H, I, J. Conidia. Scale bars: B = 20 µm, C = 10 µm, D = 20 µm, E–L = 10 µm. M– Q = 20 µm.

Materials examined: — INDIA. Maharashtra, Pune, Pimpri Chinchwad, 18.602016°N 73.744636°E, on the wall of Bathroom, 22 October 2023, KC Rajeshkumar, (culture NFCCI 6156).

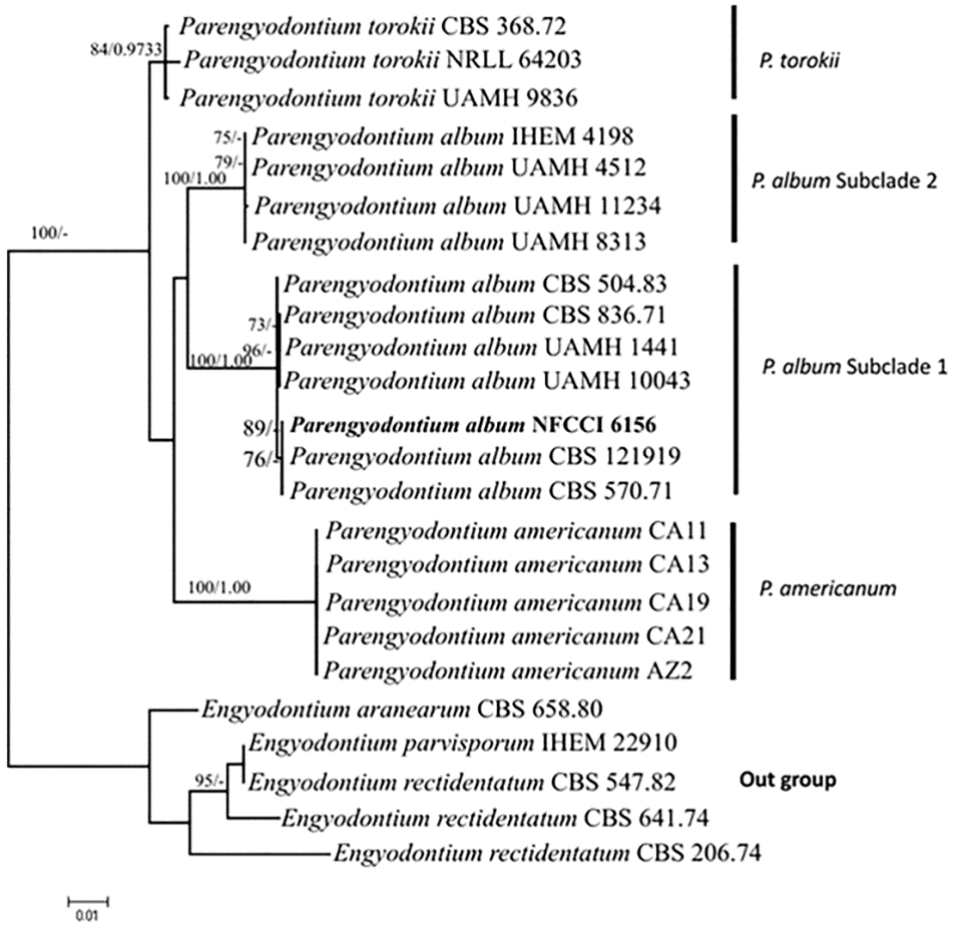

Figure 2. Maximum likelihood (ML) phylogenetic tree obtained from an IQ-TREE analysis of species from *Parengyodontium* based on LSU, ITS, and *tef1α* sequences. Strains of the species under study are shown in bold text. Subclades are indicated on the right side of the tree in blocks. Branch support values from 1000 non-parametric bootstraps for IQ-TREE (ML-BS) and posterior probability values from the Bayesian analysis (BY-PP) are shown at the nodes (ML-BS>70%/BY-PP>0.9). The tree is rooted with members of *Engyodontium*.

Notes:*P. album* NFCCI 6156, clusters with *P. album* CBS 121919 and *P. album* CBS 57071 within *P. album* subclade 1, supported by 100% ML and 1.00 BY-PP values. Morphologically, the strain closely resembles other isolates of *P. album*. Compared with the type description, the conidiophores of *P. album* NFCCI 6156 (22–26 × 1.6–1.8 µm) are slightly larger than those of *P. album* CBS H-22418 (10–24 × 1.5–2.5 µm). Similarly, the conidia of *P. album* NFCCI 6156 (2.1–2.7 × 1.6–2.0 µm) are larger than those of *P. album* CBS H-22418 (1.1–2.5 × 1.4–3.2 µm). Despite these dimensional differences, the overall shape and characteristics of the conidia remain consistent. Based on these morphological similarities and strong molecular support, the present strain is identified as *P. album*. A comparison summary of the species currently recognised under *Parengyodontium* is presented in Table 2.

Table 2. Comparative morphology of *Parengyodontium* species.

