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Endophytism of *Penicillium* Species in Woody Plants

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Abstract: The genus *Penicillium* is ubiquitous and its species are commonly recovered from every kind of substrate and environmental conditions. Therefore, not surprisingly, *Penicillium* strains are commonly reported in investigations dealing with fungal endophytic assemblages of plants in both natural and anthropic contexts. As such they are implicated in more or less effective relationships with the host, and involved in applicative issues concerning plant protection and the production of bioactive compounds to be exploited as pharmaceuticals. The available data on occurrence, biocenotic role, production and bioactivities of secondary metabolites of *Penicillium* strains which have been isolated as endophytes from woody plants are reviewed in the present paper in the aim to introduce the state of the art to researchers involved in this particular field.

Keywords: Bioactive metabolites, endophytes, fungal diversity, mutualism, *Penicillium*, plant protection.

INTRODUCTION

Endophytes are defined as organisms that colonize living, internal tissues of plants without causing any immediate, overt negative effect [1]. So close is the association with their hosts that they have been depicted to form an integral part of the ‘extended phenotype’ or symbiotic community of plant species [2, 3]. Their occurrence in plant tissues may result upon the establishment of quite complex ecological and trophic relationships ranging from an adaptation of saprophytism also defined as ‘balanced antagonism’ [4], where the microbe remains quiescent at more or less circumscribed sites awaiting to colonize host tissues eventually damaged by biotic or abiotic stresses, to a true mutualism, established when the microbe is somehow allowed to spread within the host offering in turn some kind of ecological or physiological advantage. In a sense, such a variation in the kind of relationships makes the concept of endophytism purely topographical, and reflects the existence of a wide range of micro-organisms that are more or less adapted to this biocenotic condition, hence more or less regularly associated to a particular plant species.

Until recently, the role of microbes in the organization of plant communities has been neglected. However, improvements in the ability to isolate, identify, and monitor endophytes have enabled researchers to more thoroughly consider the complex ecological relationships with their hosts. Thus, it is now generally agreed that microbial endophytes interact with plants at genetic and physiological levels, and that these interactions substantially influence plant fitness, with potential effects on vegetation dynamics.

Virtually spread in every plant on earth, endophytic fungi are influenced in their occurrence and detection by a multiplicity of extrinsic and intrinsic factors, such as the phytogeographic context, the habitat and its microclimatic and anthropic modifications, the plant taxa, the age and specificity of the colonized tissue, the number of samples used for isolations, the timing of the sampling activities, the isolation media, etc. Figures are therefore pure guesswork, and the tentatively-estimated astonishing number of over one million species is much higher than all the fungal species currently known [5, 6]. Within such a multitude, *Penicillium* represents one of the most commonly reported taxa, including species able to adapt to the most varied environmental conditions. Their well-known ability to produce a plethora of bioactive secondary metabolites has stimulated a multiplicity of research activities addressed to investigate both the involvement in plant protection based on a possible induction of antagonistic effects toward agents of biotic adversities, and the opportunities for applications in human medicine, considering the relevance of natural products for the development of novel antibiotic, immunosuppressant, and anticancer drugs. This paper offers an overview on the occurrence of endophytic *Penicillium* species in woody plants, with reference to their ecological role and implications in bioprospecting.

TAXONOMIC CONTEXT

Until recently *Penicillium* indicated the anamorphic stage of ascomycetous fungi belonging to the genera *Eupenicillium* and *Talaromyces* (Eurotiales, Trichocomaceae). Nevertheless, it traditionally prevailed in nomenclature by reason of a more general occurrence of the anamorph, which in most cases represents the form that can be isolated and cultured in the laboratory. A fundamental

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taxonomic revision based on a detailed phylogenetic analysis [7, 8] has brought to the separation of the biverticillate species (*Penicillium* subgenus *Biverticillium*) in *Talaromyces*, which has been kept in the Trichocomaceae. At the same time species in the other subgenera and in the former genera *Chromocleista*, *Eladia*, *Hemicarpenteles*, *Thysanophora* and *Torulomyces*, forming a single clade, have been placed in *Penicillium sensu stricto*, as well including the teleomorphic taxa formerly ascribed to *Eupenicillium*, and segregated to the family Aspergillaceae.

By reason of this rearrangement, species that have been repeatedly reported for their endophytic occurrence, such as *Thysanophora penicillioides*, are included in this review with their updated name (Table **1**); conversely, species of *Talaromyces* are not considered, together with unclassified strains provisionally reported as *Penicillium* sp. whose morphological description conforms with the symmetric biverticillate condition [9].

Additional nomenclatural problems may derive from an increasing number of new reports and the examination by specialists of deposited strains, which occasionally disclose synonymy with other taxa deserving priority, or are even typified as novel species. Species treated in this paper are cited under their latest accepted denomination, which therefore does not necessarily correspond to the one used in the pertinent references. However, considering the ongoing taxonomic revision based on the application of biomolecular techniques, further changes in the species status of some taxa may not have timely considered in this manuscript.

The present review is also limited to strains/species which have been recovered after a surface disinfection of the plant samples intended to prevent the isolation of epiphytes. Therefore data based on isolations carried out through alternative methods, such as serial washings [10, 11], are not considered.

ENDOPHYTIC *PENICILLIUM* SPECIES AND THEIR RELATIONSHIPS WITH HOST PLANTS

Phytopathological Implications

According to the above definition, plant pathogens should not be included in the category of endophytes. However, many fungal pathogens present a latent stage which may account for their occurrence in symptomless plant organs [12], a reason why it is relevant to mention species which have been reported for such an aptitude. Disease caused by *Penicillia* on woody plants is particularly inherent to species known as agents of fruit rots, such as *P. aurantiogriseum*, *P. commune*, *P. crustosum*, *P. digitatum*, *P. expansum*, *P. glabrum*, *P. implicatum*, *P. italicum*, *P. solitum* and *P. ulaiense*, whose incidence is generally low in the field, but may dramatically increase after harvesting [13-19].

Additional concern for plant pathologists derives from the possible release of mycotoxins which may accumulate in plants and/or their edible products. The ability by *P. expansum* to produce patulin is particularly considered in apples, a few stone fruits and grapes, and the finding of this mycotoxin in symptomless fruits has raised concerns for a possible intake deriving from latent strains [20, 21]. To this regard no circumstantial evidence has resulted so far, despite a reported endophytic ability of this species (Table **1**).

Likewise, a conjecture has been advanced that the presence of ochratoxin A in coffee derives by its accumulation before harvesting as a metabolic product of fungal endophytes. The occurrence of endophytic *Penicillium* species in *Coffea* spp. has been quite well documented, with the recovery of as many as 16 species from different plant parts and cultivation areas, together with additional unidentified isolates (Tables **1** and **2**). Isolates of four *Penicillium* species were found to be able to produce just small quantities of ochratoxin A (Table **3**), reflecting a negligible contribution to the presence of this mycotoxin in processed coffee [22]. However, similar investigations on additional mycotoxins known to be produced by species such as *P. citrinum* should be carried out for a more thorough assessment of the actual relevance of endophytic *Penicillium* strains in view of an eventual contamination of the processed product. It is quite meaningful to note that the research activity carried out on this particular subject has brought to the description of a new species, *P. coffeae*, after an isolation from a peduncle of a single plant of *Coffea arabica* grown at an experimental field in the island of Oahu [23]. Nevertheless, the intriguing assumption of this taxon as a Hawaiian endemism has been excluded by a novel isolation from sago starch in the Balima region of Papua New Guinea [24].

