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Review

Current Knowledge on the Fungal Degradation Abilities Profiled through Biodeteriorative Plate Essays

João Trovão [1,*] and António Portugal [1,2]

[1] Centre for Functional Ecology, Department of Life Sciences, University of Coimbra, 3004-531 Coimbra, Portugal; aportuga@bot.uc.pt
[2] Fitolab-Laboratory for Phytopathology, Instituto Pedro Nunes, 3030-199 Coimbra, Portugal
* Correspondence: jtrovaosb@gmail.com

Abstract: Fungi are known to contribute to the development of drastic biodeterioration of historical and valuable cultural heritage materials. Understandably, studies in this area are increasingly reliant on modern molecular biology techniques due to the enormous benefits they offer. However, classical culture dependent methodologies still offer the advantage of allowing fungal species biodeteriorative profiles to be studied in great detail. Both the essays available and the results concerning distinct fungal species biodeteriorative profiles obtained by amended plate essays, remain scattered and in need of a deep summarization. As such, the present work attempts to provide an overview of available options for this profiling, while also providing a summary of currently known fungal species putative biodeteriorative abilities solely obtained by the application of these methodologies. Consequently, this work also provides a series of checklists that can be helpful to microbiologists, restorers and conservation workers when attempting to safeguard cultural heritage materials worldwide from biodeterioration.

Keywords: biodeterioration; cultural heritage; deteriorative action; enzymatic activity; fungi

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1. Introduction

The Fungal Kingdom comprises a highly diverse eukaryotic group able to inhabit every ecological niche available on the Planet [1]. The growth and biological activity of fungal species in cultural heritage materials is known to develop serious damages by means of biodeterioration (the undesirable modifications of a valuable material occurring by the action of living organisms) [2,3]. Fungi are highly versatile, ubiquitous, chemoheterotrophic microorganisms, being able to grow in a vast number of materials and contributing to the development of various biodeterioration phenomena [2,3]. Such modifications are a result from fungal species settling, development and exploitation of various organic and inorganic compounds present in historic art-pieces and monuments [2–15]. The fungal biodeterioration of books, paper, parchment, textiles, photographs, paintings, sculptures and wooden materials occurs due to the aesthetic modifications, mechanical pressure and exoenzymatic action [2]. Various components of these materials such as cellulose, collagen, linen, glues, inks, waxes and organic binders can be oxidized, hydrolyzed, dissolved, stained or structurally modified as a result of the action of fungal enzymes, pigments and organic acids [2,3,7–11]. A typical and widely known example of these phenomena is known as "foxing", the development of red-brownish localized spots, hypothesized to be a result from fungal proliferation and metabolization of organic acids, oligosaccharides and proteic compounds that can stain and modify the constituent materials of many paper-based and photographic supports [3,8,13]. Another example of microorganism's attack of organic materials is related to the biodeterioration of human remains, mummies and funerary materials, where opportunistic, saprotrophic and highly cellulolytic and proteolytic taxa are able to thrive and trough their actions severely alter them [2,14,15]. Complementarily, historic relics mainly composed of inorganic components such as stone, frescoes, glass and ceramics can also suffer deep aesthetical, physical and chemical modifications resulting from fungal grow and action [2–6,12,16]. In these supports, deterioration is caused by hyphae penetration into the substrate, the production and release of extracellular destructive organic acids, enzymes and metabolites and by the the formation of distinct colored outlines as a result of fungi high pigment contents, contribution to biofilm development and chemical reactions with inorganic compounds [2–6].

Due to the known biodeterioration problems arising from their proliferation, the accurate species identification and a consequent deteriorative profiling of isolates are crucial steps towards the development and the establishment of proper protective measures for the diverse cultural heritage treasures around the world. With the recent development of innovative culture independent methodologies such as -omics technologies, molecular data is becoming increasingly more valuable for the identification of the microbes, the characterization of their metabolic functions and their deteriorative byproducts [17]. Methodologies such as metagenomics, transcriptomics, metabolomics and proteomics revolutionized the field and are increasingly allowing understanding of microbial diversity, but also species specific and holistic contributions to various materials biodeterioration phenomena [17]. These methods are particularly relevant considering that traditional cultivation dependent methodologies hold the disadvantage of being unable to correctly infer microorganism's abundance and only allow the study of active forms, failing to provide information regarding viable non-culturable and non-viable forms [17–27]. Nonetheless, classical culture dependent methodologies still offer an important advantage when compared with modern methodologies, especially when considering that the isolation of microbes allows their natural biodeteriorative profiles to be studied in great detail. Culture media plates modified to specify a positive biodeteriorative ability upon the microorganism development and deteriorative action (see Figure 1 for examples) can provide valuable data that allow the evaluation of the microorganism's putative risks to cultural heritage materials. Moreover, they also offer a highly informative, rapid and low-cost platform [28] that can help in a quick and focused decision-making process aiming to protect valuable artifacts. Currently, plate assays aiming to identify fungal deteriorative characteristics, such as calcium carbonate solubilization, mineralization and various enzymatic activities, have been proposed and somewhat widely used.

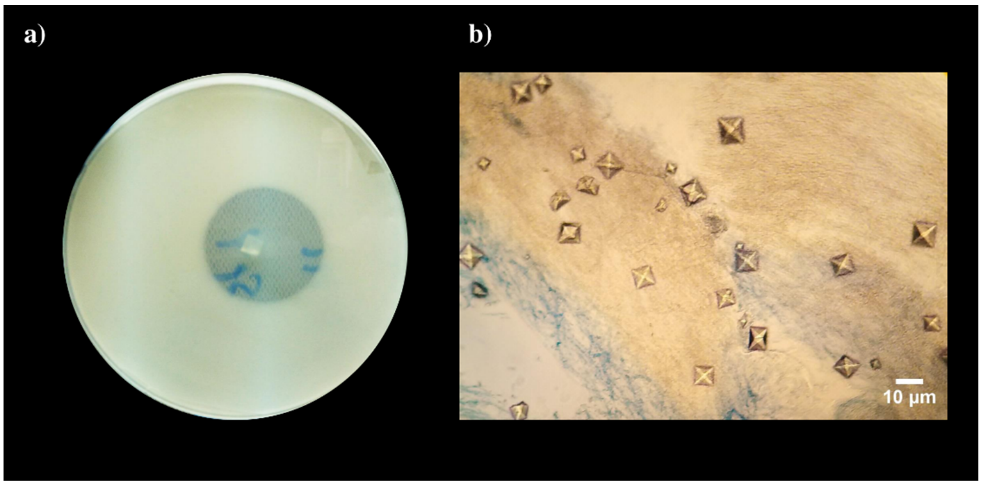

Figure 1. Examples of fungal species biodeteriogenic abilities detected through plate assays: (**a**) Calcium carbonate dissolution visualized by the development of a halo around colonies in $CaCO_3$ glucose agar; and (**b**) calcium oxalates crystals developing around fungal mycelium growing in Malt extract agar containing $CaCO_3$.

Although differences among distinct isolates, assays and incubation conditions are known and expected, the available literature concerning distinctive fungal species deteriorative profiles obtained using such methodologies remains pending a deep summarization. With this in mind, this work aims to provide an overview of available plate assays, as well as the fungal putative biodeteriorative profiles obtained solely through such tests so far. In addition, we also aimed at providing a series of quick and straight forward checklists that can be consulted by microbiologists, restorers and conservation staff, when working to safeguard important cultural heritage materials worldwide. These checklists were also annotated to contain currently accepted fungal names according to Mycobank (www.mycobank.org, last accessed on 26 April 2021) and Index Fungorum (www.indexfungorum.org, last accessed on 26 April 2021) in order to ensure an updated identification for fungi displaying such profiles, and to facilitate information sharing in the future.

2. Calcium Carbonate Solubilization or Dissolution

One of the greatest fungal effects on stone monuments is credited to their secretion of inorganic and organic acids that can alter the material properties [2–4,29–32]. In fact, carbonate weathering has been consistently linked to the excretion and action of these metabolites [33–35]. Evaluation of fungal calcium carbonate solubilization abilities in cultural heritage scenarios has been helpful to study the biodeteriorative contribution of isolates retrieved from air, mural paintings, wooden art objects, frescoes, catacombs, bricks, concrete, buildings and various limestone and plaster monuments and museums [28,33,35–44]. Fungal calcium carbonate solubilization ability screening is usually conducted with $CaCO_3$ glucose agar and adapted formulations [33]. Nonetheless, the application of Malt extract agar and Reasoner's 2A agar amended with $CaCO_3$ (CMEA and CR2A) has also been successfully achieved [35]. Moreover, Kiyuna and colleagues [37] also highlighted the utility of Glucose Yeast extract calcium carbonate agar (GYC) [45] for such evaluation. Positive $CaCO_3$ dissolution is usually evaluated by the visualization of a halo around the growing colony after a period of incubation. In addition, calcium carbonate solubilization screening can also be conducted coupled with the evaluation of the media pH modifications. For this purpose, Creatine Sucrose agar (CREA) [46] followed by the analysis of medium color changes around growing colonies, or liquid media according to the formulations provided by Borrego and colleagues [47] followed by pH analysis, can also be applied. A quick overview of the known fungal species able of $CaCO_3$ dissolution points that isolates from more than fifty species have been found to display this biodeteriorative profile, with the great majority of them being *Aspergillus* and *Penicillium* species (Table 1). Both genera are known important biodeteriogens, producing various acidic molecules and contributing to the deterioration of materials [28,48]. The detection of species from these genera (as well as others for example, from *Pestalotiopsis* and *Talaromyces* among others) might indicate a putative threat to acid susceptible resources, such is the case of stone structures, mural paintings and frescoes.

Table 1. Overview of fungal species for which isolates have been identified as having $CaCO_3$ dissolution abilities in biodeteriorative plate essays.

