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

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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

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, saprotrrophic 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 extra-cellular 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 CaCO₃ glucose agar; and (b) calcium oxalates crystals developing around fungal mycelium growing in Malt extract agar containing CaCO₃.

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 summa-
rization. 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. Novákůvá, Samson, Houbranken, Frisvad and M. Košařík | 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] |
| 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 hypogean tombs | [44] |
| *Cladosporium sphaerospermum* Pers. | Mural paintings | [41] |
| *Cyphellophora* G.A. de Vries | Etruscan hypogean tombs | [44] |
| *Cyphellophora olivacea* (W. Gams) R éblová & Unter. | Etruscan hypogean tombs | [44] |
| *Exaphila* J.W. Carmich. | Etruscan hypogean 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] |
| *Paeicillomyces* Bainier | Mayan buildings and catacombs | [33,35] |
| *Parenzygodontium 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 bialide* Chalab. | Frescoes and air | [38] |
| *Penicillium brevicompactum* Dierckx | Wooded art objects, air, mural paintings, limestone tomb, dolomitic limestone wall, limestone and plaster monuments and museums | [28,36,39,41–43] |
| *Penicillium chrysogenum* Thom | Frescoes, air and mural paintings | [38,40,41] |
| *Penicillium commune* Thom | Dolomitic limestone wall | [42] |
| *Penicillium crustosum* Thom | Wooden art objects, air, dolomitic limestone wall and limestone tomb | [28,36,42] |
| *Penicillium glabrum* (Wehmer) Westling | Frescoes and air | [38] |
| *Penicillium griseofulvum* Dierckx | Frescoes and air | [38] |
| *Penicillium Ianosum* Westling | Wooden art objects, air, frescoes, concrete and bricks | [36,40] |
| *Penicillium Link* | Mayan buildings | [35] |
| *Penicillium oxalicum* Currie and Thom | Mayan buildings | [35] |
| *Penicillium polonicum* K.W. Zaleski | Mural paintings | [41] |
| *Penicillium rubens* Biourge | Frescoes and air | [36] |
| *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 saquilensis* Visagie, N. Yilmaz, Seifert and Samson | Air | [28] |
| *Trichocladium canadense* S. Hughe | Mayan buildings | [35] |
| *Trichoderma Pers.* | Mayan buildings | [35] |
| *Valsaria sparti* 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 | Unk | Air and wall paintings | [56] |
| Aspergillus aureolatus Munt.—Cvetk. and Bata | Cc | Air and wall paintings | [56] |
| Aspergillus europaecus Hubka, A. Nováková, Samson, Houbraken, Frisvad and M. Kolafik | 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 palidofulvus 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 | Cc, Unk | Air, wall paintings and stone stela | [54,56] |
| Botrytis cinerae Pers. | Unk CO | Limestone tomb | [54] |
| Chaetomium anceps (Udagawa and Cain | Unk | Air and wall paintings | [56] |
| Cladosporium cladosporioides (Fresen.) G.A. de Vries | Cc, Wd | Air and wall paintings | [56] |
| Cladosporium sphaerospermum Penz. | Cc, Wd | Mural paintings | [41] |
| Colletotrichum acutatum J.H. Simmonds | Cc (Vaterite), Cc, Hap, Phosp | Limestone monument | [53,55] |
| Fusarium proliferatum (Matsush.) Nirenberg | Cc | Air and wall paintings | [56] |
| Lasiodiplodia theobromae (Pat.) Griffon and Maubl. | Unk | Mayan buildings | [35] |
| Leptosphaeria avenaria G.F. Weber | Cc | Air and wall paintings | [56] |
| Mucor fragilis Bainier | Unk | Mayan buildings | [35] |
| Penicillium commune Thom | Cc, Wd | Mayan buildings | [41,56] |
| Phialemonium inflatum (Burnside) Dania Garcia, Perdomo, Gené, Cano and Guarro | 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 | Unk | Air and wall paintings | [56] |
| Rolellia 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] |
| Xylaria Hill ex Schrank | Unk | Mayan buildings | [35] |
| Previously identified as: 1 Phoma medicaginis; 2 Gibberella moniliformis; 3 Phaeosphaeria avenaria; 5 Penicillium mancingi; 6 Paecilomyces inflatus; 7 Thanatephorus cucumeris; 8 Hypoxylon sp.; Cc—calcium carbonate; Wd—weddelitite; Wh—whewellite; Hap—hydroxyapatite; Hyd—hydrocruzite; 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.

