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1 Parengyodontium album, a frequently reported fungal species in the cultural

2 heritage environment

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19 Abstract

Fungi are one of the main agents responsible for the biodeterioration of cultural heritage 20 21 through physical and chemical processes. The frequent isolation of certain fungal species from deteriorated materials indicates that these species appear to have a particular affinity for 22 environmental conditions occurring in cultural heritage. It is important to identify the 23 24 conditions that favour the development of such species in order to understand how to preserve 25 monuments and collections. Among these fungal species, the involvement of Parengyodontium album (Limber) Tsang et al. seems to have been underestimated until now. 26 This species is abundant in many environments and its taxonomic position has changed quite 27 frequently, which may have concealed the effect of this fungus on cultural heritage sites. This 28 29 review seeks to compile the involvement of P. album in cultural heritage biodeterioration phenomena under all the names that it has been attributed in order to effectively determine its 30 31 occurrence. This paper also aims to determine whether P. album is marginal or dominant 32 when detected on materials. Finally, the conditions that favour the development of P. album on cultural heritage objects and sites are discussed. 33

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35 Keywords

36 Parengyodontium album, Cultural heritage, Halotolerant species, Mesophilic species,
 37 Enzymes producer, Entomogenous species

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39 **1. Introduction**

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The risk encountered by cultural heritage when colonized by fungal strains is widely knownand recognized. Fungi can cause serious damage not only to buildings but also to their

contents in the case of museums or libraries, whatever the nature of the material considered 43 (Sterflinger, 2010; Sterflinger and Piñar, 2013). First, fungi can cause aesthetic damage 44 through staining or pigment discoloration (Ciferri, 1999; Krumbein, 2002), as observed when 45 black fungi grow on historical stones (Cappitelli et al., 2007; Isola et al., 2015), or in the 46 phenomenon known as "foxing" that occurs on historical papers (Sterflinger and Piñar, 2013). 47 48 This initial aesthetic damage can be followed by more serious damage to the support (Ciferri, 49 1999). Indeed, fungal growth can also lead to physical and chemical damage (Scheerer et al., 2009; Warscheid and Braams, 2000). Physical damage can occur when fungal hyphae enter 50 the support through stone pores or through decayed stone parts and then by tunnelling into 51 52 otherwise intact mineral material (Gadd, 2007). In painted surfaces, the growth of fungi through cracks and its migration below the paint layer can cause detachments (Sterflinger, 53 2010). Finally, the secretion of organic acids by fungi lead to chemical damage to the support, 54 55 meaning that fungi are able to solubilize minerals (Burford et al., 2003; Gadd, 2007; Warscheid and Braams, 2000). 56

57 Among the fungi observed in cultural heritage, we were surprised and above all intrigued by 58 the frequent observation of the fungal species Parengyodontium album (Limber) Tsang et al. in several published and unpublished studies (Leplat et al., 2017; Leplat et al., 2019). The 59 articles cited in this introduction provide a wide review of fungal biodeterioration on 60 monuments as well as in museums, yet only Gadd (2007) mentions P. album as a fungus that 61 is frequently observed on stone. This review therefore aims to determine the true occurrence 62 of *P. album* in cultural heritage and identify the factors that lead to this occurrence in cultural 63 sites. 64

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69 2. Brief history of *Parengyodontium album* taxonomy

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71 Like many other fungal species, Parengyondontium album has had several successive names and changed fungal genus several times before being referred to by its current name. This 72 species was first described as Tritirachium album (Limber, 1940). The new genus 73 Tritirachium was created to describe fungal species bearing verticillately branched 74 conidiophores like Verticillium, but which differ insofar that they have a final zigzag conidia-75 bearing portion (Fig. 1). The genus included three species including Tritirachium album, 76 77 which had been separated from a colony of Penicillium found on a book in a marine biological laboratory and had been considered as a possible contaminant. 78

The species was then renamed *Beauveria alba* and moved into the already existing *Beauveria* genus, which is also characterized by zigzag conidia-bearing portions because of the denticulation of its rachis and the absence of pigment in aerial mycelium (Saccas, 1948; Fig. 2), which characterizes *Tritirachium* species.