Current Species Name	Original Study Focus	References
Acremonium charticola (Lindau) W. Gams	Limestone and plaster monuments and museums	[39]
Actinomucor elegans (Eidam) C.R. Benjamin and Hesseltine	Mural paintings	[41]
Alternaria alternata (Fr.) Keissl.	Mural paintings	[41]
Annulohypoxylon stygium (Lév.) Y.M. Ju, J.D. Rogers and H.M. Hsie	Mayan buildings	[35]
Aspergillus amstelodami (L. Mangin) Thom and Church	Wooden art objects	[36]
Aspergillus awamori Nakaz.	Wooden art objects	[36]
Aspergillus europaeus Hubka, A. Nováková, Samson, Houbraken, Frisvad and M. Kolařík	Frescoes and air	[38]
Aspergillus glaucus (L.) Link	Limestone tomb	[43]
Aspergillus nidulans (Eidam) G. Winter	Mural paintings	[41]
Aspergillus niger Tiegh	Wooden art objects, frescoes, air, brick and concrete	[28,36,38,40]
Aspergillus versicolor (Vuill.) Tirab	Wooden art objects, mural paintings, limestone, plaster monuments and museums	[36,39,41]

Table 1. *Cont.*

Current Species Name	Original Study Focus	References
Aspergillus westerdijkiae Frisvad and Samson	Limestone tomb	[43]
Botrytis cinerea Pers.	Limestone tomb	[43]
Cephalotrichum Link [1]	Catacombs	[33]
Cladosporium Link	Etruscan hypogeal tombs	[44]
Cladosporium sphaerospermum Penz.	Mural paintings	[41]
Cyphellophora G.A. de Vries	Etruscan hypogeal tombs	[44]
Cyphellophora olivacea (W. Gams) Réblová & Unter.	Etruscan hypogeal tombs	[44]
Exophiala J.W. Carmich.	Etruscan hypogeal tombs	[44]
Kendrickiella phycomyces (Auersw.) K. Jacobs and M.J. Wingf.	Mural paintings in Tumuli	[37]
Lasiodiplodia theobromae (Pat.) Griffon and Maubl.	Mayan buildings	[35]
Lecanicillium W. Gams and Zare	Limestone and plaster monuments and museums	[39]
Paecilomyces Bainier	Mayan buildings and catacombs	[33,35]
Parengyodontium album (Limber) 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 and P.C.Y. Woo	Dolomitic limestone wall	[42]
Penicillium angulare S.W. Peterson, E.M. Bayer and Wicklow	Dolomitic limestone wall	[42]
Penicillium aurantiogriseum Dierckx	Mural paintings	[41]
Penicillium bilaiae Chalab.	Frescoes and air	[38]
Penicillium brevicompactum Dierckx	Air, limestone tomb and dolomitic limestone wall	[28,42,43]
Penicillium chrysogenum Thom	Wooden art objects, air, mural paintings, limestone tomb, dolomitic limestone wall, limestone and plaster monuments and museums	[28,36,39,41–43]
Penicillium commune Thom	Frescoes, air and mural paintings	[38,40,41]
Penicillium crustosum Thom	Dolomitic limestone wall	[42]
Penicillium glabrum (Wehmer) Westling	Wooden art objects, air, dolomitic limestone wall and limestone tomb	[28,36,42]
Penicillium griseofulvum Dierckx	Frescoes and air	[38]
Penicillium lanosum Westling	Frescoes and air	[38]
Penicillium Link	Wooden art objects, air, frescoes, concrete and bricks	[36,40]
Penicillium oxalicum Currie and Thom	Mayan buildings	[35]
Penicillium polonicum K.W. Zaleski	Mural paintings	[41]
Penicillium rubens Biourge	Frescoes and air	[38]
Penicillium scabrosum Frisvad, Samson and Stolk	Dolomitic limestone wall	[42]
Penicillium solitum Westling	Air	[28]
Penicillium viridicatum Westling	Air	[28]
Periconia byssoides Pers.	Dolomitic limestone wall	[42]
Pestalotiopsis maculans (Corda) Nag Raj	Mayan buildings	[35]
Pestalotiopsis microspora (Speg.) G.C. Zhao and Nan Li	Mayan buildings	[35]
Pseudogymnoascus pannorum (Link) Minnis and D.L. Lindner	Limestone and plaster monuments and museums	[39]
Rosellinia De Not.	Mayan buildings	[35]
Sclerotinia Fuckel	Air and frescoes	[36]
Sclerotinia sclerotiorum (Lib.) de Bary	Air and frescoes	[36]
Talaromyces amestolkiae N. Yilmaz, Houbraken, Frisvad and Samson	Dolomitic limestone wall	[42]
Talaromyces sayulitensis Visagie, N. Yilmaz, Seifert and Samson	Air	[28]
Trichocladium canadense S. Hughe	Mayan buildings	[35]
Trichoderma Pers.	Mayan buildings	[35]
Valsaria spartii Maubl.	Dolomitic limestone wall	[42]
Xylaria Hill ex Schrank [2]	Mayan buildings	[35]

Previously identified as: [1] *Doratomyces* sp.; [2] *Hypoxylon* sp.

3. Mineralization or Crystallization Development

Calcium carbonate solubilization by the action of fungal acids can often occur coupled with the recrystallization of minerals in the substrate [2,3,5,6,49–51]. Such mineralization singularities can lead to the development of various biodeterioration phenomena [52,53]. They occur from the reactions of secreted acids (especially oxalic acid) with stone cations [32] and often result in the formation of carbonates and/or calcium magnesium oxalates [5,6]. Characterization of fungal crystallization abilities in cultural heritage scenarios has been helpful to study the biodeteriorative contribution of isolates retrieved from air, limestone monuments, stone stela, wall and mural paintings [35,41–43,53–56]. Fungal mineralization ability screening is usually conducted using B4 (with calcium acetate) or modified B4 (with calcium carbonate) media and adapted formulations [57]. Moreover, $CaCO_3$ modified Malt agar, Nutrient agar (NA) with $CaCl_2$ and the above mentioned CMEA and CR2A media have also been found useful for such purposes [35,42,43,58,59]. Positive mineralization development is usually evaluated by the microscopical visualization of neo-formed minerals around or in fungal hyphae after a period of incubation. Moreover, further characterization of these crystals can also be achieved by applying analytical methodologies such as X-ray powder diffraction (XRD) and/or energy dispersive X-ray spectroscopy (EDS) in conjunction with scanning electron microscopy (SEM) methodologies. So far, circa sixty species have been found to display mineralization abilities in plate essays and, as similarly found for fungal calcium carbonate dissolution, multiple *Aspergillus* and *Penicillium* species have also denoted this biodeteriorative profile (Table 2). Such findings can be correlated with their long-known abilities to secrete oxalic acid, among various other acids [41]. Nonetheless, a relevant number of species from genera *Alternaria*, *Cladosporium*, *Colletotrichum*, *Pestalotiopsis* and *Trichoderma* putatively displaying these biodeteriorative abilities can also be verified. Typical minerals detected include calcium carbonate in the form of calcite and vaterite-calcite, weddellite, whewellite, hydroxyapatite, hydrocerussite, pyromorphite, phosphate and other still unidentified calcium oxalates and minerals. The detection of species from these genera might indicate a putative threat to materials highly susceptible to fungal acidolysis and biomineralization, such is the case of limestone monuments and murals [5,6,60].

Table 2. Overview of fungal species for which isolates have been identified as displaying mineralization abilities in biodeteriorative plate essays.

Current Species Name	Mineral Details	Original Study Focus	References
Actinomucor elegans (Eidam) C.R. Benjamin and Hesseltine	Cc, Wd	Mural paintings	[41]
Aeminium ludgeri J. Trovão, I. Tiago and A. Portugal	Cc	Dolomitic limestone wall	[42]
Alternaria alternata (Fr.) Keissl.	Unk	Air and wall paintings	[56]
Alternaria infectoria E.G. Simmons	Unk	Air and wall paintings	[56]
Annulohypoxylon stygium (Lév.) Y.M. Ju, J.D. Rogers and H.M. Hsie	Cc, Wd	Mayan buildings	[35]
Ascochyta medicaginicola Qian Chen and L. Cai [1]	Unk	Air and wall paintings	[56]
Aspergillus aureolatus Munt.—Cvetk. and Bata	Cc	Air and wall paintings	[56]
Aspergillus europaeus Hubka, A. Nováková, Samson, Houbraken, Frisvad and M. Kolařík	Unk	Air and wall paintings	[56]
Aspergillus flavipes (Bainier and R. Sartory) Thom and Church	Unk	Air and wall paintings	[56]
Aspergillus flavus Link	Cc, Wd	Air and wall paintings	[56]
Aspergillus glaucus (L.) Link	Unk CO	Limestone tomb	[54]
Aspergillus niger Tiegh	Unk, Wh	Limestone monument, air and wall paintings	[53,56]
Aspergillus ostianus Wehmer	Cc, Wd	Air and wall paintings	[56]
Aspergillus pallidofulvus Visagie, Varga, Frisvad and Samson	Cc	Air and wall paintings	[56]
Aspergillus parasiticus Speare	Cc, Wd	Air and wall paintings	[56]