| 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]       |
| *Hypochromicium* 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 Sartry | Wooden art objects           | [36]       |
| *Penicillium Link*                   | Wooden art objects           | [36]       |
| *Penicillium sacculum* E. Dale       | Wooden art objects           | [36]       |
| *Pseudogymnascus 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, esterase 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, esterase 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].

| Current Species Name | Original Study Focus | References |
|----------------------|----------------------|------------|
| Alternaria alternata (Fr.) Keissl. | Funeral accessories [70] | |
| Ascomycota Caval. -Sm. | Funeral clothes [85] | |
| Aspergillus caninus (Sigler, Doanna A. Sutton, Gibas, Summerb. and Iwen) Houbraken, Tanney, Visagie and Samson | Funeral clothes [85] | |
| Aspergillus cristatus Raper and Fennell | Funeral clothes [85] | |
| Aspergillus fumigatus Fresen. | Funeral clothes [85] | |
| Aspergillus P. Micheli ex Haller | Funeral accessories [80] | |
| Aspergillus paniceus Kwon-Chung and Fennell | Funeral clothes [85] | |
| Aspergillus sydowii (Bainier and Sartory) Thom and Church | Funeral clothes [85] | |
| Aspergillus tubingenensis Mosseray | Funeral clothes [85] | |
| Aspergillus versicolor (Vuill.) Trab. | Funeral accessories [80] | |
| Beauveria bassiana (Bals.—Criv.) Vuill. | Funeral clothes [85] | |
| Myriodontium keratinophilum Samson and Polon. | Funeral clothes [85] | |
| Penicillium breviconveptum Dierckx | Funeral clothes [85] | |
| Penicillium commune Thom | Funeral accessories [80] | |
| Penicillium crociola 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 Klyuyver and C.B. Niel | 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 avanornii Nakaz. | Wooden art objects | [36] |
| Aspergillus fischeri Wehmer ³ | Wooden art objects | [36] |
| Aspergillus fuscus 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 cladosporioides | 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] |
| Hypocrynicium 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 salmonum de Hoog | Wax seal | [84] |
| Agaricaeae Chevall. | Statue and air | [89] |
| Alternaria Nees | Statue and stone and air | [89,90] |
| Alternaria tenuissima (Kunze) Wiltshire | Stone | [90] |
| Aspergillus amstelodami (L. Mangin) Thom and Church ¹ | Air, textiles and human remains | [83] |
| Aspergillus caespitosus Raphe and Thom | Air, textiles and human remains | [83] |
| Aspergillus calidoustus Varga, Houbraken and Samson | Air, textiles and human remains | [83] |
| Aspergillus candidus Link | Textiles | [82] |
| Aspergillus clavatus Desm. | Air, textiles and human remains | [83] |
| Aspergillus fischeri Wehmer ² | Stone | [90] |
| Aspergillus flavus Link | Air, statues, textiles and human remains | [83,89] |
| Aspergillus fumigatus Fresen. | Air, statues, textiles and human remains | [83,89] |
| Aspergillus niger Tiegh | Air, statues, textiles and human remains | [83,89] |
| Aspergillus repens (Corda) Sacc. ³ | Air, textiles and human remains | [83] |
| Aspergillus sydowi (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, textiles and human remains | [83,89] |
| Aspergillus westerdijkiae Frisvad and Samson | Air, textiles and human remains | [83] |
| Aureobasidium pullulans (de Bary and Lówenthal) G. Arnaud | Wax seal | [84] |
| Bulleromyces abus Boekhout and A. Fonseca ⁴ | Wax seal | [84] |
| Cladosporium aggregatocatricatum Bensch, Crous and U. Braun | Wax seal | [84] |
| Cladosporium Link | Air, statues, textiles and human remains | [83,89] |
| Cladosporium macaroun 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 breviculus S.P. Abbott | 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 | [83] |
| Penicillium commune Thom | Air, textiles and human remains | [83] |
| Penicillium corylophilum Dierckx | Air, statues, textiles and human remains | [83,89] |
| Penicillium crustosum Thom | Air, textiles and human remains | [83] |
| Penicillium hordei Stolk | Air, textiles and human remains | [83] |
| Penicillium Link | Air, textiles and human remains | [83] |
