

Fungi Affecting Wall Paintings of Historical Value

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Wall paintings have been a cultural expression of human creativity throughout history. Their degradation or destruction represents a loss to the world's cultural heritage, and fungi have been identified as a major contributor to their decay. For this reason, it is of utmost importance to know the species involved, their distribution, the method used for their identification, and the possible relation with the environment.

frescoes deterioration

fungal diversity

fungal ecology

hypogean conservation

mural paintings biodeterioration

subterranean cultural heritage deterioration

wall paintings conservation

1. Introduction

Wall paintings are among the most representative elements of figurative artworks and have been developed by human creativity since prehistoric times ^[1]. Their technique of execution requires a layered structure consisting of a support, a ground, and a paint layer, which changed over time across different cultures (secco, such as tempera, or frescoes) ^[2]. In secco technique, which is the earliest, the preparation layers are applied, but the colors remain on the surface, whereas in the frescoes the colors are applied before the mortar dries, allowing their in-depth penetration ^[2]. The employed colors usually have a mineral origin, but some pigments can also be derived from plants. Organic compounds can later be added during restoration or because of other human activities (e.g., firing candles in the churches) ^[3].

The observed deterioration phenomena of mural paintings depend largely on the materials used and the environmental conditions ^[4]. Humidity, lighting, temperature, ventilation, and nutrients select the occurring biological agents ^{[4][5]}. Organisms belonging to all domains such as bacteria, algae, fungi, arthropods and in a lesser extent lichens, mosses, ferns, and higher plants, have been found on the surfaces of mural paintings ^{[4][6]}. Indeed, given the indoor conditions of most mural paintings, photoautotrophs are limited, while fungi and bacteria are more frequent ^[7]. Bacteria with reduced nutritional needs have been often suggested to be the first colonizers. Fungi, due to their large assortment of enzymes and the remarkable ability to thrive in a wide range of environmental conditions, have been recognized as the most common cause of biodeterioration of painted surfaces and other artworks ^{[1][8][9][10]}.

The damage is generally due to the mycelial growth on the substrate, hyphal penetration, and fruiting bodies production onto and into the substrate, all of which increase the volume and number of cracks in the pigment layer and lead to surface fragments detachments ^{[1][11]}. Fungal colonization generally starts on the surface and then moves in-depth, up to decreasing painted layer cohesion and cause exfoliations and loss of the paint ^{[12][13]}. A study carried out by Dornieden and colleagues demonstrated that some fungi, such as the so-called microcolonial black fungi, are among the most dangerous for cultural heritages and can influence the resistance to shear and torsion stress of mortar and marble, contributing to the separation of different layers of material in mural paintings ^[14]. Aesthetic damages are also frequent, due to pigment discolorations, mycelial pigmentation, and/or the release of organic pigments of different colors, depending on the species involved. Extracellular enzymes and/or organic acids are generally released into the substrate from fungal hyphae causing chemical alterations of the mineral constituents of the surfaces as well as the original pigments ^{[12][13]}. The secretion of organic acids (e.g., oxalic, citric, succinic, formic, malic, acetic, fumaric, glyoxylic, gluconic, and tartaric acids) can cause dissolution of cations and chelation of metal ions from mortar and mineral pigments, leading to the formation of stable metal complexes whose crystallization causes an increase of internal pressure resulting in cracking, peeling, and the eventual loss of mural fragments ^[15].

Awareness of microorganisms' considerable role in preserving art objects and historical buildings dates back to the 1950s ^[16]. Ionita and colleagues provided one of the first detailed descriptions of the mycoflora involved in the deterioration of mural paintings of monasteries in Moldavia, noting that it was favoured by the various nutritional sources present in the materials used for the realization of the frescoes and by local environmental parameters ^[16]. This was perhaps one of the first statements of the importance of interdisciplinary studies to prevent and control deterioration processes and define restoration and preservation strategies.

Despite the fact that the fungal role in the deterioration of frescoes has been documented by several papers, a global inventory of fungal diversity and their optimal settlement conditions is not yet available. These paintings are mainly present in confined and semi-confined environments, both hypogean and non-hypogean. A fungal alteration pattern dependent on the environmental conditions of these different sites was expected. Those present in hypogean environments are often subjected to a constant extreme humidity, promoting fungal spores germination and mycelial growth. The amount and type of available nutrients also affect the fungal growth rate and the type of fungal taxa. Nutrients may arrive from the external environment as airborne particles, and the more confined are the environments, the lower are the air spores dispersion phenomena.

2. Fungal Diversity on Wall Paintings

Even if fungi have been suggested as secondary colonizers of painted mural substrates, they are among the most common microbial life-forms present in these environments and the primary cause of their biodeterioration ^{[1][9][10]}. The wide biodiversity observed confirms the potential key role of fungi in such colonization process and suggests a combination of causes that can favor their growth. Fungi recorded belonged to species found in natural environments like soils, plants, and air. A detailed survey of their diversity and distribution should become a prerequisite before any restoration measures in order to prevent further damages ^[17]. Most records belonged to

Ascomycota, with Eurotiales as the most common order, due to the prevalence of *Aspergillus* and *Penicillium* genera. The former was one of the most frequently isolated genera, with *A. flavus* and *A. niger* among the more frequently recorded species. As reported in the literature, even from the first older papers in this field, these two genera, along with *Alternaria*, *Fusarium*, *Cladosporium*, *Mortierella*, *Chaetomium*, and *Acremonium*, are among the most common deteriogens of such paintings [1][18][11][19][17][20][21][22][23][24]. These taxa are ubiquitous, and their frequent occurrence is due to the production of numerous airborne conidia. A diversity of filamentous fungi, with the most predominant genera *Penicillium*, *Cladosporium*, *Aspergillus*, and *Trichoderma*, were also isolated from mural paintings of the Parish Church of Santo Aleixo (Portugal) [25]. Species of these genera were recorded on indoor frescoes in Romanian monasteries; their presence was favoured by the organic components and vegetal pigments used, as well as high moisture levels caused by frequent rainwater penetration, which also resulted in the formation of efflorescences [26]. *Cladosporium* species can cope with various harsh environmental conditions thanks to their low nutritional requirements (i.e., in oligotrophic conditions). Otherwise, *Chaetomium* species are proteolytic and cellulolytic ascomycetes, favoured by nutrient-rich substrates [27][28][29]. They were reported as the most frequent microfungi on the frescoes of the St. Damian Monastery in Assisi (Italy) [20] and on frescoes in a Serbian church [27]. Furthermore, a community of *Aspergillus*, *Penicillium*, *Cladosporium*, and *Chaetomium* species was recorded from Medieval wall paintings in Styria (Austria), forming spots of different colors [17]. This group of genera was dominant on two deteriorating frescos in St Clare's Refectory of the Monastery of St Damian in Assisi [20].

Hypocreales was the second most abundant order, accounting for 18% of total fungal diversity, within which *Acremonium*, *Trichoderma*, and *Fusarium* were among the most common genera. Hypocreales is one of the largest orders of filamentous ascomycetes and exhibits a broad range of ecologies, ranging from plant-associated nutritional modes to animal pathogens (e.g., insect pathogens) and mycoparasites [30]. *Neocosmospora solani*, recorded in Thailand, India, Japan, and France; *Simplicillium lamellicola*, recorded in Russia; and *Clonostachys rosea* [31][32], recorded in Japan, are examples of mycoparasitic species, while *Parengiodontium album* is an insect parasite and was recorded in several countries (Germany, Russia, Romania, Austria, Italy, and England) [33]. The recurrent presence of mites and insects pointed out their possible role in spreading fungi on painted surfaces [20][34].

The plant pathogen species *Fusarium oxysporum* has been shown to produce an extracellular pinkish pigment that disfigures and aesthetically damages colonized mural paintings and stone surfaces with permanent stains [22].