Table 2. *Cont.*

Current Species Name	Mineral Details	Original Study Focus	References
Aspergillus westerdijkiae Frisvad and Samson	Unk CO	Limestone tomb	[54]
Bionectria ochroleuca (Schwein.) Schroers and Samuels	Cc, Wh	Stone stela	[54]
Botryotrichum murorum (Corda) X. Wei Wang and Samson [2]	Cc, Unk	Air, wall paintings and stone stela	[54,56]
Botrytis cinerea Pers.	Unk CO	Limestone tomb	[54]
Chaetomium ancistrocladum Udagawa and Cain	Unk	Air and wall paintings	[56]
Cladosporium cladosporioides (Fresen.) G.A. de Vries	Unk	Air and wall paintings	[56]
Cladosporium oxysporum Berk. and M.A. Curtis	Cc, Wd	Air and wall paintings	[56]
Cladosporium sphaerospermum Penz.	Cc, Wd	Mural paintings	[41]
Cladosporium uredinicola Speg.	Cc	Air and wall paintings	[56]
Colletotrichum acutatum J.H. Simmonds	Cc (Vaterite), Cc, Hap, Phosp	Limestone monument	[53,55]
Colletotrichum gloeosporioides (Penz.) Penz. and Sacc.	Cc (Vaterite)	Limestone monument	[53]
Epicoccum nigrum Link	Cc, Wd	Air and wall paintings	[56]
Fusarium fujikuroi Nirenberg [3]	Cc	Air and wall paintings	[56]
Fusarium proliferatum (Matsush.) Nirenberg ex Gerlach and Nirenberg	Cc	Stone stela	[54]
Lasiodiplodia theobromae (Pat.) Griffon and Maubl.	Unk	Mayan buildings	[35]
Leptosphaeria avenaria G.F. Weber [4]	Cc	Air and wall paintings	[56]
Mucor fragilis Bainier	Cc, Wd	Dolomitic limestone wall	[42]
Paecilomyces Bainier	Unk	Mayan buildings	[35]
Penicillium angulare S.W. Peterson, E.M. Bayer and Wicklow	Cc, Wd, Wh	Dolomitic limestone wall	[42]
Penicillium atrosanguineum B.X. Dong [5]	Cc, Wd	Air and wall paintings	[56]
Penicillium bilaiae Chalab.	Cc, Wd	Air and wall paintings	[56]
Penicillium brevicompactum Dierckx	Cc, Wd	Dolomitic limestone wall	[42]
Penicillium chrysogenum Thom	Cc, Wd, Unk CO	Limestone tomb and mural paintings	[41,43]
Penicillium commune Thom	Cc, Wd	Air, wall and mural paintings	[41,56]
Penicillium crustosum Thom	Cc, Wd	Stone stela	[54]
Penicillium glabrum (Wehmer) Westling	Cc, Wd, Wh	Dolomitic limestone wall	[42]
Penicillium griseofulvum Dierckx	Unk	Air and wall paintings	[56]
Penicillium lanosum Westling	Cc, Wd, Unk	Air and wall paintings	[56]
Penicillium oxalicum Currie and Thom	Cc, Wd, Wh	Mayan buildings and limestone monument	[35,53]
Penicillium polonicum K.W. Zaleski	Cc, Wd	Mural paintings	[41]
Penicillium rubens Biourge	Unk	Air and wall paintings	[56]
Periconia byssoides Pers.	Cc	Dolomitic limestone wall	[42]
Pestalotiopsis maculans (Corda) Nag Raj	Unk	Mayan buildings	[35]
Pestalotiopsis microspora (Speg.) G.C. Zhao and Nan Li	Cc, Wd, Wh	Mayan buildings	[35]
Phialemonium inflatum (Burnside) Dania García, Perdomo, Gené, Cano and Guarro [6]	Cc, Cc (Vaterite), Hyd, Pyr	Stalactite in building	[59]
Plectosphaerella cucumerina (Lindf.) W. Gams	Cc, Hyd, Pyr	Stalactite in building	[59]
Rhizoctonia solani J.G. Kühn [7]	Unk	Air and wall paintings	[56]
Rosellinia De Not.	Cc, Wd	Mayan buildings	[35]
Sclerotinia sclerotiorum (Lib.) de Bary	Cc, Wd	Air and wall paintings	[56]
Stereum hirsutum (Willd.) Pers.	Cc, Wd	Dolomitic limestone wall	[42]
Trichocladium canadense S. Hughes	Unk	Mayan buildings	[35]
Trichoderma atroviride P. Karst.	Cc, Wd	Dolomitic limestone wall	[42]
Trichoderma harzianum Rifai	Cc	Stone stela	[54]
Trichoderma Pers.	Unk	Mayan buildings	[35]
Xylaria Hill ex Schrank [8]	Unk	Mayan buildings	[35]

Previously identified as: [1] *Phoma medicaginis*; [2] *Chaetomium murorum*; [3] *Gibberella moniliformis*; [4] *Phaeosphaeria avenaria*; [5] *Penicillium manginii*; [6] *Paecilomyces inflatus*; [7] *Thanatephorus cucumeris*; [8] *Hypoxylon* sp.; Cc—calcium carbonate; Wd—weddellite; Wh—whewellite; Hap—hydroxyapatite; Hyd—hydrocerussite; Phosp—phosphate; Pyr—pyromorphite; Unk CO—Unidentified calcium oxalates; Unk—Unidentified mineralization's.

4. Enzymatic Action

Fungal ligninolytic action is often considered a threat to wooden structures [61–66]. Cultural heritage materials constructed with these materials can be affected by fungal hyphae penetration but also by the action of various exoenzymes [67]. Moreover, brown and white rot fungi are known to contribute to these substrates' deterioration and degradation in various contexts [68]. So far, fungal ligninolytic ability characterization in cultural heritage scenarios has been helpful to study the biodeteriorative contribution of isolates retrieved from air, wooden materials and art objects [61,69,70]. Ligninolytic ability screening can be conducted using media with Azure B (lignin peroxidase), Phenol Red (Mn peroxidase), Remazol Brilliant Blue R (laccase) [71–74] or, alternatively, by applying Potato Dextrose agar supplemented with guaiacol (PDA-guaiacol) [61,70]. Positive ligninolytic ability is usually evaluated by the clearance of the media specific color (Azure B, Phenol Red and Remazol Brilliant Blue R) or by the development of reddish-brown zones (PDA-guaiacol) after a period of incubation. As pointed by Pangallo and colleagues [36,69], data regarding ligninolytic abilities of filamentous fungi in biodeterioration contexts is still somewhat scarce. Nonetheless, as evidenced by Table 3, almost thirty species have been found to display these biodeteriorative abilities. Moreover, mainly species of genera *Aspergillus*, *Chaetomium*, *Cladosporium* and *Penicillium* represent the bulk of the currently studied lignin deteriorating fungi. As such, the detection of species from these genera might indicate a putative threat to lignin materials, such as the case of some types of paper and wood art pieces and objects.

Table 3. Overview of fungal species for which isolates have been identified as displaying ligninolytic abilities in biodeteriorative plate essays.

Current Species Name	Original Study Focus	References
Alternaria consortialis (Thüm.) J.W. Groves and S. Hughes [1]	Wooden art objects	[36]
Arthrinium phaeospermum (Corda) M.B. Ellis	Wooden art objects	[36]
Aspergillus amstelodami (L. Mangin) Thom and Church [2]	Wooden art objects	[36]
Aspergillus awamori Nakaz.	Wooden art objects	[36]
Aspergillus fischeri Wehmer [3]	Wooden art objects	[36]
Aspergillus flavus Link	Wooden art objects	[36]
Aspergillus fumigatus Fresen.	Wooden art objects	[36]
Aspergillus niger Tiegh	Wooden art objects	[36]
Aspergillus terreus Thom	Wooden art objects and air	[36,69]
Aspergillus ustus (Bainier) Thom and Church	Wooden art objects	[36]
Aspergillus versicolor (Vuill.) Tirab.	Wooden art objects	[36]
Beauveria bassiana (Bals.—Criv.) Vuill.	Wooden art objects	[36]
Chaetomium elatum Kunze	Wooden art objects	[36]
Chaetomium globosum Kunze	Wooden art objects and air	[36,69]
Cladosporium cladosporioides (Fresen.) G.A. de Vries	Wooden objects and air	[69]
Cladosporium herbarum (Pers.) Link	Wooden art objects	[36]
Cladosporium Link	Wooden art objects	[36]
Hypochnicium J. Erikss.	Wooden materials	[61]
"*Neocosmospora*" *solani* (Mart.) L. Lombard and Crous [4]	Wooden materials	[70]
Penicillium chrysogenum Thom	Wooden art objects	[36]
Penicillium expansum Link	Wooden art objects	[36]
Penicillium glabrum (Wehmer) Westling	Wooden art objects	[36]
Penicillium herquei Bainier and Sartory	Wooden art objects	[36]
Penicillium Link	Wooden art objects	[36]
Penicillium sacculum E. Dale	Wooden art objects	[36]
Pseudogymnoascus pannorum (Link) Minnis and D.L. Lindner [5]	Wooden art objects	[36]
Trichoderma viride Pers.	Wooden art objects	[36]

Previously identified as: [1] *Alternaria consortiale*; [2] *Eurotium amstelodami*; [3] *Neosartorya fischeri*; [4] *Fusarium solani*; [5] *Chrysosporium pannorum*.

Fungi can also have an important role in the attack of animal-based objects, adhesives and additives. Textile materials such as silk and wool can suffer microbial mediated biodeterioration processes by the action of deteriorating enzymes [75,76]. In particular, the silks fibroin and sericin can both be the target of microbial attack [77]. Moreover, wool keratins can also be the target of attack by microbes [77]. Evaluation of fibroinolytic and keratinolytic action in cultural heritage scenarios has been helpful to study mummies, funeral clothes and accessories biodeterioration [78–80]. Moreover, fungal chitinolytic and pectinolytic action has also been pinpointed as a threat to Ancient Yemeni mummies preserved with diverse organic compounds [81]. Additionally, esterease action profiling has also been helpful to study isolates retrieved from wax seals, air, textiles and human remains [82–84]. Fibroinolytic screening can be conducted using fibroin agar, with the fibroinolytic action being evaluated by the isolates ability to grow in the culture-amended plates [85]. Moreover, keratinolytic action can be evaluated using feather broth and keratin medium and positive ability can be verified by media turbidity changes [79,85]. On the other hand, chitinolytic activity can be evaluated using powdered chitin agar [86] and pectinolytic activities can be evaluated with media containing pectin [87]. Both these deteriorative activities can be estimated and quantified [81]. Additionally, esterease action can be studied using Tributyrin agar and Tween 80 agar [83,84,88]. Their action can be detected by the development of clear zones (Tributyrin agar) or by the precipitation of insoluble salts and compounds (Tween 80) around colonies. As occurring with ligninolytic action, data regarding filamentous fungi fibroinase and keratinolytic action is still infrequent. Twenty-three species were found to be able of fibroinolytic activity, while more than twenty-five were found to have keratinolytic action. Again, *Aspergillus* and *Penicillium* species also dominate these biodeteriorative profiles (Tables 4 and 5). Moreover, various *Alternaria* species also displayed putative keratinolytic abilities. On the other hand, chitinolytic abilities have been identified for *Aspergillus niger* and *Penicillium* sp., while pectinolytic action has been identified in a slightly more diversified range of fungal genera and species (*Aspergillus candidus*, *Mucor circinelloides*, *Penicillium echinulatum*, *Scopulariopsis koningii*, *Stachybotrys chartarum* and *Trichoderma hamatum*) [81]. In parallel, fifty species have been identified as displaying estereolytic action, with a great dominance of *Aspergillus* and *Penicillium* species (Table 6). Understandably, the detection of these fungal species on crypt environments, human remains, buried materials, mummies, wax seals, textiles and clothes denotes a putative threat to these materials [3].

Table 4. Overview of fungal species for which isolates have been identified as displaying fibrinolytic abilities in biodeteriorative plate essays.