| Penicillium polonicum K.W. Zaleski | Air, textiles and human remains | [83] |
| Pseudoscopulariopsis hibernica (A. Mangan) Sand. -Den., Gené and Cano | Air, textiles and human remains | [83] |
| Rhizopus arrhizus A. Fisch. | Air, textiles and human remains | [83] |
| Rhizopus microsporus Tiegh. | Air, textiles and human remains | [83] |
| Rhizopus stolonifer (Ehrenb.) Vuill. | Air, textiles and human remains | [83] |
| Sordaria fimicola (Roberge ex Desm.) Ces. and De Not. | Air, textiles and human remains | [83] |
| Talaromyces purpureogenous Samson, N. Yilmaz, Houbraken, Spiereb., Seifert, Peterson, Varga and Frisvad | Air, textiles and human remains | [83] |
| Thyronectria austroamericana (Speg.) Seeler | Air, textiles and human remains | [83] |
| Trichoderma parawiridelescens Jaklitsch, Samuels and Voglmayr | Air, textiles and human remains | [83] |

Previously identified as: 1 Eurotium amstelodami; 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 photographic 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 salmoncum de Hoog | Wax seal | [84] |
| Acrostalagmus lutheolus (Link) Zare, W. Gams and Schroers | Albumen photographic materials | [93] |
| Agaricaeae Chevall. | Statue and air | [89] |
| Alternaria malis Roberts | Wooden organ and pipes | [94] |
| Alternaria Nees | Statue and air | [89] |
| Alternaria tenusissima (Kunze) Wiltshire | Statue and air | [89] |
| Aspergillus anstelodami (L. Margin) Thom and Church | 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 | Wooden organ and pipes | [94] |
| 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 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 | Air, textiles and human remains                           | [84]             |
| *Bjerkandera adusta* (Willd.) P. Karst.      | Air, textiles and human remains                           | [84]             |
| *Bulleromyces albus* Boekhout and A. Fonseca ⁵ | Air, textiles and human remains                           | [84]             |
| *Chaetomium elatum* Kunze              | Air, textiles and human remains                           | [84]             |
| *Cladosporium aggregatocatricatum* Bensch, Crous and U. Braun | Air, textiles and human remains                           | [94]             |
| *Cladosporium cladosporioides* (Fresen.) G.A. de Vries | Air, textiles and human remains, albumen photographic materials, wooden organ and pipes | [44,83]          |
| *Cladosporium Link*                     |                                                          |                  |
| *Cladosporium macrocarpum* Preuss       |                                                          |                  |
| *Coprinellus xanthothrix* (Romagn.) Vilgalys, Hopple and Jacq. Johnson | Air, textiles and human remains                           | [83]             |
| *Coprinopsis cinea* (Schaeff.) Redhead, Vilgalys and Moncalvo | Air, textiles and human remains                           | [83]             |
| *Cyphellophora G.A. de Vries*           | Air, textiles and human remains                           | [83]             |
| *Cyphellophora oliveacea* (W. Gams) Réblová & Unter. | Air, textiles and human remains                           | [83]             |
| *Epilococcus linkii*                    | Air, textiles and human remains                           | [83]             |
| *Exophiala angulospora* Iwatsu, Udagawa & Takase | Air, textiles and human remains                           | [83]             |
| *Exophiala J.W. Carmich.*               | Air, textiles and human remains                           | [83]             |
| *Eurotium amstelodami* Wehmer ³         | Air, textiles and human remains                           | [83]             |
| *Eurotium cristatum* (Vuill.)           | Air, textiles and human remains                           | [83]             |
| *Eurotium repens* (Bainier) Sacc. ⁴    | Air, textiles and human remains                           | [83]             |
| *Eurotium versicolor* (Vuill.) Tirab    | Air, textiles and human remains                           | [83]             |
