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1 ***Parengyodontium album*, a frequently reported fungal species in the cultural**
2 **heritage environment**

3

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19 **Abstract**

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

34

35 **Keywords**

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

38

39 **1. Introduction**

40

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

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

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.
59 in several published and unpublished studies (Leplat et al., 2017; Leplat et al., 2019). The
60 articles cited in this introduction provide a wide review of fungal biodeterioration on
61 monuments as well as in museums, yet only Gadd (2007) mentions *P. album* as a fungus that
62 is frequently observed on stone. This review therefore aims to determine the true occurrence
63 of *P. album* in cultural heritage and identify the factors that lead to this occurrence in cultural
64 sites.

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69 **2. Brief history of *Parengyodontium album* taxonomy**

70

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

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

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

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

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

95

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

97

98 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
101 shows that it is a ubiquitous fungal species (Fig. 3). It has been found on a Chilean world
102 heritage site in southern America (Ortiz et al., 2014), in a Cuban museum in central America
103 (Borrego and Molina, 2019), and in a show cave in north America (Vaughan et al., 2011). The
104 fungus has also been isolated across Europe from Portugal to Russia, with observations of its
105 presence in England, Spain, France, Germany, Italy and Poland (Jeffries, 1986; Liñán et al.,
106 2018; Nugari et al., 2009; Pfendler et al., 2018; Piotrowska et al., 2014; Ponizovskaya et al.,
107 2019; Schabereiter-Gurtner et al., 2001; Trovão et al., 2019). Finally, *P. album* has also been
108 detected in Africa and in Asia, but not in a cultural heritage-related environment (Jaouani et
109 al., 2014; Zhang et al., 2013).

110

111 3.2. *Parengyodontium album*: a species which develops on a great diversity of cultural 112 sites and materials

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

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

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

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

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

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

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

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

173

174 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
177 in cultural heritage, without necessarily being considered to play a determining role in their
178 development. Amongst these symptoms, the presence of soluble salt efflorescence has been
179 the most frequently cited in relation to the fungus (Ponizovskaya et al., 2019; Trovão et al.,
180 2019). The most commonly observed is gypsum, which can occur alone or be associated with
181 organic compounds. However, *P. album* has also been isolated from calcium salts of oxalate,
182 carbonate and chloride (Lepinay et al., 2017; Mihajlovski et al., 2019; Saiz-Jimenez, 1993;
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
185 patina (Berner et al., 1997; Nugari et al., 2009), ochre discoloration (Berner et al., 1997), dark
186 stains or black spots (Bastian et al., 2009; Sáiz-Jiménez and Samson, 1981) and green-black
187 patina (Principi et al., 2011; Trovão et al., 2019). The fungus has also been associated with
188 white covering that is visibly of fungal origin (Bastian et al., 2009; Leplat et al., 2017).

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

191 The abundance of *P. album* when detected on cultural heritage varied as much as the
192 symptoms encountered or the materials affected. In some cases, *P. album* was the most
193 abundant species isolated from deterioration symptoms, while in other cases only traces of the
194 fungus were detected. In other studies, *P. album* was detected at varying levels of abundance
195 along with other species. For example, *P. album* has often been the most abundant detected
196 species when salt efflorescence (a coating caused by the migration of soluble salt contained in
197 a porous material to the surface) was present (Ponizovskaya et al., 2019; Trovão et al., 2019),
198 but in other cases this species was noted simply as a relatively abundant secondary species
199 (Lepinay et al., 2017; Mihajlovski et al., 2019; Sáiz-Jiménez and Samson, 1981). Nugari et al.
200 (2009) failed to isolate the fungus on culture medium during their study of the pink patina on
201 the Crypt of the Original Sin and finally identified it through SEM, yet it was the most
202 abundant fungal species isolated by Berner et al. (1997) from a pink patina sample of the
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
205 discoloration in the same study. However, these elements can indicate that this environment is
206 globally favourable to the growth of *P. album*. The fungus has been abundantly isolated from
207 the air of monuments when it was tested, and this was especially true of hypogean
208 environments: *P. album* was one of the most abundant airborne fungi isolated in Roman
209 catacombs of St. Domitilla and in the Nerja cave (Liñán et al., 2018; Saarela et al., 2004),
210 while it was only a secondary species in an air sample taken from a library in Venice
211 (Micheluz et al., 2017).

212

213

214

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

217

218 The microbial colonization of cultural heritage depends on environmental factors such as
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
223 an environment which is sometimes poor in nutrients, such as stone (Gadd, 2007; Sterflinger,
224 2010). The central necessity is therefore to identify the common factors in the identified
225 cultural heritage sites that can lead to the development of *P. album*.