Current Species Name	Original Study Focus	References
Alternaria alternata (Fr.) Keissl.	Funeral accessories	[70]
Ascomycota Caval. -Sm.	Funeral clothes	[85]
Aspergillus caninus (Sigler, Deanna A. Sutton, Gibas, Summerb. and Iwen) Houbraken, Tanney, Visagie and Samson [1]	Funeral clothes	[85]
Aspergillus cristatus Raper and Fennell [2]	Funeral clothes	[85]
Aspergillus fumigatus Fresen.	Funeral clothes	[85]
Aspergillus P. Micheli ex Haller	Funeral accessories	[80]
Aspergillus puniceus Kwon-Chung and Fennell	Funeral clothes	[85]
Aspergillus sydowii (Bainier and Sartory) Thom and Church	Funeral clothes	[85]
Aspergillus tubingensis Mosseray	Funeral clothes	[85]
Aspergillus versicolor (Vuill.) Tirab.	Funeral accessories	[80]
Beauveria bassiana (Bals.—Criv.) Vuill.	Funeral clothes	[85]
Myriodontium keratinophilum Samson and Polon.	Funeral clothes	[85]
Penicillium brevicompactum Dierckx	Funeral clothes	[85]
Penicillium commune Thom	Funeral accessories	[80]
Penicillium crocicola T. Yamam.	Funeral clothes	[85]
Penicillium crustosum Thom	Funeral clothes	[85]
Penicillium expansum Link	Funeral clothes	[85]
Penicillium granulatum Bainier	Funeral accessories	[80]
Penicillium Link	Funeral accessories	[80]
Penicillium roseopurpureum Dierckx	Funeral clothes	[85]
Penicillium spinulosum Thom	Funeral clothes	[85]
Sporobolomyces roseus Kluyver and C.B. Niel [3]	Funeral accessories	[80]
Xenochalara juniperi M.J. Wingf. and Crous	Funeral clothes	[85]

Previously identified as: [1] *Phialosimplex caninus*; [2] *Eurotium cristatum*; [3] *Sporidiobolus metaroseus*.

Table 5. Overview of fungal species for which isolates have been identified as displaying keratinolytic abilities in biodeteriorative plate essays.

Current Species Name	Original Study Focus	References
Alternaria consortialis (Thüm.) J.W. Groves and S. Hughes [1]	Wooden art objects	[36]
Arthrinium phaeospermum (Corda) M.B. Ellis	Wooden art objects	[36]
Aspergillus amstelodami (L. Mangin) Thom and Church [2]	Wooden art objects	[36]
Aspergillus awamori Nakaz.	Wooden art objects	[36]
Aspergillus fischeri Wehmer [3]	Wooden art objects	[36]
Aspergillus flavus Link	Wooden art objects	[36]
Aspergillus fumigatus Fresen.	Wooden art objects	[36]
Aspergillus niger Tiegh	Wooden art objects	[36]
Aspergillus terreus Thom	Wooden art objects and air	[36,69]
Aspergillus ustus (Bainier) Thom and Church	Wooden art objects	[36]
Aspergillus versicolor (Vuill.) Tirab.	Wooden art objects	[36]
Beauveria bassiana (Bals.—Criv.) Vuill.	Wooden art objects	[36]
Chaetomium elatum Kunze	Wooden art objects	[36]
Chaetomium globosum Kunze	Wooden art objects and air	[36,69]
Cladosporium cladosporioides (Fresen.) G.A. de Vries	Wooden objects and air	[69]
Cladosporium herbarum (Pers.) Link	Wooden art objects	[36]
Cladosporium Link	Wooden art objects	[36]
Hypochnicium J. Erikss.	Wooden materials	[61]
"Neocosmospora" solani (Mart.) L. Lombard and Crous [4]	Wooden materials	[70]
Penicillium chrysogenum Thom	Wooden art objects	[36]
Penicillium expansum Link	Wooden art objects	[36]
Penicillium glabrum (Wehmer) Westling	Wooden art objects	[36]
Penicillium herquei Bainier and Sartory	Wooden art objects	[36]
Penicillium Link	Wooden art objects	[36]
Penicillium sacculum E. Dale	Wooden art objects	[36]
Pseudogymnoascus pannorum (Link) Minnis and D.L. Lindner [5]	Wooden art objects	[36]
Trichoderma viride Pers.	Wooden art objects	[36]

Previously identified as: [1] *Alternaria consortiale;* [2] *Eurotium amstelodami;* [3] *Neosartorya fischeri;* [4] *Fusarium solani;* [5] *Chrysosporium pannorum.*

Table 6. Overview of fungal species for which isolates have been identified as displaying estereolytic abilities in biodeteriorative plate essays.

Current Species Name	Original Study Focus	References
Acrodontium salmoneum de Hoog	Wax seal	[84]
Agaricaceae Chevall.	Statue and air	[89]
Alternaria Nees	Statue, stone and air	[89,90]
Alternaria tenuissima (Kunze) Wiltshire	Statue and air	[89]
Aspergillus amstelodami (L. Mangin) Thom and Church [1]	Stone	[90]
Aspergillus caespitosus Raper and Thom	Air, textiles and human remains	[83]
Aspergillus calidoustus Varga, Houbraken and Samson	Air, textiles and human remains	[83]
Aspergillus candidus Link	Air, textiles and human remains	[83]
Aspergillus clavatus Desm.	Textiles	[82]
Aspergillus fischeri Wehmer [2]	Air, textiles and human remains	[83]
Aspergillus flavus Link	Stone	[90]
Aspergillus fumigatus Fresen.	Air, statues, textiles and human remains	[83,89]
Aspergillus niger Tiegh	Stone	[90]
Aspergillus repens (Corda) Sacc. [3]	Air, textiles and human remains	[83]
Aspergillus sydowii (Bainier and Sartory) Thom and Church	Air, textiles and human remains	[83]
Aspergillus terreus Thom	Air, textiles and human remains	[83]
Aspergillus ustus (Bainier) Thom and Church	Air, textiles and human remains	[83]
Aspergillus venenatus Jurjević, S.W. Peterson and B.W. Horn	Air, textiles and human remains	[83]
Aspergillus versicolor (Vuill.) Tirab.	Air, statues, textiles and human remains	[83,89]
Aspergillus westerdijkiae Frisvad and Samson	Air, textiles and human remains	[83]
Aureobasidium pullulans (de Bary and Löwenthal) G. Arnaud	Wax seal	[84]
Bulleromyces albus Boekhout and Á. Fonseca [4]	Wax seal	[84]
Cladosporium aggregatocicatricatum Bensch, Crous and U. Braun	Wax seal	[84]
Cladosporium Link	Air, textiles and human remains	[83]
Cladosporium macrocarpum Preuss	Statue and air	[89]
Cladosporium tenuissimum Cooke	Textiles	[82]

Table 6. *Cont.*

Current Species Name	Original Study Focus	References
Coprinellus xanthothrix (Romagn.) Vilgalys, Hopple and Jacq. Johnson	Air, textiles and human remains	[83]
Coprinopsis cinerea (Schaeff.) Redhead, Vilgalys and Moncalvo	Statue and air	[89]
Curvularia Boedijn	Stone	[90]
Fusarium Link	Stone	[90]
Fusarium sporotrichioides Sherb.	Statue and air	[89]
Hypoxylon fragiforme (Pers.) J. Kickx f.	Textiles	[82]
Microascus brevicaulis S.P. Abbott [5]	Air, textiles and human remains	[83]
Nigrospora oryzae (Berk. and Broome) Petch	Air, textiles and human remains	[83]
Penicillium chrysogenum Thom	Air, textiles and human remains	[82,83]
Penicillium commune Thom	Air, textiles and human remains	[83]
Penicillium corylophilum Dierckx	Textiles, statue and air	[82,89]
Penicillium crustosum Thom	Air, statues, textiles and human remains	[83,89]
Penicillium griseofulvum Dierckx	Air, textiles and human remains	[83]
Penicillium hordei Stolk	Air, textiles and human remains	[83]
Penicillium Link	Statue and air	[89]
Penicillium polonicum K.W. Zaleski	Air, textiles and human remains	[83]
Pseudoscopulariopsis hibernica (A. Mangan) Sand. -Den., Gené and Cano [6]	Air, textiles and human remains	[83]
Rhizopus arrhizus A. Fisch. [7]	Air, textiles and human remains	[83]
Rhizopus microsporus Tiegh.	Air, textils, human remains, statue and air	[83,89]
Rhizopus stolonifer (Ehrenb.) Vuill.	Air, textiles and human remains	[83]
Sordaria fimicola (Roberge ex Desm.) Ces. and De Not.	Statue and air	[89]
Talaromyces purpureogenus Samson, N. Yilmaz, Houbraken, Spierenb., Seifert, Peterson, Varga and Frisvad	Stone	[90]
Thyronectria austroamericana (Speg.) Seeler [8]	Statue and air	[89]
Trichoderma paraviridescens Jaklitsch, Samuels and Voglmayr	Statue and air	[89]

Previously identified as: [1] *Eurotium amsteldomi*; [2] *Neosartorya fischeri*; [3] *Eurotium repens*; [4] *Bullera alba*; [5] *Scopulariopsis brevicaulis*; [6] *Scopulariopsis hibernica*; [7] *Rhizopus oryzae*; [8] *Pleonectria austroamericana*.

Fungal lipolytic action can have an important impact on the biodeterioration of parchment and leather related materials [91]. Fungi can attack lipids and take advantage of fatty materials as a mean to obtain carbon (while also contributing to the material deterioration) [92]. Fungal lipolytic ability characterization in cultural heritage scenarios has been helpful to study the biodeteriorative contribution of isolates retrieved from air, textiles, human remains, wax seals, albumen photographical materials, statues, wooden organs and pipes [83,84,89,93,94]. Lipolytic ability screening can be mainly conducted using Spirit Blue agar and Nile blue, and the positive action can be identified by the development of a halo around the colonies, after a period of incubation [89]. Circa sixty species were found to be able of lipolytic action (Table 7). As similarly verified in other deteriorative analyses, *Aspergillus* and *Penicillium* species are still predominant in these profiles. The detection of these fungal species on materials rich in fatty compounds, such as wax seals and photographic materials should be considered putatively hazardous.

Table 7. Overview of fungal species for which isolates have been identified as displaying lipolytic abilities in biodeteriorative plate essays.