Phylum Basidiomycota was present with several occasional species, mostly represented by one or two records, and comprises litter, soil, and wood-saprotrophs, ectomycorrhizal, epiphyte, and plant-pathogen species. Their occurrence must be regarded as sporadic, potentially aided by root penetration. The possible role of roots as a carrier for rhizosphere microorganisms, like a dripping line for water condensation, and as an organic carbon source by root exudates has been hypothesized [35][36]. A Basidiomycete was also recorded at the entrance of Roman catacombs [37], possibly due to spores carried by water infiltrations and germinating using organic nutrients from the soil and/or the phototrophic biofilm.

Mucoromycota was present with few species and records, and black meristematic fungi were also rarely recorded. These latter may grow on a wide range of substrates and are resistant to a variety of environmental stresses, as well as being widely distributed epi- and endolithically on monuments [38][39]. Although the biodiversity of black fungi on historical monuments is not fully elucidated, recent samplings indicate that they are also present on wall paintings and that their rare finding could be linked to the isolation protocols used, generally favoring fast-growing species [124]. Two new species of the genus *Neodevrisia* have been found in the restricted sampling area of the Vallerano cave, and another, still undescribed, from Maijishan grottoes [40][41][42]. *Scolecobasidium lascauxensis* and *S. anomalus* were isolated and described from black stains in Lascaux Cave, France [43][44], while the chaetothyrialean black fungi *Cladophialophora*, *Exophiala*, and *Phialophora* have been reported from different sites [45][46][47][48].

Yeasts have been rarely reported, such as *Saccharomycetales* (Ascomycota) that usually grow by individual yeast cells or *Rhodotorula* spp. (Basidiomycota) often linked to pink/orange stains due to the release of carotenoids [25][49]. A complete list of species isolated from wall paintings has been reported by Zucconi and colleagues [link with Table 1]

Table 1. List of the fungal entries retrieved from the different papers grouped by genera, in association with the corresponding references and the environmental categories where they have been registered.

Genus	Fungal Name	References	Environment
<i>Acremoniella</i>	<i>Acremoniella atra</i>	[16]	C-NHE
<i>Acremonium</i>	<i>Acremonium camptosporum</i>	[50]	NC-HE
	<i>Acremonium charticola</i>	[51][17][52][53]	NC-HE, C-NHE
	<i>Acremonium masseei</i>	[45][54]	C-HE
	<i>Acremonium murorum</i> (syn. <i>Gliomastix murorum</i>)	[45][46][54][55][56]	C-HE, NC-HE
	<i>Acremonium rutilum</i> (syn. <i>A. roseum</i>)	[16]	C-NHE
	<i>Acremonium cf. rutilum</i>	[17]	C-NHE
	<i>Acremonium sp.</i>	[45][51][17][52][53][47][57] [58][40][20][59]	C-HE, NC-HE, C-NHE
<i>Acrodontium</i>	<i>Acrodontium crateriforme</i>	[31]	C-NHE
<i>Acrophialophora</i>	<i>Acrophialophora fusispora</i> (syn. <i>A. nainiana</i>)	[55][56]	NC-HE
<i>Acrostalagmus</i>	<i>Acrostalagmus luteoalbus</i> (syn. <i>Verticillium lateritium</i>)	[60]	C-NHE

Genus	Fungal Name	References	Environment
<i>Acrothecium</i>	<i>Acrothecium</i> sp.	[61]	O-SPE
<i>Actinomucor</i>	<i>Actinomucor elegans</i>	[62]	C-HE
<i>Akanthomyces</i>	<i>Akanthomyces lecanii</i> (syn. <i>Verticillium lecanii</i>)	[17][57][63]	NC-HE, C-NHE
<i>Allophoma</i>	<i>Allophoma labilis</i> (syn. <i>Phoma labilis</i>)	[64]	SC-NHE
<i>Alternaria</i>	<i>Alternaria alternata</i> (syn. <i>A. tenuis</i> and <i>Ulocladium alternariae</i>)	[16][65][55][66][19][56][52] [20][60][62][64][67][26][68] [35][32][69]	All environments
	<i>Alternaria angustiovoidea</i>	[70]	C-NHE
	<i>Alternaria chartarum</i> (syn. <i>Ulocladium chartarum</i>)	[16][71]	C-NHE
	<i>Alternaria dianthi</i>	[19]	C-NHE
	<i>Alternaria longipes</i>	[19]	C-NHE
	<i>Alternaria longissima</i>	[55][19][56]	NC-HE, C-NHE
	<i>Alternaria oudemansii</i> (syn. <i>Ulocladium oudemansii</i>)	[21]	NC-HE, C-NHE
	<i>Alternaria tenuissima</i>	[16][27][46][19][20][35][72]	NC-HE, C-NHE, O-SPE
	<i>Alternaria</i> sp. (syn. <i>Ulocladium</i> sp.)	[73][18][16][45][65][51][53] [20][74][28]	C-HE, NC-HE, C-NHE, O-SPE
<i>Amphinema</i>	<i>Amphinema</i> sp.	[75]	C-NHE
<i>Amyloporia</i>	<i>Amyloporia sinuosa</i> (syn. <i>Antrodia sinuosa</i>)	[18]	C-NHE
<i>Antrodia</i>	<i>Antrodia</i> sp.	[75]	C-NHE
<i>Apiotrichum</i>	<i>Apiotrichum</i> sp. (syn. <i>Hyalodendron</i> sp.)	[57]	C-NHE
<i>Arachnomyces</i>	<i>Arachnomyces</i> sp.	[40]	NC-HE
<i>Armillaria</i>	<i>Armillaria</i> sp.	[75]	C-NHE
<i>Arthrinium</i>	<i>Arthrinium arundinis</i>	[52]	C-NHE

Genus	Fungal Name	References	Environment
	<i>Arthrinium phaeospermum</i> (syn. <i>Papularia sphaerosperma</i>)	[55][56]	NC-HE
	<i>Arthrinium</i> sp.	[20][28]	C-NHE; O-SPE
<i>Arthrobotrys</i>	<i>Arthrobotrys</i> sp.	[45]	C-HE
<i>Ascochyta</i>	<i>Ascochyta medicaginicola</i> (syn. <i>Phoma medicaginis</i>)	[15][68]	O-SPE
	<i>Ascochyta</i> sp.	[72]	C-NHE
<i>Ascotricha</i>	<i>Ascotricha guamensis</i>	[56]	NC-HE
<i>Aspergillus</i>	<i>Aspergillus aeneus</i>	[76]	SC-NHE
	<i>Aspergillus amstelodami</i> (syn. <i>Eurotium amstelodami</i>)	[20][26][72]	C-NHE
	<i>Aspergillus aureolatus</i>	[15][68]	O-SPE
	<i>Aspergillus auricomus</i>	[27]	O-SPE
	<i>Aspergillus candidus</i>	[55][56][17][77]	C-HE, NC-HE, C-NHE
	<i>Aspergillus clavatus</i>	[50]	C-HE
	<i>Aspergillus creber</i>	[15][68]	O-SPE
	<i>Aspergillus echinulatus</i>	[16]	C-NHE
	<i>Aspergillus europaeus</i>	[15][68]	O-SPE
	<i>Aspergillus fischeri</i> (syn. <i>Neosartorya fischeri</i>)	[21]	NC-HE; C-NHE
	<i>Aspergillus flavipes</i>	[15][68]	O-SPE
	<i>Aspergillus flavus</i> (syn. <i>A. oryzae</i>)	[73][14][15][55][78][19][56] [68][35][77][79][80][81][82] [83][84][85]	C-HE, NC-HE, C-NHE, O-SPE
	<i>Aspergillus fumigatus</i>	[78][19][51][20][71][86][87] [22][88]	C-HE, NC-HE, C-NHE
	<i>Aspergillus glaucus</i> group	[88]	C-NHE
	<i>Aspergillus ivoriensis</i>	[76]	SC-NHE