De Hoog (1978) created the genus *Engyodontium* and incorporated *Beauveria alba* under the
name *Engyodontium album* (or *Engyodontium albus*). This change made the genus *Beauveria*more homogeneous by limiting it to species with dense clusters of short branches and fertile
cells on undifferentiated hyphae, whereas *Beauveria alba* did not have a dense subverticillate
to verticillate branching pattern.

Finally, Tsang et al. (2016) found that *Engyodontium album* was phylogenetically and chemotaxonomically different to the three other species making up the genus *Engyodontium* and created the new genus *Parengyodontium* for the sole species *Parengyodontium album*. It was the first time that the species was renamed for other reasons than morphological features.

The study of this new genus also revealed that the species *Parengyondontium album* probably 92 93 includes several subclades. This article will exclusively use the name Parengyodontium album to describe this fungus. 94

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3. Occurrence of *Parengyodontium album* in cultural heritage 96

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3.1 Parengyodontium album: a worldwide distributed species

99 Whatever the name used to describe it, Parengyodontium album has frequently been reported 100 in historical buildings, museums, libraries and touristic sites. Its detection around the world shows that it is a ubiquitous fungal species (Fig. 3). It has been found on a Chilean world 101 heritage site in southern America (Ortiz et al., 2014), in a Cuban museum in central America 102 (Borrego and Molina, 2019), and in a show cave in north America (Vaughan et al., 2011). The 103 104 fungus has also been isolated across Europe from Portugal to Russia, with observations of its presence in England, Spain, France, Germany, Italy and Poland (Jeffries, 1986; Liñán et al., 105 2018; Nugari et al., 2009; Pfendler et al., 2018; Piotrowska et al., 2014; Ponizovskaya et al., 106 107 2019; Schabereiter-Gurtner et al., 2001; Trovão et al., 2019). Finally, P. album has also been detected in Africa and in Asia, but not in a cultural heritage-related environment (Jaouani et 108 al., 2014; Zhang et al., 2013). 109

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3.2. *Parengyodontium album*: a species which develops on a great diversity of cultural sites and materials 112

113 The most commonly reported occurrences of Parengyodontium album are in religious monuments such as churches, cathedrals or monasteries (Table 1). A number of different 114 materials are affected by the presence of the fungus in these monuments. The first of these 115

materials is wall paintings: the fungus has been isolated on wall paintings located in the 116 "aerial parts" of the monuments (Jeffries, 1986; Sáiz-Jiménez and Samson, 1981; Sampo and 117 Mosca, 1989) and also in the underground parts of the monuments such as the crypts 118 119 (Gorbushina and Petersen, 2000; Leplat et al., 2017; Fig. 4). The stone structure of buildings is also affected, as shown by the isolation of the fungus from the bare stone inside 120 (Karpovich-Tate and Rebrikova, 1991; Pfendler et al., 2018; Pinheiro et al., 2018) and outside 121 the monument (Saiz-Jimenez, 1993; Trovão et al., 2019). Historical glasswork is also 122 affected, as shown by the isolation of *P. album* from the windows of Stockkämpfen church 123 (Schabereiter-Gurtner et al., 2001). 124

Caves are the second kind of cultural sites in which P. album have frequently been reported. 125 The term "cave" covers a wide variety of different geological cases that vary from large caves 126 that are several hundred meters deep to small sites that are around ten-meters deep or even 127 simple rock shelters. The caves in which P. album has been isolated represent different 128 aspects of cultural interest, ranging from caves known for their Paleolithic ornamentation, 129 130 such as Lascaux cave in France (Bastian et al., 2010) to more recent Byzantine-style 131 ornamentation, such as the crypt of the Original Sin in Italy (Nugari et al., 2009) and show caves visited for their geological interest (Vaughan et al., 2011). Like in religious monuments, 132 P. album was isolated in caves from wall paintings (Nugari et al., 2009), or directly from the 133 bare rock (Bastian et al., 2010; Lepinay et al., 2017; Mihajlovski et al., 2019; Nováková, 134 2009; Vaughan et al., 2011). The novel difference observed in comparison with religious sites 135 is that P. album has been abundantly detected not only on surfaces but also in the atmosphere 136 of the caves (Leplat et al., 2019; Liñán et al., 2018; Marvanová et al., 1992; Nováková, 2009). 137 Finally, *P. album* was reported on a historical wood staircase located in a mine that dates back 138 to the bronze and iron age in Austria (Piñar et al., 2016), an environment that is comparable to 139