Current Species Name	Original Study Focus	References
Acrodontium salmoneum de Hoog	Wax seal	[84]
Acrostalagmus luteoalbus (Link) Zare, W. Gams and Schroers	Albumen photographic materials	[93]
Agaricaceae Chevall.	Statue and air	[89]
Alternaria mali Roberts	Wooden organ and pipes	[94]
Alternaria Nees	Statue and air	[89]
Alternaria tenuissima (Kunze) Wiltshire	Statue and air	[89]
Aspergillus amstelodami (L. Mangin) Thom and Church [1]	Air, textiles, human remains, wooden organ and pipes	[83,94]
Aspergillus caespitosus Raper and Thom	Air, textiles and human remains	[83]
Aspergillus calidoustus Varga, Houbraken and Samson	Air, textiles and human remains	[83]
Aspergillus candidus Link	Air, textiles and human remains	[83]
Aspergillus cristatus Raper and Fennell [2]	Wooden organ and pipes	[94]

Table 7. *Cont.*

Current Species Name	Original Study Focus	References
Aspergillus fischeri Wehmer [3]	Air, textiles, statues and human remains	[89,93]
Aspergillus fumigatus Fresen.	Air, textiles, statues and human remains	[83,89]
Aspergillus repens (Corda) Sacc. [4]	Air, textiles and human remains	[83]
Aspergillus sydowii (Bainier and Sartory) Thom and Church	Air, textiles, human remains, wooden organ and pipes	[83,94]
Aspergillus terreus Thom	Air, textiles and human remains	[83]
Aspergillus ustus (Bainier) Thom and Church	Air, textiles and human remains	[83]
Aspergillus venenatus Jurjević, S.W. Peterson and B.W. Horn	Air, textiles and human remains	[83]
Aspergillus versicolor (Vuill.) Tirab	Air, textiles, human remains, albumen photographic materials, wooden organ and pipes	[83,89,93,94]
Aspergillus westerdijkiae Frisvad and Samson	Air, textiles and human remains	[83]
Aureobasidium pullulans (de Bary and Löwenthal) G. Arnaud	Wax seal	[84]
Bjerkandera adusta (Willd.) P. Karst.	Albumen photographic materials	[83]
Bulleromyces albus Boekhout and Á. Fonseca [5]	Wax seal	[84]
Chaetomium elatum Kunze	Albumen photographic materials	[83]
Cladosporium aggregatocicatricatum Bensch, Crous and U. Braun	Wax seal	[84]
Cladosporium cladosporioides (Fresen.) G.A. de Vries	Wooden organ and pipes	[94]
Cladosporium Link	Air, textiles, human remains and Etruscan hypogeal tombs	[44,83]
Cladosporium macrocarpum Preuss	Statue and air	[89]
Coprinellus xanthothrix (Romagn.) Vilgalys, Hopple and Jacq. Johnson	Air, textiles and human remains	[83]
Coprinopsis cinerea (Schaeff.) Redhead, Vilgalys and Moncalvo	Statue and air	[89]
Cyphellophora G.A. de Vries	Etruscan hypogeal tombs	[44]
Cyphellophora olivacea (W. Gams) Réblová & Unter.	Etruscan hypogeal tombs	[44]
Epicoccum nigrum Link	Wooden organ and pipes	[94]
Exophiala angulospora Iwatsu, Udagawa & T. Takase	Etruscan hypogeal tombs	[44]
Exophiala J.W. Carmich.	Etruscan hypogeal tombs	[44]
Fusarium sporotrichioides Sherb.	Statue and air	[89]
Microascus brevicaulis S.P. Abbott [6]	Air, textiles and human remains	[83]
Mucor plumbeus Bonord.	Albumen photographic materials	[93]
Nigrospora oryzae (Berk. and Broome) Petch	Air, textiles and human remains	[83]
Paecilomyces maximus C. Ram	Wooden organ and pipes	[94]
Penicillium chrysogenum Thom	Air, textiles and human remains	[83]
Penicillium commune Thom	Air, textiles and human remains	[83]
Penicillium corylophilum Dierckx	Statue and air	[89]
Penicillium crustosum Thom	Air, textiles, statues and human remains	[83,89]
Penicillium digitatum (Pers.) Sacc.	Air, textiles and human remains	[83]
Penicillium griseofulvum Dierckx	Air, textiles and human remains	[83]
Penicillium hordei Stolk	Air, textiles and human remains	[83]
Penicillium Link	Albumen photographic materials, statues and air	[89,93]
Penicillium polonicum K.W. Zaleski	Air, textiles and human remains	[83]
Penicillium thomii Maire	Albumen photographic materials	[93]
Phlebia Fr.	Albumen photographic materials	[93]
Pleosporales Luttr. ex M.E. Barr	Albumen photographic materials	[93]
Pseudoscopulariopsis hibernica (A. Mangan) Sand. -Den., Gené and Cano [7]	Air, textiles and human remains	[83]
Rhizopus arrhizus A. Fisch. [8]	Air, textiles and human remains	[83]
Rhizopus microsporus Tiegh.	Air, textiles, human remains, statues and air	[83,89]
Rhizopus stolonifer (Ehrenb.) Vuill.	Air, textiles and human remains	[83]
Sordaria fimicola (Roberge ex Desm.) Ces. and De Not.	Statue and air	[89]
Talaromyces flavus (Klöcker) Stolk and Samson	Air, textiles and human remains	[83]
Thyronectria austroamericana (Speg.) Seeler [9]	Statue and air	[89]
Trichoderma harzianum Rifai	Air, textiles and human remains	[83]
Trichoderma paraviridescens Jaklitsch, Samuels and Voglmayr	Statue and air	[89]
Trichothecium roseum (Pers.) Link	Albumen photographic materials	[93]

Previously identified as: [1] *Eurotium amstelodami*; [2] *Eurotium cristatum*; [3] *Neosartorya fischeri*; [4] *Eurotium repens*; [5] *Bullera alba*; [6] *Scopulariopsis brevicaulis*; [7] *Scopulariopsis hibernica*; [8] *Rhizopus oryzae*; [9] *Pleonectria austroamericana*.

Fungal proteolytic action can contribute to the biodeterioration of proteinaceous materials, such is the case of artistic natural binders. In addition, some conservation approaches also employ similar materials that can be targeted by microbial biodeterioration [38]. Fungal proteolytic ability characterization in cultural heritage scenarios has been helpful to study the biodeteriorative contribution of isolates retrieved from air, funeral clothes and accessories, graphic documents, materials present in libraries and museums, frescoes, textiles, human remains, mummies, mural paintings, cinematographic films, wax seals, paper, parchment, wooden organs and pipes [28,38,41,78–80,83–85,93,95–100]. Proteolytic ability screening can be mainly conducted using Gelatin agar (R2A-Gel), Casein agar (CN), Milk Nutrient agar (MilkNA) and media containing rabbit glue [78,94,96]. After a period of incubation, positive proteolytic ability can be detected by flooding of agar plates with 10% tannin solution and the visualization of the formed hydrolysis zones [101]. Over one hundred and thirty species have been found to be able of promoting protein attack (Table 8). As similarly verified in other enzymatic activities, *Aspergillus* and *Penicillium* species also dominate this biodeteriorative profile. Nonetheless, a significant number of species from genera *Alternaria*, *Cladosporium* and *Talaromyces* displaying these characteristics can also be confirmed. Detection of these fungal species on proteinaceous materials will putatively result in their accentuated biodeterioration.

Table 8. Overview of fungal species for which isolates have been identified as displaying proteolytic abilities in biodeteriorative plate essays.

Current Species Name	Original Study Focus	References
Acrodontium salmoneum de Hoog	Wax seal	[84]
Acrostalagmus luteoalbus (Link) Zare, W. Gams and Schroers	Albumen photographic materials	[93]
Actinomucor elegans (Eidam) C.R. Benjamin and Hesseltine	Mural paintings	[41]
Alternaria alternata (Fr.) Keissl.	Air, mural paintings, mummies, funeral accessories, cinematographic films	[41,79,80,95,98]
Alternaria mali Roberts	Mummies, wooden organ and pipes	[79,94]
Alternaria Nees	Mummies and funeral clothes	[79,85]
Alternaria solani Sorauer	Mummies	[79]
Alternaria tenuissima (Kunze) Wiltshire	Mummies	[79]
Ascomycota Caval. -Sm.	Funeral clothes	[85]
Aspergillus alliaceus Thom and Church	Air and graphic documents	[98,100]
Aspergillus amstelodami (L. Mangin) Thom and Church	Air, wooden organ and pipes	[28,94]
Aspergillus aureolatus Munt.—Cvetk. and Bata	Frescoes and air	[38]
Aspergillus auricomus (Guég.) Saito	Air and graphic documents	[100]
Aspergillus caespitosus Raper and Thom	Air, textiles and human remains	[83]
Aspergillus candidus Link	Air, graphic documents, photographs, maps, textiles and human remains	[83,84,98–100]
Aspergillus caninus (Sigler, Deanna A. Sutton, Gibas, Summerb. and Iwen) Houbraken, Tanney, Visagie and Samson [1]	Funeral clothes	[85]
Aspergillus chevalieri (L. Mangin) Thom and Church [2]	Air, graphic documents, photographs, maps and materials present in libraries and museums	[96,99,100]
Aspergillus creber Jurjević, S.W. Peterson and B.W. Horn	Air	[28]
Aspergillus cristatus Raper and Fennell [3]	Funeral clothes, wooden organ and pipes	[85,94]
Aspergillus europaeus Hubka, A. Nováková, Samson, Houbraken, Frisvad and M. Kolařík	Frescoes and air	[28,38]
Aspergillus flavipes (Bainier and R. Sartory) Thom and Church	Air	[98]
Aspergillus flavus Link [4]	Air, frescoes, mummies, photographs, maps and materials present in libraries and museums	[38,47,78,79,96,99,100]
Aspergillus fumigatus Fresen.	Air, materials present in libraries and museums, paper and parchment and funeral clothes	[85,96,97]
Aspergillus japonicus Saito	Air and graphic documents	[100]
Aspergillus jensenii Jurjević, S.W. Peterson and B.W. Horn	Air	[28]
Aspergillus nidulans (Eidam) G. Winter	Air, materials present in libraries and museum, mural paintings and cinematographic films	[41,95,96]
Aspergillus niger Tiegh	Frescoes, air, textiles, human remains, photographs, maps, paper and parchment, graphic documents, materials present in libraries and museums	[38,73,96–100]
Aspergillus ostianus Wehmer	Frescoes, air and graphic documents	[38,100]
Aspergillus P. Micheli ex Haller [5]	Air and mural paintings	[41,47]
Aspergillus penicillioides Speg.	Air and graphic documents	[100]
Aspergillus proliferans G. Sm.	Air	[28]
Aspergillus protuberus Munt. -Cvetk.	Air	[28]
Aspergillus pseudodeflectus Samson and Mouch.	Funeral clothes	[85]
Aspergillus puniceus Kwon-Chung and Fennell	Funeral clothes	[85]