Genus	Fungal Name	References	Environment
	<i>Aspergillus japonicus</i>	[22]	C-HE
	<i>Aspergillus melleus</i>	[76]	SC-NHE
	<i>Aspergillus multicolor</i>	[76]	SC-NHE
	<i>Aspergillus nidulans</i> (syn. <i>Emericella nidulans</i>)	[55][78][19][56][20][62][71] [80][81][22]	C-HE, NC-HE, C-NHE
	<i>Aspergillus niger</i>	[73][14][25][15][55][78][19] [56][60][61][64][67][26][68] [82][84][85][87][89][90][91]	All environments
	<i>Aspergillus niger group</i>	[20]	C-NHE
	<i>Aspergillus ochraceus</i>	[51][60][76]	C-HE, C-NHE, SC-NHE
	<i>Aspergillus ostianus</i>	[15][68][76]	SC-NHE, O- SPE
	<i>Aspergillus pallidofulvus</i>	[15][68]	O-SPE
	<i>Aspergillus parasiticus</i>	[15][68]	O-SPE
	<i>Aspergillus penicilloides</i>	[92]	C-HE
	<i>Aspergillus petrakii</i>	[76]	SC-NHE
	<i>Aspergillus proliferans</i>	[55][56]	NC-HE
	<i>Aspergillus protuberus</i>	[76]	SC-NHE
	<i>Aspergillus puniceus</i>	[76]	SC-NHE
	<i>Aspergillus repens</i>	[16][53]	C-NHE
	<i>Aspergillus restrictus</i>	[72][93]	C-HE, C-NHE
	<i>Aspergillus sclerotiorum</i>	[86]	C-NHE
	<i>Aspergillus spectabilis</i> (syn. <i>Emericella spectabilis</i>)	[76]	SC-NHE
	<i>Aspergillus stellatus</i> (syn. <i>Emericella variegolor</i>)	[76]	SC-NHE
	<i>Aspergillus sydowii</i>	[55][56][17][62][63][21][79]	C-HE, NC-HE, C-NHE

Genus	Fungal Name	References	Environment
	<i>Aspergillus terreus</i>	[66][78][19][56][22]	C-HE, NC-HE, C-NHE
	<i>Aspergillus unguis</i>	[86]	C-NHE
	<i>Aspergillus ustus</i>	[20][76]	C-NHE, SC-NHE
	<i>Aspergillus versicolor</i>	[14][55][19][56][17][53][57] [20][60][62][26][71][76][77] [79][80][81][22][91][93][43] [94]	C-HE, NC-HE, C-NHE, SC-NHE
	<i>Aspergillus wentii</i>	[55][19][56]	NC-HE, C-NHE
	<i>Aspergillus sp.</i>	[18][95][25][27][45][46][96] [58][40][20][61][74][75][79] [85][87][91][23][97][98][99] [24][100][49][101][102]	C-HE, NC-HE, C-NHE, O-SPE
<i>Aureobasidium</i>	<i>Aureobasidium pullulans</i>	[19][53][57][40][60][63][35]	NC-HE, C-NHE
<i>Beauveria</i>	<i>Beauveria bassiana</i>	[31]	C-NHE
	<i>Beauveria sp.</i>	[40][63]	NC-HE, C-NHE
<i>Bispora</i>	<i>Bispora sp.</i>	[28]	O-SPE
<i>Bjerkandera</i>	<i>Bjerkandera adusta</i>	[87]	C-NHE
<i>Blastobotrys</i>	<i>Blastobotrys aristatus</i>	[17]	C-NHE
<i>Blastomyces</i>	<i>Blastomyces sp.</i>	[93]	C-HE
<i>Botryotrichum</i>	<i>Botryotrichum atrogriseum</i>	[14][26][69]	NC-HE, C-NHE
	<i>Botryotricum domesticum</i>	[70]	C-NHE
	<i>Botryotrichum murorum</i> (syn. <i>Chaetomium murorum</i>)	[15][16][20][26][68]	C-NHE, O-SPE
<i>Botrytis</i>	<i>Botrytis cinerea</i>	[52][53][57][20][79]	C-NHE
<i>Brunneochlamydosporium</i>	<i>Brunneochlamydosporium nepalense</i> (syn. <i>Acremonium nepalense</i>)	[51][43]	C-HE
<i>Burgoa</i>	<i>Burgoa sp.</i>	[45]	C-HE
<i>Candida</i>	<i>Candida takamatsuzukensis</i>	[45][103]	C-HE

Genus	Fungal Name	References	Environment
	<i>Candida tumulicola</i>	[45][103]	C-HE
	<i>Candida sp.</i>	[45][46][28]	C-HE, NC-HE
<i>Capronia</i>	<i>Capronia coronata</i>	[43]	C-HE
<i>Cephalotrichum</i>	<i>Cephalotrichum verrucisporum</i> (syn. <i>Doratomyces verrucisporus</i>)	[45][46]	C-HE
	<i>Cephalotrichum sp.</i> (syn. <i>Doratomyces sp.</i>)	[45][46]	C-HE
<i>Cephalosporium</i>	<i>Cephalosporium sp.</i>	[97][99]	C-NHE
<i>Chaetomium</i>	<i>Chaetomium ancistrocladum</i>	[15][68]	O-SPE
	<i>Chaetomium elatum</i>	[52]	C-NHE
	<i>Chaetomium globosum</i>	[16][27][65][19][56][51][53] [20][62][26]	C-HE, NC-HE, C-NHE, O-SPE
	<i>Chaetomium piluliferum</i> (syn. <i>Botryotrichum piluliferum</i>)	[16][26]	C-NHE
	<i>Chaetomium sp.</i>	[12][27][96][19][17][52][57] [20][28][80][81][82]	NC-HE, C- NHE, O-SPE
<i>Chondrostereum</i>	<i>Chondrostereum sp.</i>	[75]	C-NHE
<i>Chrysosporium</i>	<i>Chrysosporium pseudomerdarium</i>	[43]	C-HE
	<i>Chrysosporium sp.</i>	[59][63][21][104]	C-HE, NC-HE, C-NHE, O-SPE
<i>Circinella</i>	<i>Circinella muscae</i> (syn. <i>Circinella sydowii</i>)	[26]	C-NHE
<i>Cladophialophora</i>	<i>Cladophialophora tumulicola</i>	[46][48]	C-HE
<i>Cladosporium</i>	<i>Cladosporium cladosporioides</i>	[27][55][66][78][19][56][51] [53][20][60][62][35][69][77] [79][43][41][105]	C-HE, NC-HE, C-NHE, O-SPE
	<i>Cladosporium cucumerinum</i>	[20][60][62]	C-HE, C-NHE
	<i>Cladosporium herbarum</i>	[16][55][19][56][17][20][62] [26][32][72][91]	C-HE, NC-HE, C-NHE
	<i>Cladosporium macrocarpum</i>	[70]	NC-HE