that of caves. After wall paintings, stone, and glasswork, wood is therefore another kind ofsupport that can be colonized by *P. album*.

142 The third group of cultural sites in which the presence of P. album has been reported is composed of all types of sepulchral site, *i.e.* from hypogean tombs dating from Etruscan and 143 Roman times (Saarela et al., 2004; Sprocati et al., 2008) to the tombstones of an historical 144 145 Jewish cemetery (Krumbein et al., 1996). In environmental terms, hypogean tombs are cut in the rock and are thus are similar to caves, while tombstones show similar features to the 146 external face of religious monuments, both being made of stone that is typically exposed to an 147 148 urban environment. The phenomenon observed in caves has also been reported in the Christian catacomb of St. Domitillus in Rome, where *P. album* isolated from the air as well as 149 from the wall paintings on marble, limestone and plaster supports (Saarela et al., 2004). 150

More recent historical buildings erected during the 20th century are also affected by the 151 presence of the fungus, which has been found in the barracks of the Auschwitz-Birkenau 152 camp in Poland and in buildings at the Humberstone and Santa Laura saltpeter works in Chile 153 (Koziróg et al., 2014; Ortiz et al., 2014; Piotrowska et al., 2014). In Auschwitz, P. album was 154 isolated from mineral components such as plaster and brick and also from wooden parts. 155 Similarly, P. album was isolated from wood in a building at Santa Laura saltpeter works; this 156 is surprising given the location of the buildings in the Atacama Desert, an extreme 157 environment characterized by dry conditions. 158

Finally, museums and libraries are also affected by the presence of the fungus, as shown by the isolation of *P. album* inside several of these buildings (Borrego and Molina, 2019; Micheluz et al., 2017; Ponizovskaya et al., 2019; Principi et al., 2011; Trovão et al., 2013). In some cases, the fungus has been detected on the internal stone or plaster walls of the museums (Ponizovskaya et al., 2019), while it has been detected directly on artworks in other cases (Borrego and Molina, 2019). These include samples of remarkable artworks such as Leonardo

da Vinci's Atlantic Codex (Principi et al., 2011), indicating that P. album can also be detected 165 166 on paper. The fungus was indirectly detected in the Archives of the University of Coimbra, where it was isolated from an Araneae during a survey about arthropod-disseminated fungi 167 (Trovão et al., 2013), and was also detected in an airborne form in the Library of Humanities 168 of the Ca' Foscari University of Venice (Micheluz et al., 2017). 169

170 To resume, Parengyodontium album has been detected on a wide variety of cultural heritage supports ranging from wall paintings, stone, plaster and brick to glass, wood and paper, and is 171 even observed in an airborne form. 172

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3.3 Parengyodontium album: associated symptoms and relative abundance on cultural 175 heritage

176 Parengyodontium album has been associated with several different symptoms of deterioration in cultural heritage, without necessarily being considered to play a determining role in their 177 development. Amongst these symptoms, the presence of soluble salt efflorescence has been 178 the most frequently cited in relation to the fungus (Ponizovskaya et al., 2019; Trovão et al., 179 2019). The most commonly observed is gypsum, which can occur alone or be associated with 180 181 organic compounds. However, P. album has also been isolated from calcium salts of oxalate, carbonate and chloride (Lepinay et al., 2017; Mihajlovski et al., 2019; Saiz-Jimenez, 1993; 182 183 Sáiz-Jiménez and Samson, 1981). The second kind of symptoms associated with P. album is 184 discoloration and patina (modification of the support colour) of various colors, including pink patina (Berner et al., 1997; Nugari et al., 2009), ochre discoloration (Berner et al., 1997), dark 185 stains or black spots (Bastian et al., 2009; Sáiz-Jiménez and Samson, 1981) and green-black 186 187 patina (Principi et al., 2011; Trovão et al., 2019). The fungus has also been associated with white covering that is visibly of fungal origin (Bastian et al., 2009; Leplat et al., 2017). 188