| *Microascus brevicaulis* S.P. Abbott ⁶  | Air, textiles and human remains                           | [83]             |
| *Mucor plumbeus* Bonord.               | Air, textiles and human remains                           | [93]             |
| *Nigrospora oryzae* (Berk. and Broome) Petch | Air, textiles and human remains                           | [93]             |
| *Paecilomyces maximus* C. Ram           | Air, textiles and human remains                           | [93]             |
| *Penicillium chrysogenum* Thom          | Air, textiles and human remains                           | [93]             |
| *Penicillium commune* Thom              | Air, textiles and human remains                           | [93]             |
| *Penicillium corylophilum* Dierckx     | Air, textiles and human remains                           | [93]             |
| *Penicillium crustosum* Thom            | Air, textiles and human remains                           | [93]             |
| *Penicillium digitatum* (Pers.) Sacc.   | Air, textiles and human remains                           | [83]             |
| *Penicillium griseofulvum* Dierckx     | Air, textiles and human remains                           | [83]             |
| *Penicillium hordet* Stolk              | Air, textiles and human remains                           | [83]             |
| *Penicillium Link*                      | Air, textiles and human remains                           | [83]             |
| *Penicillium polonicum* K.W. Zaleski    | Air, textiles and human remains                           | [83]             |
| *Penicillium thomii* Maire              | Air, textiles and human remains                           | [83]             |
| *Phellia* Fr.                          | Air, textiles and human remains                           | [83]             |
| *Pleosporales Luttr. ex M.E. Barr*      | Air, textiles and human remains                           | [83]             |
| *Pseudoscleraiphiopsis 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 and human remains                           | [83]             |
| *Rhizopus stolonifer* (Ehrenb.) Vuill.  | Air, textiles and human remains                           | [83]             |
| *Sordaria fimicola* (Roberge ex Desm.) Ces. and De Not. | Air, textiles and human remains                           | [83]             |
| *Talaromyces flavus* (Klöcker) Stolk and Samson | Air, textiles and human remains                           | [83]             |
| *Thyronectria austroamericana* (Speg.) Seeler ⁹ | Air, textiles and human remains                           | [83]             |
| *Trichoderma harzianum* Rifai           | Air, textiles and human remains                           | [83]             |
| *Trichoderma paravoridescens* Jaklitsch, Samuels and Voglmayr | Air, textiles and human remains                           | [83]             |
| *Trichotheceum roseum* (Pers.) Link     | Air, textiles and human remains                           | [83]             |

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 as 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 luteolus (Link) Zare, W. Gams and Schroers | Albumen photographic materials | [93] |
| Actinomucor elegans (Eidam) C.R. Benjamin and Hesseltime | 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 | Funeral clothes | [85] |
| Ascomycota Caval. -Sm. | Air and graphic documents | [86,100] |
| Aspergillus alliaceus Thom and Church | Air, wooden organ and pipes | [28,94] |
| Aspergillus amstelodami (L. Mangin) Thom and Church | Frescoes and air | [38] |
| Aspergillus auricomus (Gué.) 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, Summerr. and Iwen) Houbraken, Tanney, Visagie and Samson | Funeral clothes | [85] |
| Aspergillus chevalieri (L. Mangin) Thom and Church | 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 | Funeral clothes, wooden organ and pipes | [85,94] |
| Aspergillus cristatus Raper and Fennell | Frescoes and air | [28,38] |
| Aspergillus eurepasus Hubka, A. Novakova, Samson, Houbraken, Frisvad and M. Kolafik | Air | [98] |
| Aspergillus flavipes (Bainier and R. Sartory) Thom and Church | Air, frescoes, mummies, photographs, maps and materials present in libraries and museums | [38,47,78,79,96,99,100] |