Genus	Fungal Name	References	Environment
	<i>Cladosporium sphaerospermum</i>	[5] [6] [12] [27] [55] [19] [56] [17] [52] [53] [47] [57] [20] [31] [62] [63] [21] [72] [79]	C-HE, NC-HE, C-NHE, O-SPE
	<i>Cladosporium uredinicola</i>	[15] [68]	O-SPE
	<i>Cladosporium xylophilum</i>	[70]	C-NHE
	<i>Cladosporium</i> sp.	[11] [95] [25] [27] [45] [96] [47] [57] [58] [40] [63] [32] [21] [74] [28] [75] [81] [85] [87] [89] [91] [94] [23] [99] [24] [101] [106] [107] [108]	All environments
<i>Clonostachys</i>	<i>Clonostachys rosea</i> (syn. <i>Gliocladium roseum</i>)	[32]	C-HE
<i>Cochliobolus</i>	<i>Cochliobolus</i> <i>geniculatus</i> (syn. <i>Curvulata geniculata</i>)	[56] [86]	NC-HE, C-NHE
<i>Collariella</i>	<i>Collariella</i> <i>bostrychodes</i> (syn. <i>Chaetomium bostrychodes</i>)	[55] [56]	NC-HE
<i>Coltricia</i>	<i>Coltricia</i> sp.	[75]	C-NHE
<i>Coprinellus</i>	<i>Coprinellus aokii</i> (syn. <i>Coprinus aokii</i>)	[76]	SC-NHE
<i>Coprinopsis</i>	<i>Coprinopsis atramentaria</i>	[51]	C-HE
	<i>Coprinopsis cothurnata</i> (syn. <i>Coprinus cothurnatus</i>)	[72]	C-NHE
<i>Cordyceps</i>	<i>Cordyceps farinosa</i> (syn. <i>Isaria farinosa</i>)	[77]	C-HE
<i>Corioloopsis</i>	<i>Corioloopsis</i> sp.	[75]	C-NHE
<i>Cunninghamella</i>	<i>Cunninghamella echinulata</i>	[12] [55] [56] [52] [26]	NC-HE, C-NHE
	<i>Cunninghamella elegans</i>	[51]	C-HE
	<i>Cunninghamella</i> sp.	[45] [46]	C-HE
<i>Curvularia</i>	<i>Curvularia australiensis</i> (syn. <i>Drechslera australiensis</i>)	[55] [66] [78] [19] [56]	NC-HE, C-NHE
	<i>Curvularia hawaiiensis</i> (syn. <i>Drechslera hawaiiensis</i>)	[55] [66] [78] [19] [56]	NC-HE, C-NHE

Genus	Fungal Name	References	Environment
	<i>Curvularia lunata</i>	[55][78][19][56][86][92]	NC-HE, C-NHE
	<i>Curvularia pallescens</i>	[66][78][19][56]	NC-HE, C-NHE
	<i>Curvularia spicifera</i> (syn. <i>Drechslera spicifera</i>)	[20]	C-NHE
	<i>Curvularia</i> sp.	[85]	C-NHE
<i>Cutaneotrichosporon</i>	<i>Cutaneotrichosporon mucoides</i> (syn. <i>Trichosporon mucoides</i>)	[72]	C-NHE
<i>Cylindrocarpon</i>	<i>Cylindrocarpon</i> sp.	[45][46]	C-HE
<i>Cyphellophora</i>	<i>Cyphellophora olivacea</i>	[47]	C-HE
	<i>Cyphellophora</i> sp.	[47]	C-HE
<i>Cyphellostereum</i>	<i>Cyphellostereum</i> sp.	[75]	C-NHE
<i>Cystoderma</i>	<i>Cystoderma</i> sp.	[75]	C-NHE
<i>Devriesia</i>	<i>Devriesia</i> sp.	[40]	NC-HE
<i>Dichotomophilus</i>	<i>Dichotomophilus indicus</i> (syn. <i>Chaetomium indicum</i>)	[26]	C-NHE
<i>Didymella</i>	<i>Didymella glomerata</i> (syn. <i>Phoma glomerata</i>)	[16][52]	C-NHE
<i>Dipodascus</i>	<i>Dipodascus geotrichum</i>	[26]	C-NHE
	<i>Dipodascus</i> sp. (syn. <i>Geotrichum</i> sp.)	[59][85]	NC-HE, C-NHE
<i>Discostroma</i>	<i>Discostroma corticola</i> (syn. <i>Seimatosporium lichenicola</i>)	[15][68]	O-SPE
<i>Drechslera</i>	<i>Drechslera</i> sp.	[28]	O-SPE
<i>Emericella</i>	<i>Emericella ruber</i>	[19]	C-NHE
	<i>Emericella</i> sp.	[60][85]	C-HE, C-NHE
<i>Engyodontium</i>	<i>Engyodontium</i> sp.	[40][79]	C-HE, NC-HE, C-NHE
<i>Epicoccum</i>	<i>Epicoccum nigrum</i> (syn. <i>Epicoccum purpurascens</i>)	[15][55][19][56][20][60][68] [32]	C-HE, NC-HE, C-NHE, O-SPE

Genus	Fungal Name	References	Environment
	<i>Epicoccum</i> sp.	[96][28][23][99]	C-HE, NC-HE, C-NHE, O-SPE
<i>Eurotium</i>	<i>Eurotium halophilicum</i>	[109]	C-NHE
	<i>Eurotium herbariorum</i>	[77]	C-HE
	<i>Eurotium</i> sp.	[59][28][98][100]	C-HE, NC-HE, C-NHE
<i>Exophiala</i>	<i>Exophiala angulospora</i>	[47][48]	C-HE
	<i>Exophiala moniliae</i>	[43]	C-HE
	<i>Exophiala</i> sp.	[45][47]	C-HE
<i>Fomitopsis</i>	<i>Fomitopsis vinosa</i>	[72]	C-NHE
	<i>Fusarium chlamydosporum</i>	[62]	C-HE
	<i>Fusarium culmorum</i>	[19]	C-NHE
<i>Fusarium</i>	<i>Fusarium equiseti</i>	[64]	SC-NHE
	<i>Fusarium fujikuroi</i> (syn. <i>F. moniliforme</i>)	[66][78][56][84]	C-HE, NC-HE
	<i>Fusarium oxysporum</i>	[45][55][19][56][51][20][60] [32][76][83][110]	C-HE, NC-HE, C-NHE, SC-NHE
	<i>Fusarium proliferatum</i>	[87]	C-NHE
	<i>Fusarium sporotrichioides</i>	[51]	C-HE
	<i>Fusarium</i> sp.	[73][45][46][96][19][17][57] [59][21][74][91][24][101] [111]	C-HE, NC-HE, C-NHE
<i>Fuscoporia</i>	<i>Fuscoporia</i> sp.	[75]	C-NHE
<i>Fusidium</i>	<i>Fusidium viride</i>	[31]	C-NHE
<i>Ganoderma</i>	<i>Ganoderma</i> sp.	[75]	C-NHE
<i>Gliomastix</i>	<i>Gliomastix tumulicola</i> (syn. <i>Acremonium tumulicola</i>)	[45][54]	C-HE
	<i>Gliomastix</i> sp.	[32][104]	C-HE

Genus	Fungal Name	References	Environment
<i>Gloiothele</i>	<i>Gloiothele</i> sp.	[75]	C-NHE
<i>Helminthosporium</i>	<i>Helminthosporium</i> sp.	[28][85][91]	C-NHE, O-SPE
<i>Humicola</i>	<i>Humicola fuscoatra</i>	[60]	C-NHE
	<i>Humicola udagawae</i>	[51]	C-HE
	<i>Humicola</i> sp.	[19]	C-NHE
<i>Hyphodontia</i>	<i>Hyphodontia alutaria</i>	[75]	C-NHE
	<i>Hyphodontia</i> sp.	[75]	C-NHE
<i>Hyphodontiella</i>	<i>Hyphodontiella</i> sp.	[75]	C-NHE
<i>Hypholoma</i>	<i>Hypholoma</i> sp.	[75]	C-NHE
<i>Idriella</i>	<i>Idriella</i> sp.	[32]	C-HE
<i>Kendrickiella</i>	<i>Kendrickiella phycomyces</i>	[45][46][112]	C-HE
<i>Kernia</i>	<i>Kernia geniculotricha</i>	[76]	SC-NHE
	<i>Kernia hippocrepida</i>	[76]	SC-NHE
<i>Lactarius</i>	<i>Lactarius</i> sp.	[75]	C-NHE
<i>Lecanicillium</i>	<i>Lecanicillium psalliotae</i>	[51][69]	C-HE, NC-HE
	<i>Lecanicillium</i> sp.	[77]	C-HE
<i>Leptobacillium</i>	<i>Leptobacillium muralicola</i>	[50]	NC-HE
<i>Leptosphaeria</i>	<i>Leptosphaeria</i> sp.	[28]	O-SPE
<i>Leptosphaerulina</i>	<i>Leptosphaerulina</i> sp.	[74]	NC-HE
<i>Macrophomina</i>	<i>Macrophomina phaseolina</i>	[55][19][56]	NC-HE
<i>Malbranchea</i>	<i>Malbranchea</i> sp.	[20]	C-NHE
<i>Mammaria</i>	<i>Mammaria echinobotryoides</i>	[92]	C-HE
<i>Memnoniella</i>	<i>Memnoniella</i> sp.	[19]	C-NHE
<i>Metapochonia</i>	<i>Metapochonia bulbillosa</i> (syn. <i>Verticillium bulbillosum</i>)	[59]	C-HE, NC-HE
	<i>Metapochonia suchlasporia</i>	[63]	NC-HE, C-NHE