189 Finally, *P. album* has been isolated from powdered historical stones (Karpovich-Tate and190 Rebrikova, 1991).

191 The abundance of P. album when detected on cultural heritage varied as much as the symptoms encountered or the materials affected. In some cases, P. album was the most 192 abundant species isolated from deterioration symptoms, while in other cases only traces of the 193 fungus were detected. In other studies, P. album was detected at varying levels of abundance 194 195 along with other species. For example, P. album has often been the most abundant detected species when salt efflorescence (a coating caused by the migration of soluble salt contained in 196 197 a porous material to the surface) was present (Ponizovskaya et al., 2019; Trovão et al., 2019), but in other cases this species was noted simply as a relatively abundant secondary species 198 (Lepinay et al., 2017; Mihajlovski et al., 2019; Sáiz-Jiménez and Samson, 1981). Nugari et al. 199 200 (2009) failed to isolate the fungus on culture medium during their study of the pink patina on the Crypt of the Original Sin and finally identified it through SEM, yet it was the most 201 abundant fungal species isolated by Berner et al. (1997) from a pink patina sample of the 202 203 chapel of Herberstein Castle. This result does not suffice to confirm a role of P. album in the 204 development of the pink patina, as the fungus was also abundantly isolated from ochre discoloration in the same study. However, these elements can indicate that this environment is 205 206 globally favourable to the growth of *P. album*. The fungus has been abundantly isolated from the air of monuments when it was tested, and this was especially true of hypogean 207 environments: P. album was one of the most abundant airborne fungi isolated in Roman 208 209 catacombs of St. Domitilla and in the Nerja cave (Liñán et al., 2018; Saarela et al., 2004), while it was only a secondary species in an air sample taken from a library in Venice 210 211 (Micheluz et al., 2017).

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4. Particularities of cultural heritage environments that favour the development of *Parengyodontium album*

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The microbial colonization of cultural heritage depends on environmental factors such as 218 219 water availability, pH, climatic exposure, nutrient sources and the capacity of microorganisms 220 to withstand possible sources of stress such as desiccation or UV radiation (Scheerer et al., 221 2009; Warscheid and Braams, 2000). Parengyodontium album is a chemoorganotrophic 222 organism, and its development is dependent on its capacity to obtain organic compounds from an environment which is sometimes poor in nutrients, such as stone (Gadd, 2007; Sterflinger, 223 2010). The central necessity is therefore to identify the common factors in the identified 224 cultural heritage sites that can lead to the development of *P. album*. 225

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4.1 *Parengyodontium album*: a species adapted to salty, moist environments

One of the principle factors in the growth of *P. album* seems to be the presence of salts on the 228 229 supports it colonizes. Although the preceding paragraph notes that the fungus has been 230 abundantly isolated directly from salt efflorescences, salts were also often present but not necessarily visible in other sites where the fungus grew. For example, the phenomenon of 231 pink patina on historical stones and wall painting has been well documented to date. 232 233 Parengyodontium album is not the main agent of these discolorations, which are often related to bacterial biofilms (Piñar et al., 2014). Sites affected by pink patina all have problems of 234 water infiltration and salt crystallization, two phenomena that often occur simultaneously. 235 Problems of moisture and of water infiltration have also been widely observed on the walls of 236 monuments from which *P. album* has been isolated (Berner et al., 1997; Karpovich-Tate and 237