Table 8. *Cont.*

Current Species Name	Original Study Focus	References
Aspergillus sydowii (Bainier and Sartory) Thom and Church	Air, mural paintings, funeral clothes, wooden organ and pipes and materials present in libraries and museums	[28,41,85,94,96]
Aspergillus tabacinus Nakaz., Y. Takeda, Simo and A. Watan.	Air and materials present in libraries and museums	[28]
Aspergillus tamarii Kita	Air and materials present in libraries and museums	[96]
Aspergillus terreus Thom	Air and materials present in libraries and museums	[96]
Aspergillus tubingensis Mosseray	Funeral clothes	[85]
Aspergillus unguis (Émile-Weill and L. Gaudin) Thom and Raper	Air and graphic documents	[100]
Aspergillus unilateralis Thrower	Air and graphic documents	[100]
Aspergillus ustus (Bainier) Thom and Church	Cinematographic films	[95]
Aspergillus versicolor (Vuill.) Tirab	Air, mural paintings, frescoes, textiles, human remains, funeral accessories, cinematographic materials, wooden organ and pipes and materials present in libraries and museums	[28,38,41,78,80,83,94–96]
Aspergillus westerdijkiae Frisvad and Samson	Air, textiles and human remains	[83]
Aureobasidium pullulans (de Bary and Löwenthal) G. Arnaud	Wax seal and mummies	[79,84]
Beauveria bassiana (Bals.—Criv.) Vuill.	Funeral clothes	[85]
Bjerkandera adusta (Willd.) P. Karst.	Frescoes, air albumen photographic materials	[38,93]
Botryotrichum murorum (Corda) X. Wei Wang and Samson [6]	Frescoes and air	[38]
Bulleromyces albus Boekhout and Á. Fonseca [7]	Wax seal	[84]
Chaetomium ancistrocladum Udagawa and Cain	Frescoes and air	[38]
Chaetomium elatum Kunze	Albumen photographic materials	[93]
Chaetomium globosum Kunze	Mural paintings	[41]
Cladosporium aggregatocicatricatum Bensch, Crous and U. Braun	Wax seal	[84]
Cladosporium cladosporioides (Fresen.)	Mural paintings, frescoes, air, mummies, graphic documents, maps, photographs, cinematographic films, wooden organ and pipes	[38,41,79,94,95,99,100]
Cladosporium cucumerinum Ellis and Arthur	Mural paintings	[41]
Cladosporium herbarum (Pers.) Link [8]	Mummies and mural painitngs	[41,81]
Cladosporium Link	Etruscan hypogeal tombs, air and mummies	[44,47,79]
Cladosporium macrocarpum Preuss	Air and frescoes	[78]
Cladosporium oxysporum Berk. and M.A. Curtis	Frescoes and air	[38]
Cladosporium pseudocladosporioides Bensch, Crous and U. Braun	Mummies	[79]
Cladosporium sphaerospermum Penz.	Mummies and mural paintings	[41,79]
Cladosporium tenuissimum Cooke	Mural paintings	[41]
Cladosporium uredinicola Speg.	Mummies, frescoes and air	[38,79]
Coprinellus xanthothrix (Romagn.) Vilgalys, Hopple and Jacq. Johnson	Air, textiles and human remains	[83]
Curvularia australiensis (Bugnic. ex M.B. Ellis) Manamgoda, L. Cai and K.D. Hyde [9]	Air and graphic documents	[100]
Curvularia Boedijn	Air	[47]
Curvularia pallescens Boedijn	Air and graphic documents	[98,100]
Cyphellophora G.A. de Vries	Etruscan hypogeal tombs	[44]
Didymella glomerata (Corda) Qian Chen and L. Cai [10]	Cinematographic films	[95]
Dipodascus Lagerh. [11]	Air	[47]
Epicoccum Link	Air and graphic documents	[100]
Epicoccum nigrum Link	Mummies, wooden organ and pipes	[79,94]
Fusarium chlamydosporum Wollenw. and Reinking	Mural paintings	[41]
Fusarium Link	Air and graphic documents	[57,100]
Fusarium oxysporum Schltdl.	Air	[98]
Hormodendrum pyri W.H. English	Wax seal	[84]
Leptosphaeria avenaria G.F. Weber [12]	frescoes and air	[38]
Meyerozyma guilliermondii (Wick.) Kurtzman and M. Suzuki [13]	Air	[98]
Microascus brevicaulis S.P. Abbott [14]	Air, textiles and human remains	[83]
Mucor racemosus Bull.	Cinematographic films, paper and parchment	[95,97]
Mucor spinosus Schrank	Paper and parchment	[97]
Myriodontium keratinophilum Samson and Polon.	Funeral clothes	[85]
Nigrospora oryzae (Berk. and Broome) Petch [15]	Air, textiles and human remains	[83,98]
Paecilomyces maximus C. Ram [16]	Wooden organ and pipes	[94]
Paecilomyces variotii Bainier	Air	[98]
Penicillium aurantiogriseum Dierckx	Mural paintings	[41]
Penicillium bilaiae Chalab.	Frescoes and air	[38]
Penicillium brevicompactum Dierckx	Air and funeral clothes	[28,85]
Penicillium camemberti Thom	Paper and parchment	[97]
Penicillium canescens Sopp	Air and graphic documents	[100]
Penicillium chrysogenum Thom	Air, mural paintings, textiles, human remains, mummies, paper, photographs, maps, parchment, graphic documents and cinematographic films	[28,41,79,83,95,97,99,100]
Penicillium citreonigrum Dierckx	Air	[28]
Penicillium citrinum Thom	Air, photographs, maps and graphic documents	[28,99,100]
Penicillium commune Thom	Air, textiles, human remains, mural paintings, funeral accessories and clothes, paper and parchment	[41,80,83,85,87]
Penicillium crocicola T. Yamam.	Funeral clothes	[85]
Penicillium crustosum Thom	Funeral clothes, wooden organ and pipes	[85,94]

Table 8. *Cont.*

Current Species Name	Original Study Focus	References
Penicillium decumbens Thom	Air, paper and parchment	[28,97]
Penicillium digitatum (Pers.) Sacc.	Air, textiles and human remains	[28,83]
Penicillium expansum Link	Air, mummies and funeral clothes	[28,79,85]
Penicillium glabrum (Wehmer) Westling	Air	[28]
Penicillium granulatum Bainier	Funeral accessories	[80]
Penicillium griseofulvum Dierckx	Air, frescoes, graphic documents, textiles and human remains	[38,83,100]
Penicillium hordei Stolk	Air, textiles and human remains	[83]
Penicillium janczewskii K.W. Zaleski	Air, maps, photographs and graphic documents	[99,100]
Penicillium Link	Air, frescoes, albumen photographic materials and funeral accessories	[57,78,80,93]
Penicillium olsonii Bainier and Sartory	Mural paintings	[41]
Penicillium polonicum K.W. Zaleski	Air, textiles, mural paintings and human remains	[41,83]
Penicillium raistrickii G. Sm.	Mummies	[79]
Penicillium roseopurpureum Dierckx	Mummies and funeral clothes	[79,85]
Penicillium simplicissimum (Oudem.) Thom [17]	Air, maps, photographs and graphic documents	[99,100]
Penicillium solitum Westling	Air	[28]
Penicillium spinulosum Thom	Funeral clothes	[85]
Penicillium viridicatum Westling	Air, paper and parchment	[28,97]
Penicillium waksmanii K.W. Zaleski	Air and graphic documents	[100]
Pestalotia De Not.	Air and graphic documents	[100]
Phoma herbarum Westend.	Paper and parchment	[97]
Pleurotus ostreatus (Jacq.) P. Kumm. [18]	Albumen photographic materials	[93]
Pseudozyma prolifica Bandoni	Mural paintings	[31]
Rhizopus microsporus Tiegh. [19]	Air, textiles and human remains	[83]
Sarocladium W. Gams and D. Hawksw. [20]	Air, graphic documents and albumen photographic materials	[93,98,100]
Sporobolomyces roseus Kluyver and C.B. Niel [21]	Funeral Accessories	[80]
Stemphylium vesicarium (Wallr.) E.G. Simmons	Mummies	[79]
Talaromyces aculeatus (Raper and Fennell) Samson, N. Yilmaz, Frisvad and Seifert	Mural paintings	[41]
Talaromyces rugulosus (Thom) Samson, N. Yilmaz, Frisvad and Seifert	Wooden organ and pipes	[94]
Talaromyces sayulitensis Visagie, N. Yilmaz, Seifert and Samson	Air	[28]
Trichoderma harzianum Rifai	Air, textiles and human remains	[83]
Trichoderma longibrachiatum Rifai	Cinematographic films	[95]
Trichoderma viride Pers.	Air	[98]
Trichothecium roseum (Pers.) Link	Albumen photographic materials	[93]
Xenochalara juniperi M.J. Wingf. and Crous	Funeral clothes	[85]

Previously identified as: [1] *Phialosimplex caninus*; [2] *Eurotium chevalieri*; [3] *Eurotium cristatum*; [4] *Aspergillus oryzae*; [5] *Emericella* sp.; [6] *Chaetomium murorum*; [7] *Bullera alba*; [8] *Cladosporium herbarium*; [9] *Bipolaris australiensis*; [10] *Phoma glomerata*; [11] *Geotrichum* sp.; [12] *Phaeosphaeria avenaria*; [13] *Candida guilliermondii*; [14] *Scopulariopsis brevicaulis*; [15] *Nigrospora sphaerica*; [16] *Paecilomyces formosus*; [17] *Penicillium janthinellum*; [18] *Pleurotus pulmonarius*; [19] *Rhizopus microsporus var. oligosporus*; [20] *Cephalosporium* sp.; [21] *Sporidiobolus metaroseus*.