Genus	Fungal Name	References	Environment
Meyerozyma	(syn. <i>Verticillium suchlasporium</i>)		
	<i>Meyerozyma guilliermondii</i>	[70]	NC-HE
Microascus	<i>Microascus brevicaulis</i> (syn. <i>Scopulariopsis brevicaulis</i>)	[16][63][77]	C-HE, NC-HE, C-NHE
	<i>Microascus chartarum</i> (syn. <i>Scopulariopsis chartarum</i>)	[21]	NC-HE, C-NHE
	<i>Microascus cirrosus</i>	[76]	SC-NHE
	<i>Microascus</i> sp.	[77]	C-HE
Microdochium	<i>Microdochium lycopodium</i>	[51]	C-HE
Monilinia	<i>Monilinia</i> sp. (syn. <i>Monilia</i> sp.)	[91]	C-NHE
Monocillium	<i>Monocillium</i> -like	[45]	C-HE
Monodictys	<i>Monodictys castaneae</i> (syn. <i>Stemphylium macrosporoideum</i>)	[16]	C-NHE
	<i>Monodictys</i> sp.	[19][32]	C-HE, C-NHE
Mortierella	<i>Mortierella alpina</i>	[59]	NC-HE
	<i>Mortierella ambigua</i>	[51]	C-HE
	<i>Mortierella parvispora</i> (syn. <i>M. gracilis</i>)	[19]	C-NHE
	<i>Mortierella</i> sp.	[59][32]	C-HE, NC-HE
Mucor	<i>Mucor plumbeus</i> (syn. <i>M. spinosus</i>)	[16]	C-NHE
	<i>Mucor racemosus</i> (syn. <i>M. globosus</i>)	[55][56][59][70]	NC-HE
	<i>Mucor silvaticus</i>	[55][56]	NC-HE
	<i>Mucor</i> sp.	[45][20][32][74][91][49]	C-HE, NC-HE, C-NHE
Myxotrichum	<i>Myxotrichum stipitatum</i>	[20]	C-NHE
	<i>Myxotrichum</i> sp.	[20]	C-NHE
Nectria	<i>Nectria</i> sp.	[11]	C-NHE

Genus	Fungal Name	References	Environment
Neocosmospora	Neocosmospora solani (syn. Fusarium solani)	[45][55][19][86][104][110]	C-HE, NC-HE, C-NHE
	Neodevriesia modesta (syn. Devriesia modesta)	[41][42]	O-SPE
Neodevriesia	Neodevriesia simplex (syn. Devriesia simplex)	[41][42]	O-SPE
	Neodevriesia sp.	[40]	NC-HE
Neosartorya	Neosartorya sp.	[21]	NC-HE, C-NHE
Neosetophoma	Neosetophoma cerealis (syn. Coniothyrium cerealis)	[79]	C-NHE
Neurospora	Neurospora intermedia	[86]	C-NHE
	Neurospora sp.	[91]	C-NHE
Nigrospora	Nigrospora oryzae (syn. N. sphaerica)	[55][56][91]	C-HE, NC-HE, C-NHE
	Nigrospora sp.	[55][91]	NC-HE, C-NHE
Oidiodendron	Oidiodendron cereale	[79]	C-NHE
	Oidiodendron tenuissimum	[60]	C-NHE
Ophiostoma	Ophiostoma sp.	[45]	C-HE
Paecilomyces	Paecilomyces variotii	[55][66][78][19][56][71]	NC-HE, C-NHE
	Paecilomyces sp.	[96][20][77][85][91][104]	C-HE, NC-HE, C-NHE
Parengyodontium	Parengyodontium album (syn. Beauveria alba, Tritirachium album, and Engyodontium album)	[12][16][17][52][53][47][57] [31][63][69][77][101][108] [33][113][114]	C-HE, NC-HE, C-NHE
Penicillium	Penicillium aethiopicum	[76]	SC-NHE
	Penicillium albicans	[49]	C-NHE
	Penicillium aurantiogriseum (syn. P. verrucosum var. cyclopium)	[12][53][57][62]	C-HE, C-NHE
	Penicillium brevicompactum	[17][52][20][77][79][101]	C-HE, NC-HE, C-NHE

Genus	Fungal Name	References	Environment
	<i>Penicillium camemberti</i>	[49]	C-NHE
	<i>Penicillium canescens</i> (syn. <i>P. raciborski</i>)	[52][49]	C-NHE
	<i>Penicillium carneum</i>	[76]	SC-NHE
	<i>Penicillium chrysogenum</i> (syn. <i>P. notatum</i>)	[12][16][52][53][20][62][67] [70][76][79][90][23][49] [115][116]	C-HE, NC-HE, C-NHE, SC- NHE
	<i>Penicillium citreonigrum</i> (syn. <i>P. citreoviride</i>)	[27][32]	C-HE, O-SPE
	<i>Penicillium citrinum</i>	[19][56][52][32][86][49]	C-HE, NC-HE, C-NHE
	<i>Penicillium commune</i>	[62][64][77][49]	C-HE, C-NHE, SC-NHE
	<i>Penicillium concentricum</i>	[76]	SC-NHE
	<i>Penicillium coprobium</i>	[76]	SC-NHE
	<i>Penicillium corylophilum</i>	[58][24]	C-NHE
	<i>Penicillium daleae</i>	[24]	C-NHE
	<i>Penicillium decumbens</i>	[12][52][49]	C-NHE
	<i>Penicillium dierckxii</i> (syn. <i>P. fellutanum</i>)	[20]	C-NHE
	<i>Penicillium digitatum</i>	[75]	C-NHE
	<i>Penicillium dipodomyicola</i>	[76]	SC-NHE
	<i>Penicillium expansum</i>	[20][60]	C-NHE
	<i>Penicillium fuscoglaucum</i>	[70]	C-NHE
	<i>Penicillium glabrum</i> (syn. <i>P. frequentans</i>)	[12][17][20][60][75][49] [101]	NC-HE, C-NHE
	<i>Penicillium granulatum</i>	[19]	C-NHE
	<i>Penicillium griseofulvum</i>	[20][68][35][76]	C-NHE, SC- NHE
	<i>Penicillium herquei</i>	[20]	C-NHE