Rebrikova, 1991; Leplat et al., 2017; Pfendler et al., 2018; Simonovicova et al., 2003). 238 239 Moreover, airborne P. album has been repeatedly reported in caves, an environment known for relative humidity values that can sometimes approach 100 % (Liñán et al., 2018; 240 241 Nováková, 2009). This affinity of P. album for humid, salty environments is not a surprise since the fungus has often been isolated from the marine environment, including marine 242 sediments (Chellappan et al., 2006; Kirichuk et al., 2012; Yao et al., 2014; Zhang et al., 243 2013), marine sponges (Wu et al., 2016), or directly from sea water (Pindi, 2012). P. album is 244 therefore regarded as a halotolerant fungus that can grow on synthetic media supplemented 245 with NaCl 20 % (Ali et al., 2013; Jaouani et al., 2014). 246

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4.2 Parengyodontium album: a mesophilic species

Little data is available concerning the effect of temperature on the growth of 249 250 Parengyodontium album. The fungus is generally considered mesophilic (Airaudi and Marchisio, 1996; Xia et al., 2018). Although P. album is capable of surviving at sub-zero 251 temperatures, as proved by multiple observations of this species in Arctic and Antarctic 252 environments, it is unable to grow at 0 °C (Bergero et al., 1999; Caretta et al., 1994; Zucconi 253 et al., 2012). The lowest temperatures at which this fungus can grow seem to be around 4 or 5 254 255 °C, temperatures at which P. album developed in some cases but not in others (Fernandes et al., 2008; Jaouani et al., 2014). The P. album samples that had not grown at low temperatures, 256 germinated when temperatures were increased to 25 °C, suggesting that the fungus was 257 258 inhibited at low temperatures without being killed. Parengyodontium album is generally not capable of growing at temperatures above 31 °C. The only exception is the strains belonging 259 to subclade 2 of the three subclades defined by Tsang et al. (2016), which can grow at 35 °C. 260 261 This temperature range for growth ranging from approximately 5 to 30 °C and the capacity of the fugus to survive at low temperatures make P. album a species that is well adapted to the 262

environmental conditions of cultural heritage monuments. Notably, *P. album* survives on
monuments subjected to cold winters, then grows when weather becomes milder (Piotrowska
et al., 2014), or grows in sites such as caves that remain relatively cool throughout the year
(Nováková, 2009).

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4.3 Parengyodontium album: a species capable of feeding on various nutrient sources 268 As chemoorganotrophic organisms, P. album cannot develop without the presence of organic 269 matter as a nutrient in the environment. For example, it has been proposed that P. album can 270 271 feed on the organic pollutants in black crusts (Sáiz-Jiménez, 1997). Phototrophic organisms 272 such as algae, cyanobacteria or lichens are generally considered as the primary colonizers in environments that are poor in nutrients, such as stone (Dakal and Cameotra, 2012; Scheerer et 273 al., 2009; Warscheid and Braams, 2000). The accumulation of the photosynthetic biomass 274 275 created by the development of theses primary colonizers provides a suitable environment for 276 the growth of heterotrophic organisms. Parengyodontium album appears to be one such recipient of this microbial succession (Karpovich-Tate and Rebrikova, 1991), and is able to 277 recolonize supports on remaining dead biofilms following UVc treatments (Pfendler et al., 278 2018). 279

Parengyodontium album has also been shown capable of feeding on products used in 280 restoration of wall paintings. Cappitelli et al. (2004) noted that the fungus could develop on 281 several synthetic resins, and Sampo and Mosca (1989) isolated a fungal species that probably 282 283 belonged to P. album and was capable of growing on calcium caseinate and liquifying animal glue. Indeed, it is well known that *P. album* is an enzyme producer. It is used for the industrial 284 285 production of proteinase K, which acts as serine endopeptidase and induces a keratin hydrolysis activity (Ebeling et al., 1974; Jany et al., 1986). The use of proteinase K produced 286 by *P. album* to facilitate the hydrolysis of animal glue on paper artwork during a restoration 287

process is somewhat ironic given the otherwise damaging effect of this fungus in the cultural 288 289 heritage domain (Micheli et al., 2018). This keratinolytic activity and the capacity of the fungus to produce cytotoxic polyketides led to the recognition of P. album as an emerging 290 291 opportunistic pathogen (Tsang et al., 2016). The keratinolytic activity could also become an issue for the conservation of antique textiles (Błyskal, 2009). Besides the production of 292 protease, *P. album* has also been recognized as a producer of α -amylase, esterase, phosphatase 293 294 lipase and chitinase (Ali et al., 2014; Jaouani et al., 2014; Karpovich-Tate and Rebrikova, 295 1991). A number of studies have shown these enzymes to be effective under high salinity conditions (Ali et al., 2014; Jaouani et al., 2014), which could explain the favourable 296 297 development of *P. album* on monuments affected by salt crystallization.