Fungal cellulolytic action is known to contribute to the biodeterioration of paper, canvas oil paintings, binders and photographic materials [3]. Moreover, cellulolytic action abilities characterization in cultural heritage scenarios has been helpful to study the biodeteriorative contribution of isolates retrieved from air, albumen photographic materials, mummies, funeral accessories, wooden art objects, organs and pipes, wax seals, graphic documents, stone, drawings, lithographs, paintings, textiles, human remains, maps, photographs, paper and other materials present in libraries and museums [28,36,69,79,81–83,96–100,102–105]. Cellulolytic ability screening can be conducted using Czapek-Dox agar supplemented with hydroxyethyl cellulose [69], Congo Red agar [79], Mandels and Reese medium with carboxymethyl cellulose (CMC) [106] or media containing sterilized filter paper [47]. Positive evaluation of cellulolytic ability can be assessed by the visualization of hydrolyzed areas or after congo red application and treatment. Over one hundred and fifty fungal species have been found to have cellulolytic abilities (Table 9). The great majority of species belonged to genera *Alternaria*, *Aspergillus*, *Chaetomium*, *Cladosporium*, *Penicillium* and *Talaromyces*. As such, detection of these fungal species on cellulolytic materials including paper, paintings and photographic materials, should be perceived as putatively threatening from a biodeterioration standpoint.

Table 9. Overview of fungal species for which isolates have been identified as displaying cellulolytic abilities in biodeteriorative plate essays.

Current Species Name	Original Study Focus	References
Acremonium alabamense Morgan-Jones	Air	[98]
Acrostalagmus luteoalbus (Link) Zare, W. Gams and Schroers	Albumen photographic materials	[93]
Alternaria alternata (Fr.) Keissl.	Air, mummies and funeral accessories	[79,80,98]
Alternaria chartarum Preuss [1]	Mummies	[81]
Alternaria consortialis (Thüm.) J.W. Groves and S. Hughes [2]	Wooden art objects	[36]
Alternaria mali Roberts	Mummies, wooden organ and pipes	[79,94]
Alternaria Nees	Air and graphic documents, stone and mummies	[47,79,90,91]
Alternaria solani Sorauer	Mummies	[79]
Alternaria tenuissima (Kunze) Wiltshire	Air and mummies	[79,102]
Arthrinium arundinis (Corda) Dyko and B. Sutton	Drawings and lithographs	[94]
Arthrinium phaeospermum (Corda) M.B. Ellis	Wooden art objects	[36]
Ascomycota Caval. -Sm.	Funeral clothes and oainting	[85,103]
Ascotricha Berk.	Painting	[103]
Ascotricha chartarum Berk.	Painting	[103]
Aspergillus alliaceus Thom and Church	Air and graphic documents	[98,100]
Aspergillus amstelodami (L. Mangin) Thom and Church [3]	Air, stone, wooden organ, pipes and objects	[28,36,69,90,94]
Aspergillus auricomus (Guég.) Saito	Air and graphic documents	[100]
Aspergillus caespitosus Raper and Thom	Air, textiles and human remains	[83]
Aspergillus calidoustus Varga, Houbraken and Samson	Air, textiles and human remains	[28,83]
Aspergillus candidus Link	Air, textiles, mummies, graphic documents, maps, photographs and human remains	[81,83,98–100]
Aspergillus chevalieri (L. Mangin) Thom and Church [4]	Air, photographs, maps and graphic documents	[99,100]
Aspergillus clavatus Desm.	Air and textiles	[82,102]
Aspergillus creber Jurjević, S.W. Peterson and B.W. Horn	Air	[28]
Aspergillus cristatus Raper and Fennell [5]	Funeral clothes, wooden organ and pipes	[85,94]
Aspergillus fischeri Wehmer [6]	Air, textiles and human remains	[83]
Aspergillus flavipes (Bainier and R. Sartory) Thom and Church	Air	[98,102]
Aspergillus flavus Link [7]	Air, stone, paintings, graphic documents, photographs, maps, paintings, library and museums	[28,47,90,96,98–100,102,104]
Aspergillus fumigatus Fresen.	Air, textiles, paper, parchment, funeral clothes, libraries, museums and human remains	[83,85,96,97]
Aspergillus japonicus Saito	Air and graphic documents	[100]
Aspergillus jensenii Jurjević, S.W. Peterson and B.W. Horn	Air	[28]
Aspergillus melleus Yukawa	Air	[28]
Aspergillus niger Tiegh	Air, stone, paintings, libraries, museums, graphic documents, photographs, maps, drawings and lithographs	[28,90,96,98–100,102,104,105]
Aspergillus ostianus Wehmer	Air and graphic documents	[100]
Aspergillus P. Micheli ex Haller	Air	[47]
Aspergillus penicillioides Speg.	Air and graphic documents	[100]
Aspergillus protuberus Munt. -Cvetk.	Air	[28]
Aspergillus pseudodeflectus Samson and Mouch.	Funeral clothes	[85]
Aspergillus sydowii (Bainier and Sartory) Thom and Church	Air, textiles, human remains, funeral clothes, libraries, museums, wooden organ and pipes	[28,83,85,94,96]
Aspergillus tabacinus Nakaz., Y. Takeda, Simo and A. Watan.	Air	[28]
Aspergillus tamarii Kita	Air and materials present in libraries and museums	[96]

Table 9. *Cont.*

Current Species Name	Original Study Focus	References
Aspergillus terreus Thom	Air, textiles, wooden art objects, libraries, museums and human remains	[36,69,83,96,102]
Aspergillus unguis (Émile-Weill and L. Gaudin) Thom and Raper	Air and graphic documents	[100]
Aspergillus unilateralis Thrower	Air and graphic documents	[100]
Aspergillus ustus (Bainier) Thom and Church	Mummies and wooden art objects	[36,81]
Aspergillus venenatus Jurjević, S.W. Peterson and B.W. Horn	Air, textiles and human remains	[83]
Aspergillus versicolor (Vuill.) Tirab	Air, wooden art objects, textiles, human remains, albumen photographic materials, drawings, lithographs, wooden organ and pipes	[28,36,83,93,94,102, 105]
Aspergillus westerdijkiae Frisvad and Samson	Air, textiles and human remains	[83]
Aureobasidium pullulans (de Bary and Löwenthal) G. Arnaud	Mummies	[81]
Bjerkandera adusta (Willd.) P. Karst.	Paper, parchment and albumen photographic materials	[93,97]
Chaetomium elatum Kunze	Air, wooden art objects and albumen photographic materials	[36,93,102]
Chaetomium globosum Kunze	Wooden art, air, paintings, libraries, museums, drawings and lithographs	[36,69,96,103,105]
Chaetomium thermophilum La Touche	Mummies	[81]
Cladosporium aggregatocicatricatum Bensch, Crous and U. Braun	Wax seal	[84]
Cladosporium angustisporum Bensch, Summerell, Crous and U. Braun	Drawings and lithographs	[105]
Cladosporium cladosporioides (Fresen.)	Air, wooden art objects, mummies, libraries, museums, graphic documents, photographs, maps, drawings. lithographs, wooden organ and pipes	[36,69,79,94,96,98–100,102,105]
Cladosporium herbarum (Pers.) Link [8]	Air and mummies	[81,102]
Cladosporium Link	Etruscan hypogeal tombs, air, textiles, human remains, wooden art objects, mummies, drawings and lithographs	[36,44,57,79,83,105]
Cladosporium oxysporum Berk. and M.A. Curtis	Air and materials present in libraries and museums	[96,102]
Cladosporium pseudocladosporioides Bensch, Crous and U. Braun	Mummies	[79]
Cladosporium sphaerospermum Penz.	Mummies, air and materials present in libraries and museums	[79,82,92,96,105]
Cladosporium tenuissimum Cooke	Textiles, mummies, drawings and lithographs	[79,82,105]
Cladosporium uredinicola Speg.	Mummies	[79]
Collariella bostrychodes (Zopf) X. Wei Wang and Samson [9]	Air and materials present in libraries and museums	[96]
Colletotrichum kahawae J.M. Waller and Bridge	Drawings and lithographs	[105]
Coniochaeta cipronana Coronado-Ruiz, Avendaño, Escudero-Leyva, Conejo-Barboza, P. Chaverri and Chavarría	Drawings and lithographs	[105]
Coprinellus xanthothrix (Romagn.) Vilgalys, Hopple and Jacq. Johnson	Air, textiles and human remains	[83]
Curvularia australiensis (Bugnic. ex M.B. Ellis) Manamgoda, L. Cai and K.D. Hyde [10]	Air and graphic documents	[100]
Curvularia Boedijn	Air and stone	[47,90]
Curvularia clavata B.L. Jain	Air	[102]
Curvularia eragrostidis (Henn.) J.A. Mey.	Air and graphic documents	[98,100]
Curvularia lunata (Wakker) Boedijn	Air and materials present in libraries and museums	[86,102]
Curvularia pallescens Boedijn	Air and graphic documents	[98,100,102]