Genus	Fungal Name	References	Environment
	<i>Penicillium italicum</i>	[64]	SC-NHE
	<i>Penicillium javanicum</i> (syn. <i>Eupenicillium javanicum</i>)	[21]	NC-HE, C-NHE
	<i>Penicillium lanosum</i>	[15][68][105]	NC-HE, O-SPE
	<i>Penicillium lilacinum</i>	[16][26]	C-NHE
	<i>Penicillium meleagrinum</i>	[51][79]	C-HE, C-NHE
	<i>Penicillium miczynskii</i>	[59]	SC-NHE
	<i>Penicillium olsonii</i>	[62]	C-HE
	<i>Penicillium oxalicum</i>	[60][32]	C-HE, C-NHE
	<i>Penicillium pancosmium</i>	[51]	C-HE
	<i>Penicillium paneum</i>	[45][76][117]	C-HE, SC-NHE
	<i>Penicillium polonicum</i>	[62]	C-HE
	<i>Penicillium purpurescens</i>	[19]	C-NHE
	<i>Penicillium purpurogenum</i>	[79][49]	C-NHE
	<i>Penicillium restrictum</i>	[49]	C-NHE
	<i>Penicillium simplicissimum</i> (syn. <i>P. janthinellum</i>)	[32][49]	C-HE, C-NHE
	<i>Penicillium spinulosum</i> (syn. <i>P. nigricans</i>)	[12][52][93]	C-HE, C-NHE
	<i>Penicillium thomii</i>	[49]	C-NHE
	<i>Penicillium turbatum</i>	[64]	SC-NHE
	<i>Penicillium verrucosum</i>	[17][20]	C-NHE
	<i>Penicillium vulpinum</i>	[76]	SC-NHE
	<i>Penicillium</i> sp.	[18][11][95][25][45][46][65] [55][19][57][58][40][20][59] [31][32][71][74][75][80][85] [87][22][89][91][94][97][98] [99][24][101][106]	C-HE, NC-HE, C-NHE
<i>Pestalotia</i>	<i>Pestalotia</i> sp.	[65]	C-NHE

Genus	Fungal Name	References	Environment
<i>Phialophora</i>	<i>Phialophora</i> sp.	[45][46][57][59]	C-HE, C-NHE
<i>Phlebia</i>	<i>Phlebia</i> sp.	[75]	C-NHE
<i>Pholiota</i>	<i>Pholiota</i> sp.	[75]	C-NHE
<i>Phoma</i>	<i>Phoma</i> sp.	[45][19]	C-HE, C-NHE
<i>Physalacria</i>	<i>Physalacria</i> sp.	[75]	C-NHE
<i>Pleospora</i>	<i>Pleospora</i> sp.	[28]	O-SPE
<i>Postia</i>	<i>Postia</i> sp.	[75]	C-NHE
<i>Preussia</i>	<i>Preussia terricola</i>	[77]	C-HE
	<i>Preussia</i> sp.	[77]	C-HE
<i>Pseudogymnoascus</i>	<i>Pseudogymnoascus pannorum</i> (syn. <i>Geomyces pannorum</i> and <i>Chrysosporium pannorum</i>)	[17][57][31]	C-NHE
<i>Pseudozyma</i>	<i>Pseudozyma prolifica</i>	[62]	C-HE
<i>Purpureocillium</i>	<i>Purpureocillium lilacinus</i> (syn. <i>Paecilomyces lilacinus</i>)	[25][51][60]	C-HE, C-NHE
<i>Pyrenophora</i>	<i>Pyrenophora bisepitata</i> (syn. <i>Drechslera bisepitata</i>)	[55][56]	NC-HE
<i>Radulomyces</i>	<i>Radulomyces</i> sp.	[75]	C-NHE
<i>Rhinocladiella</i>	<i>Rhinocladiella</i> -like	[45]	C-HE
<i>Rhizoctonia</i>	<i>Rhizoctonia solani</i> (syn. <i>Thanatephorus cucumeris</i>)	[15][55][56][68]	NC-HE, O-SPE
<i>Rhizopus</i>	<i>Rhizopus stolonifer</i> (syn. <i>R. nigricans</i>)	[55][19][56][64][35][83][84]	C-HE, NC-HE, C-NHE
	<i>Rhizopus</i> sp.	[96][106]	NC-HE, C-NHE
<i>Rhodotorula</i>	<i>Rhodotorula glutinis</i>	[60]	C-NHE
	<i>Rhodotorula mucilaginosa</i>	[75]	C-NHE
	<i>Rhodotorula</i> sp.	[11][95][75][79][89][24]	C-NHE
<i>Russula</i>	<i>Russula</i> sp.	[75]	C-NHE

Genus	Fungal Name	References	Environment
Sagenomella	<i>Sagenomella griseoviridis</i>	[46]	C-HE
	<i>Sagenomella striatispora</i>	[46]	C-HE
	<i>Sagenomella</i> sp.	[58]	NC-HE
Sarocladium	<i>Sarocladium bacillisporum</i> (syn. <i>Acremonium bacillisporum</i>)	[101]	NC-HE
	<i>Sarocladium kiliense</i> (syn. <i>Acremonium kiliense</i>)	[16][63]	NC-HE, C-NHE
	<i>Sarocladium strictum</i> (syn. <i>Acremonium</i> cfr. <i>strictum</i>)	[45][63]	C-HE, NC-HE, C-NHE
Schizophyllum	<i>Schizophyllum commune</i>	[74]	C-NHE
	<i>Schizophyllum</i> sp.	[76]	C-NHE
Schizopora	<i>Schizopora paradoxa</i> (syn. <i>Hyphodontia paradoxa</i>)	[74]	C-NHE
Scolecobasidium	<i>Scolecobasidium anomalum</i> (syn. <i>Ochroconis anomala</i>)	[44]	C-HE
	<i>Scolecobasidium lascauxensis</i>	[43][44]	C-HE
	<i>Scolecobasidium tshawytschae</i> (syn. <i>Ochroconis tshawytschae</i>)	[20]	C-NHE
Scopulariopsis	<i>Scopulariopsis brevicaulis</i>	[16][26]	C-NHE
	<i>Scopulariopsis fusca</i>	[17]	C-NHE
	<i>Scopulariopsis</i> sp.	[20][59][90][99]	NC-HE, C-NHE
Scytalidium	<i>Scytalidium</i> sp.	[80][81]	C-NHE
Simplicillium	<i>Simplicillium lamellicola</i> (syn. <i>Verticillium lamellicola</i>)	[31]	C-NHE
Skeletocutis	<i>Skeletocutis</i> sp.	[76]	C-NHE
Sordaria	<i>Sordaria humana</i>	[55][56]	NC-HE
Sphaerostilbella	<i>Sphaerostilbella</i> sp. (syn. <i>Gliocladium</i> sp.)	[45][49][104]	C-HE, C-NHE
Sporothrix	<i>Sporothrix</i> sp.	[58][24]	NC-HE, C-NHE

Genus	Fungal Name	References	Environment
<i>Sporotrichum</i>	<i>Sporotrichum</i> sp.	[53][57]	C-NHE
<i>Stachybotrys</i>	<i>Stachybotrys chartarum</i> (syn. <i>S. atra</i>)	[16][19][31][67][93]	NC-HE, C-NHE
	<i>Stachybotrys cylindrosporus</i>	[16]	C-NHE
	<i>Stachybotrys echinatus</i> (syn. <i>Memnoniella echinata</i>)	[55][19][56]	NC-HE
	<i>Stachybotrys</i> sp.	[12][96][19]	NC-HE, C-NHE
<i>Stagonosporopsis</i>	<i>Stagonosporopsis lupini</i>	[70]	C-NHE
<i>Stemphylium</i>	<i>Stemphylium botryosum</i>	[53]	C-NHE
	<i>Stemphylium pyriforme</i>	[26]	C-NHE
	<i>Stemphylium</i> sp.	[49]	C-NHE
<i>Stereum</i>	<i>Stereum</i> sp.	[75]	C-NHE
<i>Syncephalastrum</i>	<i>Syncephalastrum</i> sp.	[85]	C-NHE
<i>Talaromyces</i>	<i>Talaromyces aculeatus</i>	[62]	C-HE
	<i>Talaromyces flavus</i>	[51][79]	C-HE
	<i>Talaromyces pinophilus</i> (syn. <i>Penicillium pinophilum</i>)	[67][101]	C-HE, NC-HE
	<i>Talaromyces rugulosus</i> (syn. <i>Penicillium rugulosum</i>)	[77][79][116]	C-HE, C-NHE
	<i>Talaromyces variabilis</i> (syn. <i>Penicillium variabile</i>)	[79]	C-NHE
<i>Thysanorea</i>	<i>Thysanorea papuana</i>	[43]	C-HE
<i>Tilletiopsis</i>	<i>Tilletiopsis</i> sp.	[79]	C-NHE
<i>Torrubiella</i>	<i>Torrubiella alba</i> (syn. <i>Lecanicillium aranearum</i>)	[101]	NC-HE
	<i>Torrubiella</i> sp.	[77][101]	C-HE, NC-HE
<i>Torula</i>	<i>Torula herbarum</i>	[26]	C-NHE
	<i>Torula</i> sp.	[20]	C-NHE