226

227 **4.1 *Parengyodontium album*: a species adapted to salty, moist environments**

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

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

247

248 4.2 *Parengyodontium album*: a mesophilic species

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

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

267

268 4.3 *Parengyodontium album*: a species capable of feeding on various nutrient sources

269 As chemoorganotrophic organisms, *P. album* cannot develop without the presence of organic
270 matter as a nutrient in the environment. For example, it has been proposed that *P. album* can
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
273 environments that are poor in nutrients, such as stone (Dakal and Cameotra, 2012; Scheerer et
274 al., 2009; Warscheid and Braams, 2000). The accumulation of the photosynthetic biomass
275 created by the development of these primary colonizers provides a suitable environment for
276 the growth of heterotrophic organisms. *Parengyodontium album* appears to be one such
277 recipient of this microbial succession (Karpovich-Tate and Rebrikova, 1991), and is able to
278 recolonize supports on remaining dead biofilms following UVc treatments (Pfendler et al.,
279 2018).

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

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

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

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

317

318 **5. Concluding remarks**

319

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

336

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338

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545

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

Cultural heritage site	Material affected									Reference
	Stone	Wall paintings	Wood	Plaster	Brick	Glass	Paper	Air	Arthropod	
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)
Laugerie-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)
Latrone cave, France								■		(Leplat et al., 2019)
Bayol cave, France								■		(Leplat et al., 2019)
Narja cave, Spain								■		(Liñán et al., 2018)
Zbrašov aragonite caves, Czech Republic								■		(Marvanová et al., 1992)
Biblioteca di area umanistica (BAUM), Italy								■		(Micheluz et al., 2017)
Sorcerer'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)
Church 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 17 th 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

549

550 Figure 1: Taxonomy of *Parengyodontium album* over time (graphics program: Inkscape).

551 The figure explains which factors led to taxonomical changes of *Parengyodontium album*
552 from its first description until it was renamed by Tsang et al. The green annotations indicate
553 the similarities between *P. album* and the genera to which it is compared whereas the red
554 annotations indicate the dissimilarities.

555

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

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

561

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

563 The map shows the global distribution of *P. album* as well as the variety of environments
564 from which the fungus has been isolated.

565

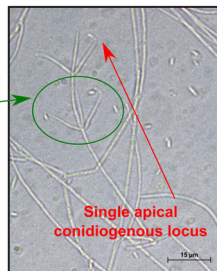
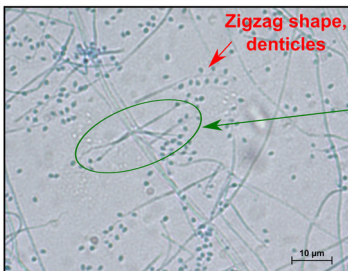
566 Figure 4: Wall paintings of the crypt of Saint-Savin-sur-Gartempe Abbey church, affected by
567 *Parengyodontium album*.

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

Tritirachium album

Verticillium sp.

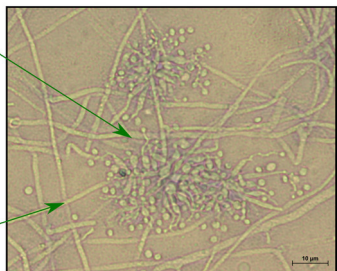
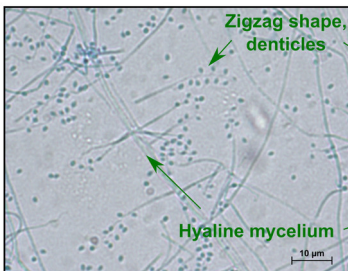
Limber 1940
Creation of
Tritirachium genus



Beauveria alba

Beauveria sp.

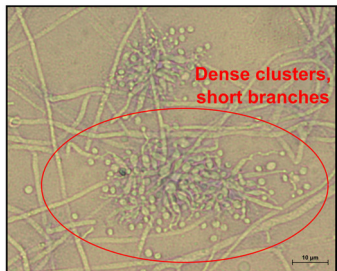
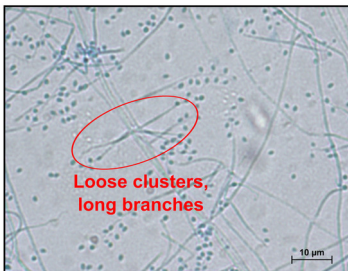
Saccas 1948
Moving in
Beauveria genus



Engyodontium album

Beauveria sp.

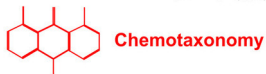
De Hoog 1978
Creation of
Engyodontium genus



Tsang et al. 2016
Creation of
Parengyodontium genus



Parengyodontium album



Similarities
Dissimilarities