Possible implications in plant health may involve *Penicillium* spp., such as *P. glabrum* and *P. paxilli*, reported to occur in insect galls or cecidia [25]. However, these strains should not be regarded as endophytes in the strict sense, considering that galls are abnormal outgrowths originated after the aggression of a pest, and that the fungal presence may more directly result after the establishment of a saprophytic, entomopathogenic, or symbiotic relationship with the latter organism [26, 27].

Mutualism

Endophytes contribute to improve host fitness through a set of beneficial effects [3]. Particularly, the production of antimicrobial metabolites and free radical-scavenging substances may enhance host's tolerance to biotic and abiotic stresses, and the concept of 'defensive mutualism' has been defined to explain endophyte-mediated plant protection through the production of a range of bioactive molecules [28]. Moreover, an adaptative relationship referable to a specific function in plant protection has been conjectured for vertically transmitted endophytes [29]. As a matter of fact, incidence of culturable fungal endophytic biodiversity may be even more substantial than it could be optimistically hoped. A meaningful example is offered by an investigation carried out on cocoa (*Theobroma cacao*) showing that about 70% endophytic strains, including *Penicillium* spp., had some extent of biocontrol effects against the agent of the black-pod rot disease (*Phytophthora palmivora*) [30].

There are a number of additional reports considering *Penicillium* in antagonism against plant pathogens, and possible applications in biological control. Examples on woody

Table 1. ***Penicillium*** **species reported for endophytic occurrence.**

Species	Host	Plant Part/Organ	Geographic Origin	Reference
P. adametzii	*Justicia wayanadensis*	leaf	Kodagu (India)	[39]
	Pinus thunbergii	root	Goseong (South Korea)	[98]
P. albidum	*Morinda pubescens*	leaf, stem	Similipal reserve (India)	[99]
P. antarcticum	*Cedrus deodara*	stem	Yamagata (Japan)	[100]
P. atramentosum	*Pinus thunbergii*	root	Uljin, Busan (South Korea)	[98]
P. aurantiogriseum	*Cupressus arizonica*	twig	Fars (Iran)	[42]
P. brasilianum	*Melia azedarach*	root	São Carlos (Brazil)	[101]
P. brevicompactum	*Alnus glutinosa*	root	Dartmoor (England, UK)	[102]
	Coffea arabica	peduncle, seed, seedling	Kunia (Hawaii)	[22, 103]
		leaf	Chinchiná (Colombia)	[22, 103]
		root	Beltsville (Maryland, USA)	[104]
	Coffea stenophylla	leaf	Hawaii	[103]
	Hevea brasiliensis	stem (sapwood)	Madre de Dios (Peru)	[105]
[1]	*Quercus robur ?*	leaf	Leipzig (Germany)	[106]
P. brocae	*Coffea arabica*	seedling (root), leaf	Kunia (Hawaii)	[22, 103]
		leaf	Chinchiná (Colombia)	[22, 103]
P. canescens	*Calotropis procera*	leaf	Taif region (Saudi Arabia)	[40]
	Ephedra nebrodensis	twig ?	Ontígola (Spain)	[107]
	Rhododendron tomentosum	leaf	Oulu (Finland)	[108]
	Pinus thunbergii	root	Uljin, Busan (South Korea)	[98]
P. chermesinum	*Kandelia kandel*	stem	Guangdong (China)	[109]
P. chrysogenum	*Adhathoda vasica*	leaf	Mandi district (India)	[110]
	Austrocedrus chilensis	branch	Las Trancas (Chile)	[111]
	Avicennia marina	root	Egypt	[112]
	Calotropis procera	leaf	Taif region (Saudi Arabia)	[40]
	Canavalia cathartica	root, leaf, pod, seed	Nethravathi River (India)	[113]
	Catha edulis	leaf	Yemen	[114]
	Cupressus arizonica	stem	Hamedan (Iran)	[42]
	Eucalyptus globulus	branch	Astroni crater (Italy)	[115]
	Hevea brasiliensis	stem (sapwood)	Madre de Dios (Peru)	[105]
	Justicia wayanadensis	leaf	Kodagu (India)	[39]
	Ostrya carpinifolia	branch	Astroni crater (Italy)	[115]
	Pinus sylvestris	root	Lithuania	[116]
	Prumnopitys andina	branch	Las Trancas (Chile)	[111]
	Salvadora oleoides	leaf/stem	Haryana (India)	[117]
	Sesbania bispinosa	all plant parts	Nethravathi River (India)	[118]
	Withania somnifera	leaf	Mandi district (India)	[110]
	Ziziphus spina-christi	leaf	Al-Jabal Al-Akhdar (Oman)	[119]
	Unidentified plant	leaf	Camino Cuzco Amazon (Peru)	[120]

Table 1. contd….

Species	Host	Plant Part/Organ	Geographic Origin	Reference
P. citreonigrum	*Picea abies*	needle	Lombardia (Italy)	[121]
	Pinus thunbergii	root	Busan (South Korea)	[98]
P. citrinum	*Abies beshanzuensis*	needle or twig	Baishanzu (China)	[3]
	Alnus glutinosa	root	Dartmoor (England, UK)	[102]
	Catha edulis	leaf	Yemen	[114]
	Ceratonia siliqua	stem	Morocco	[64]
	Coffea arabica	peduncle	Kunia (Hawaii)	[22, 103]
		seedling (root, leaf)	Beltsville (Maryland, USA)	[22]
		stem, leaf, root	Beltsville (Maryland, USA)	[104]
	Melia azedarach	stem, leaf (cortex)	Brazil	[122]
	Palicourea tetraphylla	leaf	Serra do Espinhaço (Brazil)	[123]
	Prosopis cineraria	inner bark	India	[124]
	Taxus cuspidata	bark	Changbai Mountain (China)	[125]
	Ziziphus hajnanensis	leaf	Al-Jabal Al-Akhdar (Oman)	[119]
	Ziziphus spina-christi	leaf	Al-Jabal Al-Akhdar (Oman)	[119]
P. coffeae	*Coffea arabica*	peduncle	Kunia (Hawaii)	[23]
P. commune	*Cupressus arizonica*	stem	Fars, Hamedan, Markazi (Iran)	[42]
	Espeletia sp.	trunk?	Choachí (Colombia)	[126]
	Hibiscus tiliaceus	stem	Hainan (China)	[127]
	Olea europaea	leaf or branch	Portugal	[41]
	Persea americana	root	South Africa	[128]
	Sorbus sp.	not specified	not specified	[129]
P. corylophilum	*Alnus glutinosa*	root	Dartmoor (England, UK)	[102]
	Calotropis procera	leaf	Taif region (Saudi Arabia)	[40]
	Picea glauca	needle	New Brunswick (Canada)	[43]
	Withania somnifera	stem	Karachi (Pakistan)	[130]
P. cristata *	*Azadirachta indica*	root, fruit	Varanasi (India)	[131]
	Eucalyptus citriodora	leaf	Varanasi (India)	[132]
P. crustosum	*Coffea arabica*	seed	Cacaohoatán (Mexico)	[22, 103]
		berry	Guatemala	[133]
		crown, berry	Chinchiná (Colombia)	[103]
		seed	Águas da Prata (Brazil)	[134]
	Persea americana	root	South Africa	[128]
	Quercus robur	branch	Astroni crater (Italy)	[115]
P. daleae *	*Coffea arabica*	stem, root	Beltsville (Maryland, USA)	[104]
	Pinus thunbergii	root	Goseong (South Korea)	[98]
	Taxus chinensis	leaf	Jinyun reserve (China)	[135]
P. dipodomyicola	*Palicourea tetraphylla*	leaf	Serra do Espinhaço (Brazil)	[123]
P. donkii	*Eucalyptus grandis*	twig	Tacuarembó (Uruguay)	[136]
P. echinulatum	*Carpinus betulus*	branch	Astroni crater (Italy)	[115]
	Cupressus arizonica	stem	Hamedan (Iran)	[42]
	Cupressus sempervirens	twig	Fars (Iran)	[42]
	Thuja orientalis	leaf	Hamedan (Iran)	[42]