The production of chitinase by P. album leads us to consider the entomogenous character of 298 299 this fungus. The exoskeleton of arthropods is mainly composed of chitin (Merzendorfer, 2006). The role of arthropods in the dissemination of fungal species is commonly recognized, 300 especially in environments where insects are numerous such as caves, catacombs and mural 301 302 paintings (Bastian et al., 2009; Jurado et al., 2008; Trovão et al., 2013). Dead insects also 303 provide a source of nutrients for entomogenous fungi in these nutrient-poor environments. It is well known that some of the successive fungal genera in which P. album has been classified 304 contain entomogenous species, *i.e. Beauveria* and Engyodontium (Samson et al., 2013). 305 Indeed, Beauveria bassiana and B. brongnartii are used as commercial biological control 306 agents against various pests (Butt and Copping, 2000), and Engyodontium parvisporum and 307 308 E. geniculatum have been isolated from arthropods (Gams et al., 1984). Several authors have linked the development of P. album on cultural heritage monuments to the presence of insects 309 310 (Gorbushina and Petersen, 2000; Jurado et al., 2008; Liñán et al., 2018; Nugari et al., 2009; Principi et al., 2011). Although the association between P. album and arthropods has often 311 been suggested rather than proved, the fungus has been isolated from spiders in at least three 312

different studies (Chandrashekhar and Narasimham, 1981; Martynenko et al., 2011; Trovão et
al., 2013). Given that spiders are actually a preferred host for species belonging, or having
belonged, to the *Engyodontium* genus (Gams et al., 1984), and in the knowledge that *P. album*is a chitinase producer, this association between arthropods and *P. album* is very likely.

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318 **5. Concluding remarks**

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The reviewing of multiple studies confirms that Parengyodontium album is a globally 320 321 distributed environmental fungal species that can be found in extreme environments such as polar soils. In studies dealing specifically with cultural heritage, P. album was frequently 322 isolated from deteriorated materials and from the environment of monuments, suggesting that 323 the role played by this fungal species in the biodeterioration process may have been 324 underestimated. The fungus was recovered from a wide range of supports including stone, 325 326 wood, glass and paper, and was also found in monuments in an airborne form. The presence of *P. album* was marginal in some cases, but this species was dominant in samplings of other 327 sites. The tolerance of *P. album* for salty environments could explain why it is often recovered 328 329 from cultural heritage materials which often suffer from water infiltrations and from the crystallization of soluble salts. These environments are generally poor in nutrients, but P. 330 album can feed on organic pollution, on biofilms composed of primary colonizers, and also 331 probably on certain products used for restoration processes. Finally, it is likely that P. album 332 is also capable of feeding on (dead) arthropods, and especially spiders, which are usually 333 334 abundant in caves and catacombs, or on wall paintings. Arthropods could also be a means of dissemination for the fungus in these environments. 335

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Table 1: Inventory of the cultural heritage sites sited in the article from which *Parengyodontium album* has been isolated