Sl. No.	Species	Conidiogenous cells		Conidia		References
		Shape	Size (µm)	Shape	Size (µm)	
1	*P. album*	Solitary and in whorls of 2 to 3 cells; zigzag structure of phialides	13–50	Globose to subglobose	1.5–2.9 × 1.1–1.9	Tsang *et al.*(2016); Leplat *et al.* (2022)
2	*P. torokii*	Solitary and in whorls of 2 cells; zigzag structure of phialides	21–33	Ellipsoidal to sub-cylindrical	2.0–4.1 × 1.2–1.7	Parker *et al.* (2022)
3	*P. americanum*	Pairs or solitary on a lateral stalk/stem; right-angled phialides and/or aphanophialids, usually verticillate	–	Cylindrical to globose	1.71±2.35 × 3.43 ± 2.35	Teixeira *et al.* (2020)

5. Discussion

The holotype of *Parengyodontium album* (BPI 414591), recovered from the cover of a book in Woods Hole, Massachusetts, USA, is a historical specimen from which neither an ex-type culture nor DNA material is available. To support the holotype, Tsang et al. (2016) designated CBS H-22418 (MBT 203989) as the epitype, isolated from a human brain abscess in Germany with CBS 504.83 serving as the ex-epitype culture. Other isolates of *Parengyodontium album* have been examined from a wide range of sources and geographical regions. For instance, isolate HKU48 (= NBRC 111624 = NCPF 7880) was recovered from a biopsy of a crusted skin lesion on the right shin of a human patient in Hong Kong. CBS 570.71 and UAMH 1441 were isolated from a human source in the Netherlands. CBS 836.71 was recovered from *Pisum sativum* (pea) in Israel, and CBS 121919 was reported from an uncontrolled diabetic patient with conjunctivitis in India. Additional isolates include IHEM 4198, obtained from human ear secretions in Italy, and NRRL 2312, recovered from dismal swamp soil in the USA.

Several isolates have also been recovered from human and veterinary clinical specimens in North America, including UAMH 4512 from a human eye wound, UAMH 8313 from human blood, UAMH 10043 from broodmare pleural fluid, UAMH 11234 from a human bioprosthetic valve from the prepuce of a giant panda and IFM 65407 from skin lesions of a dolphin suffering from Paracoccidioidomycosis (Kanegae et al., 2020). It has been implicated as a cause of allergic bronchopulmonary mycosis, cerebral abscess, cutaneous hyalohyphomycosis, endocarditis, fungemia, granulomatous mastitis, and keratitis in humans and cutaneous granulomatosis in dolphins. The ability of the mould to grow at human and dolphins' body temperature, production of extracellular enzymes like proteinases and keratinase and cytotoxic polyketides that inhibit vascular endothelial growth factor could play a role in the pathogenesis of infections in immunocompromised hosts. (Macêdo *et al*., 2007, Mohamed *et al., 2022*, Thamke *et al*., 2015, Tsang *et al*., 2016).

Other than being restricted to medical or veterinary specimens, *Parengyodontium album* has also been reported from a wide range of environmental and cultural heritage sites. In France, several isolates were obtained from subterranean and historical locations. For example, strain LRMH C120 was recovered from the Crypt of Saint-Savin-sur-Gartempe Abbey church (Nouvelle-Aquitaine) through surface sampling, while strains LRMH C267 and LRMH C268 originated from the Bastia Museum. From the Chauvet cave (Auvergne-Rhône-Alpes), strain LRMH C327 was isolated by surface sampling. Additionally, multiple isolates were recovered from the Cosquer cave (Provence-Alpes-Côte d'Azur) through air sampling, including LRMH C343, LRMH C345, LRMH C346, LRMH C349, LRMH C350, LRMH C355, and LRMH C358, highlighting the widespread presence of this species in cave ecosystems (Leplat et al., 2022).

A strain of *Beauveria alba* identified by Chandrashekhar et al. (1981) on the abdomen of a spider cadaver (*Achaearanea* sp.) from Madras, Tamil Nadu, is now a synonym of *P. album*, although its identification has not been validated through molecular data. Tsang et al. (2016) established *Parengyodontium* as a distinct phylogenetic lineage within the family *Cordycipitaceae* and described three sub-clades of *P. album* and described as potential cryptic species, based on significant phylogenetic differences revealed through the study of ITS, LSU and *tub2* markers, despite the lack of morphological differences.

Leplat et al. (2022) further confirmed these subclades using additional markers (SSU, *tef1α*, *rpb1* and *rpb2*), revealing some intraspecific variability within *P. album* and *P. torokii*, though insufficient to describe new species. Sequencing of *tef1α* consistently failed in *P. torokii*, whereas all *P. album* strains were successfully sequenced, suggesting primer incompatibility specific to *P. torokii*. In our study, ITS, LSU and *tef1α* sequences were successfully amplified and used for phylogenetic analyses.

The cosmopolitan distribution of this fungus and its potential to bridge the gap between environmental reservoirs and clinical infection in humans and animals represents a classic "One Health" challenge (Mackenzie et al., 2019). This study represents the first authenticated record of *P. album* from an indoor environment in India, using an integrative molecular approach. The findings underscore the urgent need for large-scale investigations on *Parengyodontium*, given its potential to emerge as an opportunistic pathogen, particularly in densely populated regions like India, where diverse strains are likely to be encountered. At the same time, *P. album* has demonstrated remarkable plastic-degrading abilities, highlighting its ecological and biotechnological significance. Research on this genus is therefore critical both for medical mycology and for environmental biotechnology applications.

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Conflict of interest

There is no conflict of interest.

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