Table 1. contd….

Species	Host	Plant Part/Organ	Geographic Origin	Reference
P. expansum	*Alnus nepalensis*	leaf	Taphou Naga (India)	[137]
	Cupressus arizonica	leaf	Hamedan (Iran)	[42]
	Excoecaria agallocha	root	Wenchang (China)	[138]
	Picea abies	needle	Lombardia (Italy)	[121]
	Sorbus sp.	not specified	not specified	[129]
	Thuja orientalis	twig	Fars (Iran)	[42]
P. fellutanum	*Pinus rigida*	needle	Daejeon (South Korea)	[139]
P. freii *	*Platycladus orientalis*	foliage	North Carolina, USA	[140]
P. glabrum	*Acer saccharum*	leaf (lamina, petiol)	Southern Quebec (Canada)	[141]
	Coffea arabica	root	Beltsville (Maryland, USA)	[104]
	Espeletia sp.	leaf	Choachí (Colombia)	[142]
	Eucalyptus nitens	twig	Canberra (Australia)	[143]
	Hevea brasiliensis	leaf	Madre de Dios (Peru)	[105]
	Manilkara bidentata	leaf	Luquillo (Puerto Rico)	[144]
	Pinus thunbergii	root	Uljin, Busan (South Korea)	[98]
	Punica granatum	fruit	Uzbekistan	[63]
	Quercus ilex	bark, twig and/or leaf	Castilla (Spain)	[145]
		leaf or twig	unspecified	[146]
	Theobroma gileri	bole (sapwood)	Esmeraldas (Ecuador)	[147]
P. glaucoalbidum[2]	*Abies alba*	needle	Switzerland	[148]
	Abies beshanzuensis	needle	Baishanzu Reserve (China)	[38]
	Fagus sylvatica	leaf	Greifswald (Germany)	[149]
	Picea abies	needle	Southern Finland	[150]
		needle	Trojmezná (Czech Rep.)	[151]
	Picea glauca	needle	Southern Québec (Canada)	[152]
P. goetzii	*Pinus ponderosa*	root	Okanogan (Washington, USA)	[153]
	Pseudotsuga menziesii	root	Okanogan (Washington, USA)	[153]
P. griseofulvum	*Palicourea tetraphylla*	leaf	Serra do Espinhaço (Brazil)	[123]
P. griseoroseum	*Coffea arabica*	seed	Aguas da Prata (Brazil)	[79]
	Picea abies	needle	Lombardia (Italy)	[121]
P. hennebertii[3]	*Picea abies*	needle	Lombardia (Italy)	[121]
P. herquei	*Melia azedarach*	fruit	Brazil	[122]
P. implicatum	*Melia azedarach*	fruit	Brazil	[122]
P. italicum	*Alnus nepalensis*	leaf	Taphou Naga (India)	[137]
	Canavalia cathartica	root, pod	Nethravathi River (India)	[113]
P. janczewskii	*Prumnopitys andina*	branch (phloem)	Las Trancas (Chile)	[111, 154]
P. janthinellum	*Coffea arabica*	root	Kunia (Hawaii)	[22]
		root	Beltsville (Maryland, USA)	[104]
	Melia azedarach	fruit	Brazil	[122]
	Pinus thunbergii	root	Busan (South Korea)	[98]
	Taxus baccata	inner bark	Arunachal Pradesh (India)	[155]
	unspecified mangrove	leaf	Karankadu (India)	[85]

Table 1. contd….

Species	Host	Plant Part/Organ	Geographic Origin	Reference
P. lagena[4]	*Bauhinia racemosa*	leaf	Nilgiri mountains (India)	[156]
	Diospyros montana	leaf	Nilgiri mountains (India)	[156]
	Elaeodendron glaucum	leaf	Nilgiri mountains (India)	[156]
	Erica arborea	root	Liguria (Italy)	[157]
	Ixora nigricans	leaf	Nilgiri mountains (India)	[156]
	Quercus ilex	root	Liguria (Italy)	[157]
P. levitum	*Avicennia marina*	root	Egypt	[112]
P. meleagrinum	*Hevea brasiliensis*	leaf	Madre de Dios (Peru)	[105]
P. multicolor	*Abies beshanzuensis*	needle or twig	Baishanzu (China)	[3]
P. miczynskii	*Taxus chinensis*	bark	Jinyun reserve (China)	[158]
P. montanense	*Pinus thunbergii*	root	Goseong (South Korea)	[98]
P. nodositatum	*Alnus cordata*	root	Santabarbara (Italy)	[159]
		root	Saou (France), Firenze (Italy)	[70]
	Alnus glutinosa	root	Dauphiné (France)	[68, 70]
		root	Holland	[72]
	Alnus incana	root	Ardenne, Savoie, Dauphiné (France)	[68-71]
	Alnus viridis	root	Savoie, Dauphiné (France)	[70]
	Linnea borealis	leaf	Oregon, USA	[73]
P. ochrochloron	*Pinus thunbergii*	root	Busan (South Korea)	[98]
P. olsonii	*Atriplex canescens*	seed	Las Cruces (New Mexico, USA)	[160]
	Coffea arabica	crown, seed, berry, leaf	Kauai, Kona, Kunia, Oahu (Hawaii)	[22, 103]
		berry, stem	Chinchiná (Colombia)	[22, 103]
		crown, berry	Puerto Rico	[103]
	Coffea congensis	peduncle	Kona (Hawaii)	[22]
	Coffea dewevrei	leaves	Kona (Hawaii)	[22]
	Coffea liberica	peduncle, leaf	Kona (Hawaii)	[22, 103]
	Picea abies	needle	Lombardia (Italy)	[121]
P. oxalicum	*Abies beshanzuensis*	needle or twig	Baishanzu (China)	[3]
	Coffea arabica	leaf	Chinchiná (Colombia)	[22, 103]
	Theobroma cacao	seed	Beltsville (Maryland, USA)	[161]
	Thuja plicata	leaf, stem	Chennai (India)	[162]
P. parvum	*Azadirachta indica*	not specified	Varanasi district (India)	[47]
P. paxilli	*Garcinia atroviridis*	leaf or branch	Southern Thailand	[163]
	Hevea brasiliensis	stem (sapwood), leaf	Madre de Dios (Peru)	[105]
P. polonicum	*Lysidice rhodostegia*	root	China	[164]
P. raciborskii	*Rhododendron tomentosum*	leaf	Oulu (Finland)	[108]
P. raistrickii	*Pinus thunbergii*	root	Busan (South Korea)	[98]
	Taxus brevifolia	inner bark	Northwestern Montana (USA)	[165]

Table 1. contd….