Genus	Fungal Name	References	Environment
Tricharina	Tricharina sp.	[74]	NC-HE
Trichocladium	Trichocladium asperum	[77]	C-HE
Trichoderma	Trichoderma harzianum	[66][78][19][56][79]	NC-HE, C-NHE
	Trichoderma sect. Longibrachiatum	[45][110]	C-HE
	Trichoderma virens (syn. Gliocladium virens)	[32]	C-HE
	Trichoderma viride	[45][26][32]	C-HE, C-NHE
	Trichoderma sp.	[25][45][46][19][58][59][85] [91][43][102][104]	C-HE, NC-HE, C-NHE
Trichothecium	Trichothecium indicum (syn. Acremonium indicum)	[55][19][56]	NC-HE
	Trichothecium roseum	[16][100]	C-NHE
Tritirachium	Tritirachium sp.	[76][91]	C-HE, C-NHE
Tubaria	Tubaria sp.	[75]	C-NHE
Tyromyces	Tyromyces sp.	[75]	C-NHE
Umbelopsis	Umbelopsis ramanniana (syn. Mortierella ramanniana)	[17][59]	NC-HE, C-NHE
Venturia	Venturia carpophila (syn. Cladosporium carpophilum)	[56]	NC-HE
Verticillium	Verticillium alboatrum	[56]	NC-HE
	Verticillium sp.	[45][31][63][32][104]	C-HE, NC-HE, C-NHE
Wallemia	Wallemia sebi	[72]	C-NHE
	Wallemia sp.	[100]	C-NHE
Westerdykella	Westerdykella sp.	[74]	NC-HE
Xylodon	Xylodon nespoli	[75]	C-NHE
	Xylodon nothofagi	[75]	C-NHE
	Xylodon raduloides	[75]	C-NHE

Genus	Fungal Name	References	Environment
<i>Zygosporium</i>	<i>Zygosporium masoni</i>	[45]	C-HE
	<i>Basidiomycota (Phylum)</i>	[74]	NC-HE
	<i>Black meristematic fungi</i>	[5][41][118]	NC-HE, O-SPE
	<i>Chaetomiaceae (Family)</i>	[74]	NC-HE
	<i>Filobasidiales</i>	[74]	NC-HE
	<i>Hyaline sterile mycelia</i>	[21]	NC-HE, C-NHE
	<i>Melanized sterile mycelia</i>	[21]	NC-HE, C-NHE
	<i>Pezizomycotina (Subphylum)</i>	[74]	NC-HE
	<i>Undetermined dark pigmented fungi</i>	[14]	O-SPE
	<i>Undetermined yeasts</i>	[20]	C-NHE
	<i>Uredinales (Order)</i>	[28]	O-SPE
	<i>Ustilaginales (Order)</i>	[28]	O-SPE

3. Geographic Distribution

Considering the geographic distribution of the data, just one site among the studied paintings comes from the Americas (the Cathedral of Havana at Cuba) [91]. The highest records were from Europe, with 70 monuments with a considerable prevalence of Italian monuments (39). A total of 26 monuments were from Asia, and the 13 from Africa were all from Egypt.

This distribution arises from the Euro-Mediterranean area starting from the old prehistoric caves to the Etruscan and Greek-Roman traditions until the decoration of Christian churches and historical buildings [2]. In the case of the Egyptian area, the recorded taxa derived from the old tombs of the Pharaohs [67][82][83][87][22], and similarly in East Asia, where paintings are mainly found in kings' and Emperors' tombs [45][46][54][51].

Researchers' results suggest that the monuments studied were often confined to restricted geographic areas. In any case, a wider geographic distribution than that recorded may be possible, as some sites/ studies could have escaped the search because of language barriers search. [link with **Figure 1**]

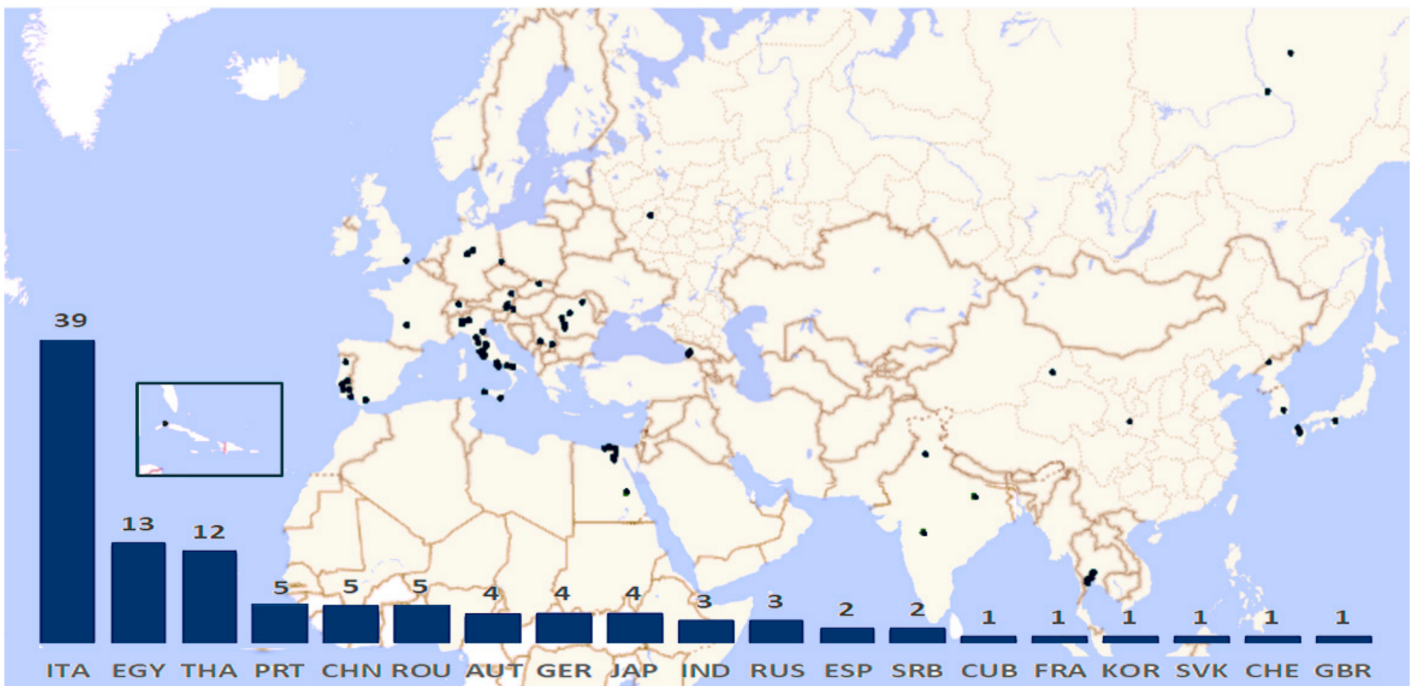


Figure 1. Geographic distribution of the reviewed study's 107 monuments. Nations are indicated with the international alpha-3 code: ITA: Italy, EGY: Egypt, THA: Thailand, PRT: Portugal, CHN: China, ROU: Romania, AUT: Austria, GER: Germany, JAP: Japan, IND: India, RUS: Russian Federation, ESP: Spain, SRB: Republic of Serbia, CUB: Cuba, FRA: France, KOR: Republic of Korea, SVK: Slovak Republic, CHE: Swiss, GBR: Great Britain. In the blue rectangle Cuba.