| Aspergillus flavus Link | 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 museums, 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 ostiarius Wehmer | Frescoes, air and graphic documents | [38,100] |
| Aspergillus P. Micheli ex Haller | Air and mural paintings | [41,47] |
| Aspergillus penicilloides Spec. | Air and graphic documents | [100] |
| Aspergillus prolificans G. Sm. | Air | [28] |
| Aspergillus protuberans Munt. –Cvetk. | Air | [28] |
| Aspergillus pseudodeflectus Samson and Mouch | Funeral clothes | [85] |
| Aspergillus puniceus Kwon-Chung and Fennell | Funeral clothes | [85] |
| Current Species Name | Original Study Focus | References |
|----------------------|----------------------|------------|
| Aspergillus sydowii (Bainier and Saratory) 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 Kila | Air and materials present in libraries and museums | [96] |
| Aspergillus terreus Thom | Funeral clothes | [83] |
| Aspergillus tubingenensis Mosseray | Air and graphic documents | [100] |
| Aspergillus unguis (Émile-Weill and L. Gaudin) Thom and Raper | Air and graphic documents | [100] |
| Aspergillus unilateralis Thrower | 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 | [28,38,41,79,80,83,94–96] |
| Aspergillus westerdijkiae Trivisad and Samson | Wax seal and mummies | [79,84] |
| Aureobasidium pullulans (de Bary and Löwenthal) G. Arnaud | Wax seal and mummies | [79,84] |
| Beauveria bassiana (Bals.—Criv.) Vuill. | Wax seal | [79,84] |
| Botryotrichum murorum (Corda) X. Wei Wang and Samson | Frescoes and air | [38] |
| Chaetomium ancistrocladum Udagawa and Cain | Frescoes and air | [38] |
| Chaetomium cladosporioides (Pers.) Link | Frescoes and air | [38] |
| Chaetomium globosum Kunze | Frescoes and air | [38] |
| Chaetomium oxysporum | Frescoes and air | [38] |
| Cladosporium aggregatocaroticatricum Berentsch, Crous and U. Braun | Frescoes and air, albumen photographic materials | [38,95] |
| Cladosporium cucumerinum Ellis and Arthur | Frescoes and air | [38] |
| Cladosporium herbarum (Pers.) Link | Frescoes and air | [38] |
| Cladosporium macrocarpum Preuss | Frescoes and air | [38] |
| Cladosporium oxysporum Berk. and M.A. Curtis | Frescoes and air | [38] |
| Cladosporium sphaerospermum Penz. | Frescoes and air | [38] |
| Cladosporium tenuissimum Cooke | Frescoes and air | [38] |
| Cladosporium unguis | Frescoes and air | [38,95] |
| Coccinellus xanthothrix (Romagn.) Vilgalys, Hopple and Jacq. Johnson | Air, textiles and human remains | [83] |
| Curvularia australiensis (Burgnic. ex M.B. Ellis) Manamgoda, L. Cai and K.D. Hyde | Air and graphic documents | [100] |
| Curvularia Boedijn | Air and graphic documents | [100] |
| Curvularia parlescens Boedijn | Air and graphic documents | [100] |
| Cyphellophora G.A. de Vries | Air and graphic documents | [100] |
| Didymella glomerata (Corda) Qian Chen and L. Cai | Air and graphic documents | [100] |
| Dipodascus lagerh. | Air and graphic documents | [100] |
| Epicoccum nigrum | Air and graphic documents | [100] |
| Fusarium chlamydosporum Wollenw. and Reinking | Air and graphic documents | [100] |
| Fusarium Link | Air and graphic documents | [100] |
| Fusarium oxysporum Schltdl. | Air and graphic documents | [100] |
| Hormodendrum pru W.H. English | Air and graphic documents | [100] |
| Leptosphaeria avenaria Dierckx | Air and graphic documents | [100] |
| Microascus brevicaulis S.P. Abbott 14 | Air and graphic documents | [100] |
| Mucor racemosus | Air and graphic documents | [95,97] |
| Mucor sp. | Air and graphic documents | [95,97] |
| Myriodontium keratinophilum Samson and Polon. | Air and graphic documents | [95,97] |
| Nigrospora oryzae (Berk. and Broome) Petch 15 | Air and graphic documents | [95,97] |
| Paecilomyces maximus C. Ram 16 | Air and graphic documents | [95,97] |
| Paecilomyces variotii Bainier | Air and graphic documents | [95,97] |
| Penicillium aurantiogriseum Dierckx | Air and graphic documents | [95,97] |
| Penicillium bilaiae Chalab. | Air and graphic documents | [95,97] |
| Penicillium brevicompactum Dierckx | Air and graphic documents | [95,97] |