Species	Host	Plant Part/Organ	Geographic Origin	Reference
P. cf. *resedanum*	*Tilia cordata ?*	leaf	Leipzig (Germany)	[106]
P. rolfsii	*Pinus thunbergii*	root	Uljin, Busan (South Korea)	[98]
P. roseopurpureum *	*Coffea arabica*	seed	Kunia (Hawaii)	[22]
	Olea europaea	leaf or branch	Portugal	[41]
	Pinus thunbergii	root	Busan (South Korea)	[98]
P. sclerotiorum	*Abies beshanzuensis*	needle or twig	Baishanzu (China)	[3]
	Alchornea castaneifolia	leaf	Tocantins (Brazil)	[166]
	Camellia sinensis	leaf, stem	Zijin hill (China)	[167]
	Coffea arabica	crown, peduncle	Kauai (Hawaii)	[22, 103]
	Eugenia aff. *bimarginata*	leaf	Tocantins (Brazil)	[166]
	Garcinia atroviridis	leaf	Yala (Thailand)	[168]
	Hevea brasiliensis	stem (sapwood)	Madre de Dios (Peru)	[105]
	Taxus chinensis	branch	Jinggang mountains (China)	[158]
P. senticosum	unspecified medicinal plant	leaf	Tirumala hills (India)	[86]
P. simplicissimum	*Alnus glutinosa*	root	Dartmoor (England, UK)	[102]
	Eucalyptus nitens	twig	Canberra (Australia)	[143]
	Melia azedarach	stem (cortex)	Brazil	[122]
P. spinulosum	*Eucalyptus nitens*	not specified	not specified	[143]
	Hevea brasiliensis	stem (sapwood)	Madre de Dios (Peru)	[105]
	Picea glauca	needle	New Brunswick (Canada)	[43]
	Taxus chinensis	bark	Jinyun reserve (China)	[158]
P. steckii	*Coffea arabica*	berry	Oahu (Hawaii)	[22, 103]
		root	Beltsville (Maryland, USA)	[22, 104]
P. sublateritium	*Calotropis procera*	stem	Karachi (Pakistan)	[169]
P. sumatrense	*Abies beshanzuensis*	needle or twig	Baishanzu (China)	[3]
	Coffea arabica	peduncle	Chiapas (Mexico)	[103]
		seed	Adjuntas (Puerto Rico)	[103]
	Vitis vinifera	not specified	Fujian (China) ?	[170]
P. thomii	*Alnus glutinosa*	root	Dartmoor (England, UK)	[102]
	Bruguiera gymnorrhiza	root	Guang Xi (China)	[171]
	Picea glauca	needle	New Brunswick (Canada)	[43]
	Terminalia chebula	leaf, stem or root	Dhaka (Bangladesh)	[172]
P. toxicarium	*Coffea arabica*	stem	Beltsville (Maryland, USA)	[104]
	Pinus rigida	needle	Daejeon (South Korea)	[139]
P. verrucosum	*Quercus robur* or *Q. cerris*	leaf, shoot, twig or bud	Trino (Italy)	[173]
P. viridicatum	*Cupressus sempervirens*	twig	Fars (Iran)	[42]
P. waksmanii	*Alnus glutinosa*	root	Dartmoor (England, UK)	[102]

[1] strain identified as *P.* cf. *biourgeianum*; [2] reported as the synonym *Thysanophora penicillioides*; [3] reported as the synonym *Thysanophora canadensis*; [4] reported as the synonym *Torulomyces lagena*; * species identification on the corresponding host is questionable;

? host, plant part or location not clearly stated in the pertinent reference.

Table 2. Occurrence of unclassified endophytic *Penicillium* strains.

Plant Species	Tissue	Geographic Location	Reference
Abies pindrow	not specified	Kashmir (India)	[174]
Acacia catechu	inner bark	Kolhapur (India)	[175]
Acanthus ilicifolius	bark	Guangdong (China)	[35]
	leaf?	India	[176]
Acer ginnala	several plant parts	Harbin (China)	[58]
Acer saccharum	leaf	Muir's Wood (Canada)	[140]
Actinidia chinensis	leaf	Sichuan (China)	[177]
Adhatoda zeylanica	bark, stem and leaf	Kudremukh range (India)	[178]
Aegiceras corniculatum	stem	Fujian (China)	[179]
	bark	Gaoqiao (China)	[180]
	bark	Fujian (China)	[181]
	branch or leaf	Zhuhai (China)	[182]
Aegle marmelos	bark, leaf	Varanasi (India)	[183]
Albizia (*Samanea) saman*	leaf	Bangkok (Thailand)	[184]
Alibertia macrophylla	leaf	Mogi-Guaçu (Brazil)	[36, 37]
Alstonia scholaris	stem?	Paschim Medinipur (India)	[185]
Annona muricata	leaf and root	Pernambuco (Brazil)	[186]
Annona squamosa	seed?	Taiwan	[187]
Anogeissus latifolia	leaf	Nilgiri mountains (India)	[156]
Antidesma madagascariense	leaf	Mauritius	[188]
Aquilaria sinensis	stem	Jinghong (China)	[189]
Aralia elata	root	Xiaoxing'anling (China)	[135]
Avicennia marina	leaf	Pichavaram (India)	[190]
Avicennia officinalis	leaf	Pichavaram (India)	[190]
Avicennia sp.	leaf	Hainan (China)	[80]
Azadirachta indica	inner bark	Mysore (India)	[191]
	leaf	Varanasi (India)	[192]
	leaf	Panchmarhi reserve (India)	[193]
Bauhinia phoenicea	bark, stem and leaf	Kudremukh range (India)	[178]
Bauhinia racemosa	leaf	Nilgiri mountains (India)	[156]
Bauhinia vahlii	leaf, stem	Paschim Medinipur (India)	[194]
Bruguiera sexangula	root	Qinglan Port (China)	[195]
Butea monosperma	leaf	Nilgiri mountains (India)	[156]
Callicarpa tomentosa	bark, stem and leaf	Kudremukh range (India)	[178]
Calophyllum inophyllum	not specified	Bangalore (India)	[196]
Camellia caduca	root, stem	Meghalaya (India)	[197]
Camellia japonica	leaf or stem	Yunnan (China)	[198]
Camellia sinensis	stem	West Java (Indonesia)	[199]
Camptotheca acuminata	stem	Anhui (China)	[200]
Careya arborea	leaf	Nilgiri mountains (India)	[156]