		Material affected							_		
Cultural heritage site	Stone		Wall paintings Wood		Plaster Brick		Paper	Air	Arthropod	Reference	
Lascaux cave, France										(Bastian et al., 2009; Bastian et al., 2010)	
Chapel of Herberstein Castle, Austria										(Berner et al., 1997)	
National Museum of Fine Arts, Cuba										(Borrego and Molina, 2019)	
Crypt of Kodersdorf parish church, Germany										(Gorbushina and Petersen, 2000)	
St. Peter and Paul church, Koenigslutter, Germany										(Gorbushina and Petersen, 2000)	
St. Martin's church, Kreiensen-Greene, Germany										(Gorbushina and Petersen, 2000)	
Canterbury Cathedral, England										(Jeffries, 1986)	
Cathedral of the Nativity of the Virgin, Pafnutii-Borovskii monastery, Russia										(Karpovich-Tate and Rebrikova, 1991)	
Concentration camp of Auschwitz II - Birkenau, Poland										(Koziróg et al., 2014; Piotrowska et al., 2014)	
An der Strangriede" cemetery in Hannover, Germany										(Krumbein et al., 1996)	
augerie-Haute shelter, France										(Lepinay et al., 2017)	
Crypt of Saint-Savin-sur-Gartempe Abbey church, France										(Leplat et al., 2017)	
Points cave, France										(Leplat et al., 2019)	
atrone cave, France										(Leplat et al., 2019)	
Bayol cave, France										(Leplat et al., 2019)	
Jarja cave, Spain										(Liñán et al., 2018)	
Ibrašov aragonite caves, Czech Republic										(Marvanová et al., 1992)	
Biblioteca di area umanistica (BAUM), Italy										(Micheluz et al., 2017)	
orcerer's cave, France										(Mihajlovski et al., 2019)	
Domica cave, Slovak Republic										(Nováková, 2009)	
Crypt of the Original Sin, Italy										(Nugari et al., 2009)	
Humberstone and Santa Laura saltpeter works, Chile										(Ortiz et al., 2014)	
hurch of Vicherey, France										(Pfendler et al., 2018)	

Staircase of Hallstatt, Austria		(Piñar et al., 2016)
Church of Boris and Gleb, Russia		(Ponizovskaya et al., 2019)
Kuskovo manor, Russia		(Ponizovskaya et al., 2019)
The State Tretyakov Gallery archive, Russia		(Ponizovskaya et al., 2019)
Leonardo da Vinci's Atlantic Codex, Italy		(Principi et al., 2011)
Roman catacombs of St. Domitilla, Italy		(Saarela et al., 2004)
Mechelen Cathedral, Belgium		(Saiz-Jimenez, 1993)
Monastery of Santa María de la Rábida, Spain		(Sáiz-Jiménez and Samson, 1981)
Ognissanti church, Italy		(Sampo and Mosca, 1989)
Church of Stockkämpfen, Germany		(Schabereiter-Gurtner et al., 2001)
Historical building from 17th century, Slovak Republic		(Simonovicova et al., 2003)
Necropolis of Tarquinia, Italy		(Sprocati et al., 2008)
Archive of the University of Coimbra, Portugal		(Trovão et al., 2013)
Kartchner caverns, USA		(Vaughan et al., 2011)

547 Grey boxes indicate the type of material from which *Parengyodontium album* has been isolated

548 **Captions for Figures**

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550	Figure 1:	Taxonomy	of Pare	engyodontium	album c	over time	(graphics	program:	Inkscape).
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The figure explains which factors led to taxonomical changes of *Parengyodontium album* from its first description until it was renamed by Tsang et al. The green annotations indicate the similarities between *P. album* and the genera to which it is compared whereas the red annotations indicate the dissimilarities.

555

Figure 2: Macroscopic picture (recto and verso) of *Parengyodontium album* on Malt extract
agar (MEA) (graphics program: Inkscape).

The figure shows the result of isolation following sterile swab sampling on the wall paintings of the crypt of Saint-Savin-sur-Gartempe Abbey church. The aerial mycelium of *P. album* is not pigmented, thus differentiating it from *Tritirachium* genus.

561

562 Figure 3: Distribution of isolation sites cited in the review (graphics program: R).

The map shows the global distribution of *P. album* as well as the variety of environmentsfrom which the fungus has been isolated.

565

Figure 4: Wall paintings of the crypt of Saint-Savin-sur-Gartempe Abbey church, affected by *Parengyodontium album.*

The picture clearly shows the presence of a white veil due to *P. album* across almost the entire surface of the vault, with the exception of small areas where the colors are more intense.







Latitude