4. Isolation and Identification Methods

Culture-based methods favor the growth of microorganisms best fitting with the laboratory conditions used (namely, culture media, temperatures, and incubation times). In this entry, researchers found that the most frequent experimental settings were favorable to fast-growing, highly-sporulating fungi, using culture media rich in easily accessible carbon sources, alongside short incubation times and optimal growth temperatures favoring their sporulation. Otherwise, lower growth temperatures (≤ 20 °C), wide temperature ranges, different isolation media, and a longer incubation time could enlarge the detectable culturable fraction.

Morphological identification was dominant since the early 2000s when molecular phylogenetic methods have been applied. This allowed a better understanding of the kingdom of Fungi, highlighting also a number of misidentifications [\[119\]](#). Nowadays, the identification by barcode regions sequencing is a common practice. Even if the nuclear ITS region has been recognized as a fungal barcode, its discriminating power changes within the taxonomical groups and other/more barcode regions are often necessary for a reliable identification [\[120\]](#). This is the case of the identification of species within large groups, as *Fusarium*, *Penicillium*, *Aspergillus*, and *Cladosporium* genera, where cryptic species can be detected only by sequencing multiple molecular markers [\[121\]](#).

In detail, *Fusarium* species determination has been best made with the combined phylogeny of protein-coding genes such as elongation factor (TEF1), RNA polymerase (RPB2) and the partial β -tubulin (BT2) gene [121]. To discriminate between *Penicillium* and *Aspergillus* species, β -tubulin (BT2) and calmodulin (cmdA) genes have been proposed as secondary barcodes, respectively [122][123]. While the most phylogenetic informative markers for *Cladosporium* were TEF1 and actin gene (actA), being ITS sequences identical for species of the same complex [124][125].

The correct identification of strains is required in order to provide restorers more information about strains' ecology and degradative potential. In this light, standardized identification protocols should be implemented.

High throughput sequencing methods have recently been applied to cultural heritage purposes. These methods represent a powerful tool to define the whole fungal diversity present but not necessarily to deepen the mechanisms and the main actors of the deterioration phenomena [126]. The combination of culture-based and molecular methods should be used to better understand deterioration processes. Indeed, pure cultured microorganisms represent the key to uncovering settlers' physiological and ecological traits and represent a resource for many in silico applications and barcoded identifications [39][127].

5. Distribution of Taxa in the Different Environments

Wall paintings in confined non-hypogean environments, characterized by varied thermo-hygrometric temperatures and air movement, were quite frequent. Hypogean (both confined and non-confined), where nutrients and humidity can favor fungal growth, were also represented.

Temperature and relative humidity are among the environmental parameters most important to microbial colonization capability, and in the case of heterotrophs, a certain amount of nutrients is also needed [4][128]. The low values of temperatures, even if are not favorable for microbial growth by themselves, have a positive effect in contributing the increase in humidity, favoring water condensation on surfaces. Walls, especially in hypogean environments, generally provide these requirements [1]. Temperatures in confined environments are generally more stable than in non-confined environments, where daily and seasonal changes may occur, with ranges that affect the microbial settlement.

Elevated moisture values and stable temperatures have been reported as ideally suited to promote microbial growth on surfaces in catacombs sites [6][101][129]. Indeed, the highest risk occurs when high humidity is coupled with high temperature values, and negative effects of rising temperatures arise only if their highest values can strongly influence the humidity values [130].

Air movement differences between confined, semi-confined, and non-confined environments were expected to alter the number and type of fungal species recorded as well as incoming nutrients from the outside environment. A great proportion of entries in the database belonged to soil and litter dwellers such as saprotrophs, producing numerous spores that are well adapted to air-borne dispersal, and therefore, air ventilation may have a significant

impact on the risk of contamination [131]. The more limited air volume movement of confined mural paintings than semi-confined ones was suggested to decrease the number of air-borne dust particles, with biofilm communities relying more on internal interactions between different microorganisms than on the external organic inputs [14].

Among the first aerobiological studies, Savulescu and Ionita reported a greater number of isolates inside the studied monasteries than outside of them, probably due to a more favorable microclimate inside the church, which favors the development of microorganisms [26]. Pangallo and colleagues proposed for the first time a comparative analysis of the microbial component of paintings and the surrounding air to gather information on the origin of fungal contamination [80]. Aside from the importance of aerobiological studies for conserving and preventing microbial attacks on indoor painted surfaces [132], these studies have received little attention. In light of the large number of fungal species potentially harmful for restorers and visitors, constant monitoring of air spore quality and concentration, as well as the use of air filters to reduce fungal spores concentrations, would be required for site conservation [21][106][132][133].

Significant correlations between taxa and the various environmental categories have not been recorded. Indeed, such data is not the result of the absence of a correlation between fungal growths and environmental conditions but can be considered as a direct consequence of several other influencing conditions that hide it. In fact, many are the ecological requirements that shape the ecological niches of the different species (i.e., the limiting factors), but the most conditioning factors are those that result in a quantity proximal to the upper or lower tolerance limit of an organism [134]. Then, for the various sites examined, some factors may become more relevant if their values are closer to the tolerance limit of certain organism, but this does not mean that other parameters do not play a role [135].

Indeed, researchers' results may be influenced by a number of variables. The different sampling techniques and isolation conditions but also the presence of numerous genera that are widespread and highly sporulating and hence present in all the environmental categories must also be considered. Moreover, the absence of evident correlations could have been determined by the absence of distinct boundaries between the categories identified, with overlapping microclimatic conditions resulting in overlaps within their respective microbial communities. Finally, the heterogeneity of the data, with taxa identified at the genus or species level, may have resulted in dispersed clusters and hampered the ability to demonstrate any relationship.

This result seems to be in line with other studies. The influence of environmental factors such as temperature, relative humidity, and the opening or closure of the temples was not evident for fungal growths on wall paintings of 12 archaeological sites in the central and western parts of Thailand [86]. Furthermore, a stronger relationship with the age of five caves in China than with the environmental conditions, such as temperature and relative humidity, was proposed to explain the observed differences in fungal communities [74]. In two distinct mural paintings, instead, the differences recorded in the microbial communities were associated to the different organic input origin (i.e., wine cellar evaporation and insect exuvia/excrements) and the microclimatic conditions. The more humid conditions favored the growth of actinomycetes, bacteria, and dark-pigmented fungi, while the other showed a biofilm, mainly dominated by xerotolerant and patchy growing sporulating fungi [14]. Differences in fungal

communities were also recorded on mural paintings of two subterranean ancient Chinese tombs dating back over 1700 years, mostly due to variations in interior temperature and relative humidity and their history and drawing techniques [62].

Other significant concerns could be related to identifying the isolated species, which was initially based solely on morphological observation. Indeed, nowadays, phylogenetic molecular approaches are routinely applied, providing a universal tool for identifying fungal species accurately.

New methodologies such as omics techniques are now available; however, they rarely provide information at the species or genus level, and there is no guarantee that the recorded taxa are actively growing. Moreover, culture-dependent approaches may not provide a real picture of the microbial diversity actively growing at the sampling time. Therefore, a combination of culture-based and molecular approaches may be needed to gain a clear picture of the actual biodiversity present on the painted surfaces as well as to have strains to investigate their potential degradative roles.

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