Table 2. contd…

Plant Species	Tissue	Geographic Location	Reference
Cassia fistula	leaf	Nilgiri mountains (India)	[156]
Casuarina equisetifolia	shoot	Puerto Rico	[201]
Cerbera manghas	stem?	China	[202]
Ceriops tagal	leaf?	China	[203]
Cinnamomum longepaniculatum	leaf	Yibin (China)	[204]
Clerodendrum serratum	bark, stem and leaf	Kudremukh range (India)	[178]
Coffea arabica	leaf	Puerto Rico	[205]
	bean	Cundinamarca, Valle del Cauca (Colombia)	[206]
	root	Ethiopia	[207]
Cordemoya integrifolia	leaf	Maccabhé (Mauritius)	[208]
Dalbergia oliveri	leaf	Viengsa (Thailand)	[209]
Daphniphyllum longeracemosum	branch	Kunming (China)	[210]
Delonix regia	leaf or stem	Yunnan (China)	[198]
Derris elliptica	root	Guangzhou (China)	[55]
Derris hancei	leaf, caudex	China	[56]
Diospyros crassifolia	fruit	Mbalmayo (Cameroon)	[211]
Dracaena cambodiana	stem	Yunnan (China)	[189]
Elaeodendron glaucum	leaf	Nilgiri mountains (India)	[156]
Eucalyptus benthami	seedling	Southern Brazil	[212]
Eucalyptus globulus	stem	Maldonado (Uruguay)	[213]
	leaf	La Coruña province (Spain)	[214]
Eucalyptus grandis	twig	Tacuarembò (Uruguay)	[136]
Fagus sylvatica	leaf	Greifswald (Germany)	[215]
Garcinia atroviridis	leaf or branch	Southern Thailand	[163]
Ginkgo biloba	bark	China	[216]
	root	China	[217]
Givotia rottleriformis	leaf	Nilgiri mountains (India)	[156]
Glochidion ferdinandi	bark	Toohey Forest (Australia)	[218]
Grewia tiliaefolia	leaf	Nilgiri mountains (India)	[156]
Helicteres isora	leaf	Nilgiri mountains (India)	[156]
Hopea hainanensis	leaf	Hainan (China)	[34]
Ixora nigricans	leaf	Nilgiri mountains (India)	[156]
Jatropha curcas	stem	China	[219]
Kandelia candel	root	Hong Kong (China)	[220]
	branch or leaf	Zhuhai (China)	[182]
	leaf	Shankou (China)	[221]
Kigelia pinnata	leaf	Chengalpattu (India)	[222]
Lagerstroemia microcarpa	leaf	Nilgiri mountains (India)	[156]
Leptospermum scoparium	leaf	Northland and Coromandel (New Zealand)	[223]
Leucopogon parviflorus	root	New South Wales (Australia)	[224]

Table 2. contd…

Plant Species	Tissue	Geographic Location	Reference
Lithocarpus (Pasania) edulis	leaf	Kagoshima (Japan), Pichavaram (India)	[225]
Lumnitzera racemosa	leaf	Puerto Rico	[190]
Madhuca indica	leaf, bark	Uttar Pradesh (India)	[226]
Manilkara bidentata	seed	São Carlos (Brazil)	[201]
Mauritia flexuosa	root	Manaus (Brazil)	[227]
Melia azedarach	root	Brazil	[78]
	leaf, root cortex	Brazil	[122]
Mitragyna javanica	leaf	Ayuthaya province (Thailand)	[228]
Moringa oleifera	leaf	Yercaud forest (India)	[229]
Morus alba	leaf	China	[230]
Murraya paniculata	leaf	São Carlos (Brazil)	[54]
Naringi crenulata	leaf	Nilgiri mountains (India)	[156]
Nothapodytes foetida	leaf, stem, seed, fruit	Agumbe forest (India)	[231]
Nyctanthes arbor-tristis	leaf, stem	Varanasi (India)	[232]
Phoradendron perrottettii	needles	Lavras (Brazil)	[233]
Picea abies	root	Lombardia (Italy)	[121]
Pinus ponderosa	needles, twigs	Mission Creek (Washington, USA)	[234]
Pinus roxburghii	not specified	Kashmir (India)	[174]
Pinus spp.	needles	Palencia province (Spain)	[235]
Pinus sylvestris	sapwood	Harjavalta (Finland)	[236]
	leaf	Western Alps (Italy)	[237]
Pinus thunbergii	root	South Korea	[98]
Plumeria rubra	leaf, twig, bark	Chennai (India)	[238]
Populus angustifolia	leaf	Weber river (Utah, USA)	[239]
Populus euphratica	leaf	Tarim River basin (China)	[240]
Populus tremula	leaf	Palencia province (Spain)	[241]
	leaf	Umeå (Sweden)	[242]
Premna tomentosa	bark	Nilgiri mountains (India)	[156]
Prosopis cineraria	root	Rajahstan (India)	[124]
Pseudotsuga menziesii	buds, leaves, twigs	Mission Creek (Washington, USA)	[234]
Quercus cerris	bark or leaf	Southern Italy	[243]
Quercus ilex	branch or twig	La Matilla (Spain)	[145]
	stem, root	Castel Fusano (Italy)	[244]
Quercus pannosa	leaf, stem	Baima Snow Mountain reserve (China)	[245]
Quercus pubescens	sapwood, heartwood	Southern Italy	[243]
Quercus robur	leaf or branch	Westerwald (Germany)	[246]
Quercus spinosa	leaf, stem	Baima Snow Mountain reserve (China)	[245]
Quercus suber	not specified	Bortigiadas (Sardinia, Italy)	[247]
Quercus variabilis	leaf	Zijin Mountain (China)	[248]
Rauwolfia serpentina	leaf, stem	Northeast India	[249]