| Penicillium camemberti Thom | Air and graphic documents | [95,97] |
| Penicillium canescens Sopp | Air and graphic documents | [95,97] |
| Penicillium chrysogenum Thom | Air, murals, paintings, textiles, human remains, mummies, paper, photographs, maps, parchment, graphic documents and cinematographic films | [28,41,79,83,95,97,99,100] |
| 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 crustosus 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 elatum (Wehmer) Westling | Air | [28] |
| Penicillium granulatum Bainier | Funeral accessories | [80] |
| Penicillium griseofulvum Diercks | Air, frescoes, graphic documents, textiles and human remains | [38,83,100] |
| Penicillium hordae 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 | Air, textiles, mural paintings and human remains | [41] |
| Penicillium polonicum K.W. Zaleski | Mummies | [79] |
| Penicillium raistrickii G. Sm. | Mummies and funeral clothes | [79,85] |
| Penicillium roseopurpureum | Air, maps, photographs and graphic documents | [99,100] |
| Penicillium solitum Westling | Air | [28] |
| Penicillium spinulosum Thom | Funeral clothes | [85] |
| Penicillium viridatum Westling | Air, paper and parchment | [28,97] |
| Penicillium waksmanii | Air and graphic documents | [100] |
| Pseudozyma prolifica | Paper and parchment | [97] |
| Phoma herbarum | Alumen photographic materials | [93] |
| Pleurotus ostreatus | Mural paintings | [31] |
| Pleurotus janthinellum | Air, textiles and human remains | [83] |
| Phialosimplex caninus | Air, graphic documents and alumen photographic materials | [93,98,100] |
| Phialosimplex caninus | Funeral Accessories | [80] |
| Phialosimplex caninus | Mummies | [79] |
| Phialosimplex caninus | Wooden organ and pipes | [94] |
| Phialosimplex caninus | Air | [28] |
| Phialosimplex caninus | Textiles and human remains | [83] |
| Phialosimplex caninus | Cinematographic films | [95] |
| Phialosimplex caninus | Air | [98] |
| Phialosimplex caninus | Alumen photographic materials | [93] |
| Phaeosphaeria avenaria | Funeral clothes | [85] |

Previously identified as: 1 Phialosimplex caninus; 2 Eurotium chevalieri; 3 Eurotium cristatum; 4 Aspergillus oryzae; 5 Emericella sp.; 6 Chaetomium murovum; 7 Bullera alba; 8 Cladosporium herbarium; 9 Bipolaris australiensis; 10 Phoma glomerata; 11 Geotrichum sp.; 12 Phaeosphaeria avenaria; 13 Candida guillermondii; 14 Scopulariopsis brevicatia; 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, alumen 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 hydroxethyl 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 lutetiusl (Link) Zare, W. Gams and Schroers | Albumen photographic materials | [99] |
| Alternaria alternata (Fr.) Keissl. | Air, mummies and funeral accessories | [79,80,98] |
| Alternaria chartarum Preuss | Mummies | [81] |
| Alternaria consoritae (Thüm.) J.W. Groves and S. Hughes | Wooden art objects | [36] |
| Alternaria nali Roberts | Mummies, wooden organ and pipes | [79,94] |
| Alternaria Nees | Air and graphic documents, stone and mummies | [47,79,90,91] |
| Alternaria solani Sorauer | Air and graphic documents | [79] |
| 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 allieus Thom and Church | Air and graphic documents | [98,100] |
| Aspergillus amstelodami (L. Mangin) Thom and Church | Air, stone, wooden organ, pipes and objects | [28,36,69,90,94] |
| Aspergillus auricomus (Gueg.) 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, mummies, graphic documents, maps, photographs and human remains | [81,83,98–100] |
| Aspergillus candidus Link | Air, photographs, maps and graphic documents | [99,100] |
| Aspergillus chevalieri (L. Mangin) Thom and Church | Air and textiles | [82,102] |
| Aspergillus creber Jurjević, S.W. Peterson and B.W. Horn | Air | [28] |
| Aspergillus cristatus Raper and Fennell | Funeral clothes, wooden organ and pipes | [85,94] |
| Aspergillus fischeri Wehmer | Air, textiles and human remains | [83] |
| Aspergillus flavipes (Bainier and R. Sartry) Thom and Church | Air | [98,102] |
| Aspergillus flavus Link | 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 melius 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 ostiarius 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 Sartry) 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] |