Table 9. *Cont.*

Current Species Name	Original Study Focus	References
Cyphellophora G.A. de Vries	Etruscan hypogeal tombs	[44]
Cyphellophora olivacea (W. Gams) Réblová & Unter.	Etruscan hypogeal tombs	[44]
Dichotomopilus indicus (Corda) X. Wei Wang and Samson [11]	Air and materials present in libraries and museums	[96]
Dipodascus Lagerh. [12]	Air	[47]
Epicoccum Link	Air and graphic documents	[100]
Epicoccum nigrum Link	Mummies, wooden organ and pipes	[79,94]
Fomes fomentarius (L.) Fr.	Textiles	[82]
Fulvia fulva (Cooke) Cif. [13]	Air	[102]
Fusarium Link	Air, stone and graphic documents	[47,90,100,102]
Fusarium oxysporum Schltdl.	Air and wooden materials	[70,98]
Fusarium proliferatum (Matsush.) Nirenberg ex Gerlach and Nirenberg	Air	[98]
Hormodendrum pyri W.H. English	Wax seal	[84]
Hypochnicium J. Erikss.	Wooden materials	[61]
Meyerozyma guilliermondii (Wick.) Kurtzman and M. Suzuki [14]	Air	[98]
Microascus brevicaulis S.P. Abbott [15]	Air, textiles and human remains	[83]
Mortierella Coem.	Wooden materials	[61]
Mucor circinelloides Tiegh.	Mummies	[81]
Mucor P. Micheli ex L.	Air	[102]
Mucor plumbeus Bonord.	Albumen photographic materials	[93]
Mucor racemosus Bull.	Air, paper and parchment	[97,98]
Mucor spinosus Schrank	Paper and parchment	[97]
"Neocosmospora" solani (Mart.) L. Lombard and Crous [16]	Wooden materials	[70]
Neurospora crassa Shear and B.O. Dodge	Air	[98,102]
Neurospora sitophila Shear and B.O. Dodge [17]	Air and materials present in libraries and museums	[96,98]
Nigrospora oryzae (Berk. and Broome) Petch	Air, textiles and human remains	[83]
Nigrospora oryzae (Berk. and Broome) Petch	Air and materials present in libraries and museums	[96,98]
Paecilomyces maximus C. Ram [18]	Wooden organ and pipes	[94]
Paecilomyces variotii Bainier	Air	[98]
Penicillium aurantiogriseum Dierckx	Air	[102]
Penicillium brevicompactum Dierckx	Air	[28]
Penicillium camemberti Thom	Paper and parchment	[97]
Penicillium canescens Sopp	Air and graphic documents	[28,100]
Penicillium carneum (Frisvad) Frisvad	Air	[28]
Penicillium chrysogenum Thom	Wooden objects, air, textiles, mummies, human remains, drawings, maps, photographs, lithographs, graphic documents and materials present in libraries and museums	[28,36,69,79,82,83,96–100,102,105]
Penicillium citreonigrum Dierckx	Air	[28]
Penicillium citrinum Thom	Air, paintings, graphic documents, photographs, maps and materials present in libraries and museums	[28,96,99,100,102,104]
Penicillium commune Thom	Air, textiles, paper, parchment, funeral clothes and human remains	[83,85,97,102]
Penicillium corylophilum Dierckx	Textiles, air and materials present in libraries and museums	[82,96]
Penicillium crocicola T. Yamam.	Funeral clothes	[85]
Penicillium crustosum Thom	Air, textiles, funeral clothes, human remains and wooden organ and pipes	[83,85,94]
Penicillium decumbens Thom [19]	Air, paper and parchment	[28,97,102]
Penicillium digitatum (Pers.) Sacc.	Air, textiles and human remains	[28,83,102]

Table 9. *Cont.*

Current Species Name	Original Study Focus	References
Penicillium expansum Link	Air, wooden art objects and funeral clothes	[28,36,69,85]
Penicillium glabrum (Wehmer) Westling	Wooden objects, air and materials present in libraries and museums	[28,69,96]
Penicillium griseofulvum Dierckx	Air, textiles, graphic documents and human remains	[83,100,102]
Penicillium herquei Bainier and Sartory	Wooden objects and air	[36,69]
Penicillium janczewskii K.W. Zaleski	Air, photographs, maps and graphic documents	[99,100]
Penicillium Link	Air, mummies, wooden art objects, albumen photographic materials, funeral accessories and paintings	[36,47,80,81,93,98–100,103]
Penicillium raistrickii G. Sm.	Mummies	[79]
Penicillium roseopurpureum Dierckx	Mummies and funeral clothes	[79,85]
Penicillium rubens Biourge	Painting	[103]
Penicillium sacculum E. Dale	Wooden objects and air	[36,69]
Penicillium sanguifluum (Sopp) Biourge	Air	[28]
Penicillium simplicissimum (Oudem.) Thom	Air, photographs, maps, graphic materials and materials present in libraries and museums	[96,99,100]
Penicillium solitum Westling	Air	[28]
Penicillium thomii Maire	Albumen photographic materials	[93]
Penicillium ulaiense H.M. Hsieh, H.J. Su and Tzean	Air	[28]
Penicillium viridicatum Westling	Paper and parchment	[97]
Penicillium waksmanii K.W. Zaleski	Air and graphic documents	[100]
Penicillium westlingii K.W. Zaleski	Drawings and lithographs	[105]
Periconia epigraphicola Coronado-Ruiz, R. E. Escudero-Leyva, G. Conejo-Barboza, P. Chaverri and M. Chavarría	Drawings and lithographs	[105]
Pestalotia De Not.	Air and graphic documents	[100]
Phlebia Fr.	Albumen photographic materials	[93]
Phoma herbarum Westend.	Paper and parchment	[97]
Pleosporales Luttr. ex M.E. Barr	Albumen photographic materials	[93]
Pleurotus ostreatus (Jacq.) P. Kumm. [20]	Albumen photographic materials	[93]
Pseudallescheria fimeti (Arx, Mukerji and N. Singh) McGinnis, A.A. Padhye and Ajello	Painting	[103]
Pseudallescheria Negr. and I. Fisch.	Painting	[103]
Pseudogymnoascus pannorum (Link) Minnis and D.L. Lindner [21]	Wooden objects and air	[36,69]
Pseudoscopulariopsis hibernica (A. Mangan) Sand. -Den., Gené and Cano [22]	Air, textiles and human remains	[83]
Rhizopus arrhizus A. Fisch. [23]	Air, textiles and human remains	[83]
Rhizopus microsporus Tiegh.	Air, textiles and human remains	[83]
Sarocladium W. Gams and D. Hawksw. [24]	Air and graphic documents	[98,100]
Sporobolomyces roseus Kluyver and C.B. Niel [25]	Funeral accessories	[80]
Stachybotrys chartarum (Ehrenb.) S. Hughes	Mummies	[81]
Stemphylium vesicarium (Wallr.) E.G. Simmons	Mummies	[79]
Syncephalastrum racemosum Cohn ex J. Schröt.	Air and materials present in libraries and museums	[96]
Talaromyces amestolkiae N. Yilmaz, Houbraken, Frisvad and Samson	Air	[28]
Talaromyces purpureogenus Samson, N. Yilmaz, Houbraken, Spierenb., Seifert, Peterson, Varga and Frisvad	Stone	[90]
Talaromyces rugulosus (Thom) Samson, N. Yilmaz, Frisvad and Seifert	Wooden organ and pipes	[94]
Talaromyces sayulitensis Visagie, N. Yilmaz, Seifert and Samson	Air	[28]

Table 9. *Cont.*

Current Species Name	Original Study Focus	References
Talaromyces verruculosus (Peyronel) Samson, N. Yilmaz, Frisvad and Seifert	Air	[28]
Trichoderma harzianum Rifai	Air, textiles and human remains	[83]
Trichoderma longibrachiatum Rifai	Drawings and lithographs	[105]
Trichoderma viride Pers.	Wooden art objects and air	[36,69,98]
Trichothecium roseum (Pers.) Link	Albumen photographic materials	[93]

Previously identified as: [1] *Ulocladium chartarum*; [2] *Alternaria consortiale*; [3] *Eurotium amsteldomi*; [4] *Eurotium chevalieri*; [5] *Eurotium cristatum*; [6] *Neosartorya fischeri*; [7] *Aspergillus oryzae*; [8] *Cladosporium herbarium*; [9] *Chaetomium bostrychodes*; [10] *Bipolaris australiensis*; [11] *Chaetomium indicum*; [12] *Geotrichum* sp.; [13] *Cladosporium fulvum*; [14] *Candida guilliermondii*; [15] *Scopulariopsis brevicaulis*; [16] *Fusarium solani*; [17] *Chrysonilia sitophila*; [18] *Paecilomyces formosus*; [19] *Penicillium funiculosum*; [20] *Pleurotus pulmonarius*; [21] *Chrysosporium pannorum*; [22] *Scopulariopsis hibernica*; [23] *Rhizopus oryzae*; [24] *Cephalosporium* sp.; [25] *Sporidiobolus metaroseus*.

5. Conclusions

As pointed and reviewed by Pyzik and colleagues [107] the application of high-throughput Next-Generation sequencing technologies has highlighted that cultural heritage materials are inhabited by various unknown microorganisms still pending taxonomic description and their biodeteriorative profiling. The material biodeterioration is known to sometimes be caused by a predominant or specific microbial group, while more often the complex biodeterioration processes are a result of the synergistic action of a group of organisms resulting from various colonization events influenced by the impacts of multiple external factors throughout a time frame [77]. Cultivation methodologies often face limitations in what regards the ability for distinct organisms to be effectively cultivated and their original biodeteriorative characteristics replicated under laboratory conditions [108]. Understandably the application of more modern molecular techniques in cultural heritage biodeterioration studies has been increasingly being used and updated for the last two decades [27,108]. Although with their own set of limitations, culture-dependent methodologies still offer three main advantages: (1) The isolation of microbes for further differential analysis; (2) the possibility to isolate, characterize and describe previously unknown taxa; and (3) the development and improvement of biological and genetic databases. These aspects are especially important when considering that even the biodeteriorative role (but also their taxonomic classification) of long known species might also need to be constantly revised, updated and reevaluated [107,109]. For instance, the inclusion of the *Fusarium solani* Species Complex in the genus *Neocosmospora* was recently reevaluated and continues to be the focus of additional studies [110].

Fungi are constantly regarded as one if not the most important microorganism groups causing cultural heritage materials biodeterioration [2,3,30]. This review highlighted that, so far, isolates from more than two-hundred fungal species have been showed to exhibit biodeteriorative abilities when studied by specific plate essays. Based on the available studies performed so far, it is possible to verify that *Aspergillus* and *Penicillium* species dominate the biodeteriorative abilities usually screened in biodeterioration contexts. With this in mind, it should be reinforced that the detection of these species in various cultural heritage materials can, under specific conditions, result in severe biodeterioration of the substrate. Nonetheless, a careful analysis of these checklists, as well as, the biodeteriorative screening of obtained isolates, wherever possible, is strongly advised. Not all isolates might display deteriorative action or display similar degradative rates and thus a proper and specific analysis in each case and/or the implementation of additional tests (e.g., molecular identification of genes involved in biodeterioration (see for example [111])) is also recommended. In conjunction with molecular approaches not relying in cultivation, they can provide a holistic evaluation of a specific biodeterioration phenomena. As pointed by Sterflinger and colleagues [112], understanding deterioration mechanisms and the main microbial perpetrators is still one of the major challenges in historic and cultural materials biodeterioration research. As such, the information summarized in this work provides a contribution that can help microbiologists, restorers, conservators and curators in their attempt to preserve cultural heritage materials for future generations.

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