Table 2. contd…

Plant Species	Tissue	Geographic Location	Reference
Rhizophora annamalayana	leaf	Vellar estuary (India)	[250]
Rhizophora apiculata	stem, root	Pichavaram (India)	[251]
Rhizophora mucronata	stem	Porong river (Java, Indonesia)	[252]
Rhododendron anthopogon	root	Kalchuman lake (Nepal)	[253]
Rhododendron spp.	leaf, stem	Baima Snow Mountain reserve (China)	[245]
Rosa hybrida	leaf or stem	Yunnan (China)	[198]
Santalum album	root	Guangdong province (China)	[254]
Schima khasiana	root, stem	Meghalaya (India)	[197]
Scurrula atropurpurea	leaf	Puncak Pass (Java, Indonesia)	[255]
Shorea obtusa	leaf	Viengsa (Thailand)	[209]
Shorea siamensis	branch or leaf	Viengsa (Thailand)	[209]
Sonneratia caseolaris	leaf	Zhuhai (China)	[182]
Stereospermum angustifolium	leaf	Nilgiri mountains (India)	[156]
Strychnos potatorum	leaf, stem	Nilgiri mountains (India)	[156]
Tabebuia argentea	leaf, stem, root	Karnataka (India)	[256]
Tamarix chinensis	leaf	Laizhou Bay (China)	[52]
Tapirira guianensis	leaf, shoot or twig	Lavras (Brazil)	[233]
Taxus baccata	inner bark	Italy	[257]
	inner bark	Arunachal Pradesh (India)	[155]
Taxus brevifolia	several plant parts	Northwestern USA	[75, 81]
Taxus chinensis	branch, bark	Jingning, Jinyun reserve (China)	[158]
Taxus cuspidata	leaf	Gunma prefecture (Japan)	[258]
Taxus globosa	bark	Sierra Alta Hidalguense (Mexico)	[259]
	leaf	Sierra Gorda Reserve (Mexico)	[76]
Tectona grandis	inner bark, twig	Bangkok (Thailand)	[184]
Terminalia arjuna	leaf	Karnataka (India)	[260]
Terminalia crenulata	bole (sapwood)	Nilgiri mountains (India)	[156]
Theobroma gileri	xylem and/or shoot	Pichincha (Ecuador)	[147]
Viscum album	leaf	DC Bungalow (India)	[261]
Vismia latifolia	leaf	French Guiana	[262]
Vitis vinifera	leaf	Austria	[263]
	leaf, twig, berry	Madrid region (Spain)	[264]
	leaf	Tenerife (Spain)	[265]
Withania somnifera	leaf	Karachi (Pakistan)	[130]
Ziziphus hajnanensis	leaf	Al-Jabal Al-Akhdar (Oman)	[119]
Ziziphus spina-christi	leaf	Al-Jabal Al-Akhdar (Oman)	[119]
Ziziphus xylopyrus	leaf	Nilgiri mountains (India)	[156]
Unspecified medicinal plants		Malnad (India)	[83]

? host, plant part or location not clearly stated in the pertinent reference.

Table 3. Secondary metabolites produced by endophytic *Penicillium* strains.

Compound	**Species**	**Reference**	**Bioactivity**
Altenuene, hydroxyaltenuene, epialtenuene	*Penicillium sp.*	[203]	#
Antarone A-B*	*P. antarcticum*	[100]	#
Arisugacin B, F, G, I*, J*	*Penicillium sp.*	[52, 221]	C, E
Arugosin I*	*Penicillium sp.*	[181]	#
Asperfumoid	*Penicillium sp.*	[34]	C, F
Asperphenamate	*P. raistrickii*	[81]	#
Asterric acid	*P. glabrum*	[63]	#
Austins: austinolide*, austinoneol*, dehydroaustin, acetoxydehydroaustin, neoaustin, isoaustinone*, preaustinoids*	*P. brasilianum*	[78, 101, 266-268]	B
Azadirachtin A-B	*P. parvum*	[47]	#
Baccatin III, deacetylbaccatin III	*P. raistrickii*	[81]	#
Bacillosporin A, C	*Penicillium sp.*	[181]	#
Benzomalvin B, C	*Penicillium sp.* *P. raistrickii*	[81]	#
Bile acids (cholic, deoxycholic, glycocholic, glycodeoxycholic)	*Penicillium sp.*	[255]	#
Brasiliamide A, B, F*	*P. brasilianum*	[101]	B
β-Carbolines	*Penicillium sp.*	[269]	#
Chermesinone A-C*	*P. chermesinum*	[109]	#
Chromans: Acetyldihydroxyhydroxypropyldimethylchroman*, acetyl-dihydroxypropylidenehydroxymethylchromanone*	*Penicillium sp.*	[210]	#
Hydroxymethoxydimethylisochroman, arohynapene D, citriquinochroman*	*P. citrinum*	[64]	C
Chromone	*Penicillium sp.*	[269]	#
Cinchona alkaloids: cinchonin, cinchonidine, quinine, quinidine	*Penicillium sp.*	[77]	#
Citreoviridin	*Penicillium sp.*	[81]	S
Citrinamide A	*P. citrinum*	[64]	#
Citrinin	*P. herquei* *P. janthinellum* *Penicillium sp.* *Penicillium sp.* *Penicillium sp.*	[270] [271] [272] [180] [220]	# B, P B # C
Citrinin H-1	*P. herquei*	[272]	B
Citrorosein	*P. janthinellum* *P. herquei*	[271] [270, 272]	# B
Clavatol	*P. commune* *P. griseoroseum*	[127] [79]	# #

Table 3. contd…

Compound	Species	Reference	Bioactivity
Curvularin	*Penicillium sp.*	[269]	#
Cyclo(Ala-Gly), cyclo(Ala-Pro), cyclo(Pro-Gly)	*P. thomii*	[171]	C
Cyclo(6,7-en-Pro-Phe)	*Penicillium sp.*	[80]	#
Cyclo(Pro-Val)	*Penicillium sp.*	[36]	E
Cycloaspeptide A	*P. raistrickii* *P. janczewskii*	[81] [33]	# C
Dechloroisochromophilone III	*P. sclerotiorum*	[273]	#
Demethyl-FR-901235*	*Penicillium sp.*	[181]	#
Diacetyltetrahydroxydimethyldiphenylmethane	*Penicillium sp.*	[210]	#
Dibutylphthalate	*P. thomii*	[171]	C
Dichloroanisic acid	*Penicillium sp.*	[34]	C, F
Dicitrinol*	*P. herquei* *P. janthinellum*	[270] [274]	# B
Diclavatol*	*P. griseoroseum*	[275]	#
Dihydrocitrinin	*P. herquei* *Penicillium sp.*	[272] [180]	# #
Dihydromethoxydimethyloxobenzopyran	*P. citrinum*	[64]	#
Dihydrotrimethylpyranone	*P. sclerotiorum*	[273]	#
Dihydroxydimethoxy(hydroxypropyl)biphenyl*	*P. thomii*	[171]	C
Dihydroxydimethyloxononadienylmethylbenzaldehyde	*P. sclerotiorum*	[273]	#
Dihydroxymethylacetophenone	*Penicillium sp.*	[210]	#
Dimethoxybiphenyl	*Penicillium sp.*	[80]	#
Dihydroxymethylphenylbutanone	*Penicillium sp.*	[195]	#
Dilation	*Penicillium sp.*	[269]	#
Dimethylisoalloxazine	*Penicillium sp.*	[34]	#
Dimethyloctadienoic acid	*P. sclerotiorum*	[273]	#
Diorcinol	*P. expansum*	[138]	#
Emodin	*P. janthinellum* *P. herquei*	[271] [270, 272]	B B, P
Eupenoxide	*Penicillium sp.*	[218]	#
Expansol A-B*	*P. expansum*	[138]	C
Fiscalin B	*P. raistrickii*	[81]	#
Furanone	*Penicillium sp.*	[49]	B
Furocoumarins: methyl(methylbutenyl)furocoumarin*, bergapten	*Penicillium sp.*	[80]	C