| 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* Thower | 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 aggregatorioides* (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 | 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 spheroaspernum* 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 | Air and materials present in libraries and museums | [96] |
| *Colletotrichum kahawae* J.M. Waller and Bridge | Drawings and lithographs | [105] |
| *Coniochaeta cipronana* Coronado-Ruíz, Avendaño, Escudero-Leyva, Conejo-Barboza, P. Chaverri and Chavarria | 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 | 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] |
| 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] |
| Dichotomopsis indicus (Corda) X. Wei Wang and Samson | Air and materials present in libraries and museums | [96] |
| Dipodascus Lagerh. | Air | [47] |
| Epicoccum Link | Air and graphic documents | [100] |
| Fomes fomentarius (L.) Fr. | Mummies, wooden organ and pipes | [79,94] |
| Fulva fulva (Cooke) Cif. | Textiles | [82] |
| Fusarium Link | Air | [102] |
| Fusarium oxysporum Schltdl. | Air, stone and graphic documents | [47,90,100,102] |
| Myrocoelia guilliermondii (Wick.) Kurtzman and M. Suzuki | Air | [98] |
| Microascus brevicaulis S.P. Abbott | 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 | Wooden materials | [70] |
| Neurospora crassa Shear and B.O. Dodge | Air | [98,102] |
| Neurospora sitophila Shear and B.O. Dodge | 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 | Wooden organ and pipes | [94] |
| Paecilomyces variotii Bainier | Air | [98] |
| Penicillium aurantiogriseum Thom | Air | [102] |
| Penicillium camemberti Thom | Air | [28] |
| Penicillium canescens Sopp | Paper and parchment | [97] |
| 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 citronigrum 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 crociola 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 | Air, paper and parchment | [28,97,102] |
| Penicillium digitatum (Pers.) Sacc. | Air, textiles and human remains | [28,83,102] |
| 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. | | [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 | | [28] |
| **Penicillium thomii** Maire | | [93] |
| **Penicillium ulaniense** H.M. Hsieh, H.J. Su and Tzean | | [28] |
| **Periconia epigraphicola** Coronado-Ruiz, R. E. Escudero-Leyva, G. Conejo-Barboza, P. Chaverri and M. Chavarría | | [28] |
| **Pestalotia** De Not. | | [28] |
| **Phomopsis herbarum** Westend. | | [28] |
| **Phlebia Fr.** | | [97] |
| **Pleosporales Luttr. ex M.E. Barr** | | [105] |
| **Phlebia** Fr. | | [105] |
| **Phlebia** Fr. | | [103] |
| **Pleurotus ostreatus** (Jacq.) P. Kumm. | | [93] |
| **Pseudallescheria fimeti** (Arx, Mukerji and N. Singh) McGinnis, A.A. Padhye and Ajello | | [93] |
| **Pseudallescheria Negr. and I. Fisch.** | | [93] |
| **Pseudogymnoascus pannorum** (Link) Minnis and D.L. Lindner | | [93] |
| **Pseudogymnoascus pannorum** (Link) Minnis and D.L. Lindner | | [93] |
| **Pseudoscleroporus hibernicus** (A. Mangan) Sand. -Den., Gené and Cano | | [83] |
| **Rhizopus arrhizus** A. Fisch. | | [83] |
| **Rhizopus microsporus** Tiegh. | | [83] |
| **Sarocladium** W. Gams and D. Hawksw. | | [100] |
| **Sporobolomyces roseus** Kuyper and C.B. Niel | | [80] |
| **Stachybotrys chartarum** (Ehrenb.) S. Hughes | | [81] |
| **Stemphylium vesicarium** (Wallr.) E.G. Simmons | | [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 sayulltensis** 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 consortiae; 3 Eurotium amsteldoni; 4 Eurotium chevalieri; 5 Eurotium cristatum; 6 Neosartorius fischeri; 7 Aspergillus oryzae; 8 Cladosporium herbarium; 9 Chaetomium bostrychoides; 10 Bipolaris australiensis; 11 Chaetomium indicum; 12 Geotrichum sp.; 13 Cladosporium fulvum; 14 Candida guilliermondii; 15 Scopulariopsis birecivula; 16 Fusarium solani; 17 Chrysosporium sipta; 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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