Table 3. contd…

Compound	Species	Reference	Bioactivity
Gallic acid	*Penicillium sp.*	[58]	#
GKK1032	*Penicillium sp.*	[272]	#
Glandicolin B	*Penicillium sp.*	[227]	B
Gliovictin,	*Penicillium sp.*	[81]	F
gliovictin-acetate	*P. janczewskii*	[154]	B, C
Griseofulvin, dechlorogriseofulvin	*Penicillium sp.*	[81]	B, F
Hydroxyacetophenone	*P. sclerotiorum*	[273]	#
Hydroxymethoxymethylphthalide	*P. crustosum*	[134]	#
Hydroxymetoxyphenylacetamide	*P. thomii*	[171]	#
Indolyl-3-acetic acid	*P. glabrum*	[63]	#
methyl ester	*P. citrinum*	[64]	#
Isocoumarin derivatives:			
Dihydroxytrimethylisocoumarin, dihydroxytetramethylisochroman	*Penicillium sp.*	[195]	C
Methoxy-, hydroxy-, dihydroxy-mellein	*P. raistrickii*	[81]	#
	Penicillium sp.	[36, 37]	E, F
Penicilisorin*	*P. sclerotiorum*	[273]	#
Leptosphaerone C*	*Penicillium sp.*	[181]	C
Lumichrome	*Penicillium sp.*	[269]	#
Methoxydimethylisoquinolinol*	*P. citrinum*	[64]	#
Methoxymethylisobenzofuranone	*Penicillium sp.*	[269]	C
Methylbenzenediols*	*Penicillium sp.*	[202]	B
		[195]	#
Methylcurvulinic acid*	*P. citrinum*	[64]	#
Methylpentendioic acid	*Penicillium sp.*	[210]	#
Methylpiperazine-dione	*Penicillium sp.*	[217]	#
Mycophenolic acid	*Penicillium sp.*	[81]	B, F
	P. crustosum	[134]	#
Neocyclocitrinols*	*P. janthinellum*	[276]	#
Ochratoxin A	*P. brevicompactum* *P. crustosum* *P. olsonii* *P. oxalicum*	[22]	#
Orcinol	*Penicillium sp.*	[36]	F
Oxaline	*Penicillium sp.*	[81]	S
Oxydimethylenebisfuraldehyde	*Penicillium sp.*	[269]	#

Table 3. contd…

Compound	Species	Reference	Bioactivity
Paspaline	*Penicillium sp.*[1]	[179]	#
Paspalitrem A	*Penicillium sp.*[1]	[179]	#
Patulin	*Penicillium sp.*	[81]	B, F, S
Paxilline	*P. paxilli*	[277]	#
Pebrolides	*Penicillium sp.*	[81]	#
Penicilazaphilone A-B*	*P. sclerotiorum*	[273]	#
Penicillenols*	*Penicillium sp.*	[180]	C
Penicillenone*	*Penicillium sp.*	[181]	C
Penicillides: hydroxydidehydropenicillide*, methyldehydroiso-penicillide*, dehydroisopenicillide, epoxydidehydropenicillide*	*Penicillium sp.*	[258]	C
Penicillone*	*P. paxilli*	[277]	F
Penicinoline*,	*Penicillium sp.*	[57]	C, I
Methylpenicinoline	*P. citrinum*	[64]	#
Peniprequinolone	*P. janczewskii*	[154]	B, C
Penitrem A-B	*P. raistrickii*	[81]	#
Phenol A	*Penicillium sp.*	[180, 195]	C
Phomopsolide A-B, dihydrophomopsolide A-B*	*Penicillium sp.*	[49]	B
Phomoxin B-C*	*Penicillium sp.*	[218]	#
Physcion	*Penicillium sp.*	[34]	F
Pseurotin A	*P. raistrickii*	[81]	#
	P. janczewskii	[33]	B, C
Pyrenocine A-B	*P. paxilli*	[277]	F
Questinol	*P. glabrum*	[63]	#
Quinolactacide, tetrahydroquinolactacide*	*P. citrinum*	[64]	#
Quinolins: hydroxyquinolinone, methoxydimethylisoquinolinol*	*P. citrinum*	[64]	#
Rhodostegone*	*P. polonicum*	[164]	#
Roquefortine C	*Penicillium sp.*	[81]	#
Rotenone	*Penicillium sp.*	[55]	I
Saponins	*Penicillium sp.*	[135]	B
Sclerotiorin	*P. sclerotiorum*	[273]	F, V
Scopoletin	*Penicillium sp.*	[80]	#
Sequoiamonascin D	*Penicillium sp.*	[181]	#
Sequoiatone A-B	*Penicillium sp.*	[181]	#
Shearinine A, D-K*	*Penicillium sp.*[1]	[179]	K

Table 3. contd…

Compound	Species	Reference	Bioactivity
Spiroquinazolines: alantrypinene B*, alanditrypinone*, alantryleunone*, alantryphenone*	*Penicillium sp.*	[54]	#
Sterequinone C	*Penicillium sp.*	[80]	#
Sterols	*Penicillium sp.* *P. thomii* *P. commune* *Penicillium sp.* *Penicillium sp.*	[81] [171] [127] [210] [203]	F # # # #
Stirylpyrones: methylbisnoryangonin*, methyldesmethoxyyangonin*	*P. glabrum*	[63]	#
Sulochrins: rhizoctonic acid, sulochrin, Monomethylsulochrin	*Penicillium sp.* *P. glabrum*	[34] [63]	C, F #
Sydonic, acetoxysydonic* and dehydrosydonic* acids	*P. expansum*	[138]	#
Talaroflavone	*Penicillium sp.*	[203]	#
Tanzawaic acid B, F, G*, H*	*P. citrinum*	[64]	#
Taxol	*P. raistrickii* *Penicillium sp.* ^{2}	[75] [76]	C
Terphenyls: dihydroxy-O-desmethylterphenyllin, O-desmethylcandidusin B, hydroxy-O-desmethylterphenyllin*, desmethylterphenyllin*, deoxy-O-desmethylcandidusin B*	*P. chermesinum*	[109]	E, G
Territrem B-C	*Penicillium sp.*	[52, 221]	E
Tetrahydroquinolactacide*	*P. citrinum*	[64]	#
Tetronic acids: viridicatic acid, terrestric acid	*P. griseoroseum*	[275]	#
Trichodermamide C* (dipeptide)	*Penicillium sp.* *P. citrinum*	[278] [64]	C #
Umbelliferone	*Penicillium sp.*	[80]	#
Vanillic acid	*P. citrinum*	[64]	#
Verruculogen verruculogen TR-2, TR-2C-11 epimer*	*P. brasilianum* *P. brasilianum*	[78] [279]	B #
Xanthones : janthinone*, hydroxyjanthinone* Fusarindin (=norlichexanthone) Methylhydroxyxanthene-carboxylates* Dihydroxyxanthone	*P. janthinellum* *P. herquei* *Penicillium sp.* *Penicillium sp.* *Penicillium sp.* *Penicillium sp.*	[271] [270, 272] [220] [272] [35] [80]	# P # # F #
Xanthoviridicatin E-F*	*P. chrysogenum*	[120]	V

*Compounds identified for the first time in these strains; ^{1}closely related to *P. janthinellum* and *P. simplicissimum*; ^{2}closely related to *P. canescens*; B=antibacterial; C=cytostatic/antiproliferative on tumor cells; E= acetylcholinesterase inhibitor; F=antifungal; G=α-glucosidase inhibitor; I=insecticidal; K=blocking calcium-activated potassium channels; P=antiprotozoal; S=brine shrimp toxic; V=antiviral; #=no activity evaluated in the pertinent reference.

woody plants are given by the efficacy of *P. glabrum* (= *P. frequentans*) against twig blight of peach trees incited by *Monilinia laxa* [31], and of *P. citrinum* and *P. expansum* against anthracnose of mango caused by *Colletotrichum gloeosporioides* [32]. Moreover, some endophytic strains have been characterized for their ability to produce antibiotic compounds (Table **3**), whose bioactivity against plant pathogens and pests has been documented in a number of cases. Examples are given by pseurotin A produced by *P. janczewskii* against the bacterial pathogens *Erwinia carotovora* and *Pseudomonas syringae* [33], and a couple of compounds produced by unidentified *Penicillium* strains, such as dichloroanisic acid against *Aspergillus niger* [34], and dimethyl-8-methoxy-9-oxo-9H-xanthene-1,6-dicarboxylate against *Fusarium oxysporum* f. sp. *cubense* [35]. More products from unidentified strains possibly involved in the defense of their host species against infection by pathogenic fungi are orcinol and 4-hydroxymellein [36], and a few dihydroisocoumarins [37]. Otherwise, the production of antifungal extrolites may be presumed based on inhibitory properties in dual cultures, which is a condition reported for a number of strains/species such as *P. citrinum, P. multicolor* and *P. oxalicum* isolated from *Abies beshanzuensis* [38], *P. adametzi* and *P. chrysogenum* from *Justicia wayanadensis* [39], *P. chrysogenum* and *P. corylophilum* from *Calotropis procera* [40], *P. commune* from olive tree (*Olea europaea*) [41], and *P. aurantiogriseum, P. commune, P. echinulatum, P. expansum* and *P. viridicatum* from cupressaceous hosts [42].

On the insect pest side, a role in protection of white spruce (*Picea glauca*) against the spruce budworm (*Choristoneura fumiferana*) has been given to endophytic fungi producing rugulosin [43], an anthraquinone compound which is also known as a secondary metabolite of a few *Penicillium* species [44]. More in general, anthraquinones are believed to contribute to the defense of plants towards pests and disease agents [45], and besides a known occurrence as plant metabolites, additional compounds of this class such as citrorosein, emodin, and physcion have been reported by several endophytic *Penicillium* strains (Table **3**). The same consideration pertains the structurally related dibenzo-γ-pyrones, or xanthones (Table **3**), which are known for their insecticidal effect and have been reported from plant species belonging to at least 20 botanical families [46]. The azadirachtins, tetranortriterpene limonoids typical of the neem tree (*Azadirachta indica*) and related species in the Meliaceae, represent a well known example of natural insecticide mainly acting as an antifeedant and a growth disruptor, which have been recently found to be produced by an endophytic strain of *P. (Eupenicillium) parvum* [47]. Likewise, antifeedant effects against the elm bark beetles (*Scolyuts* spp.) have been reported for the phomopsolides, pyranone compounds first characterized from *Phomopsis oblonga* [48], and later extracted from liquid cultures of an unidentified endophytic *Penicillium* strain [49]. Insecticidal properties have been also pointed out for the brasiliamides by an endophytic strain of *P. brasilianum*, which were found to induce convulsive effects in silkworms (*Bombyx mori*) [50] similar to those referable to penitrems [51] and other tremorgenic meroterpenoids of *Penicillium*. The latter class of compounds also includes the arisugacins and the territrems recently reported by a strain from *Tamarix chinensis* [52]. Alanditrypinone and related spiroquinazoline alkaloids, well known for their insecticidal activity [53], have been found as secondary metabolites of a strain (*Eupenicillium* sp.) recovered from leaves of *Murraya paniculata* [54]. Moreover, strains (*Penicillium* sp.) recovered from root of *Derris elliptica* [55], and from leaf of *Derris hancei* [56], have been reported to produce metabolites displaying insecticidal activity against larvae of noxious moths (*Plutella xylostella* and *Spodoptera litura*), and against the turnip aphid (*Lipaphis erysimi*). Rotenone, or a related product, was identified among these compounds [55]. Finally, insecticidal activity against the melon and cotton aphid (*Aphis gossypii*) has been reported for penicinoline, a novel pyrrolyl 4-quinolinone alkaloid produced by another unidentified strain [57].

Besides a direct antibiotic role, some endophyte metabolites are also considered to possibly act as elicitors inducing enhanced plant protection against biotic adversities. Production of gallic acid by an endophytic *Penicillium* strain has been reported with reference to such a positive effect [58]. Other endophytes may influence plant development in consequence of their ability to release phytohormones, among which gibberellins, primarily known as fungal metabolites, are particularly considered for their implication in overcoming the adverse effects of abiotic stresses [59]. Within *Penicillium*, production of gibberellins has been observed by endophytic strains from herbaceous plants [60-62], while so far there is no direct evidence for strains recovered from trees and shrubs. Conversely, production of auxins has been reported by endophytic strains of *P. glabrum* [63] and *P. citrinum* [64], respectively from pomegranate (*Punica granatum*) and carob tree (*Ceratonia siliqua*).

Mutualism may also involve at least part of the multitude of *Penicillium* strains/species inhabiting rhizosphere which are supposed to be eventually involved in mycorrhizal relationships on tree roots. Actually, this symbiotic context is mostly conjectural, considering that a review of the huge literature available on the subject [65] refers an unproved establishment of *Penicillium* strains in the root tissues. A notable exception is represented by the particular interaction occurring on alder roots, consisting in the induction of the formation of myconodules confined at the outer cortical layer. A fungus inducing myconodules on *Alnus incana* was first identified as *P. albidum* [66]. Afterwards, isolates recovered from roots of *Alnus glutinosa* were ascribed to the closely related *P. nigricans* [67], currently treated as a synonym of *P. janczewskii*. The identity of alder isolates as a new species was later advanced [68], and the name *Penicillium nodositatum* proposed [69]. It was found to be phylogenetically related to species in the subgenus *Biverticillium* [70], but not included in the mentioned taxonomic revision by Samson, *et al.* [8]. Considering the unknown functions of myconodules and the absence of any apparent damage to alder plants despite the observed death of cortical cells following fungal infection, *P. nodositatum* has been defined as a neutral microsymbiont [71]. Other observations have pointed out that it may rather act as a competitor at the root infection sites against actinorhizae promoted by *Frankia* strains establishing a mutualistic interaction based on nitrogen fixation [68, 72]. The association with alder roots resulting in samplings from several European countries (Table **1**) was indicative of an occurrence of this species confined to *Alnus* spp.; however, this hypothesis is destined to be abandoned in consequence of a more recent finding as an endophyte in leaves of twinflower (*Linnea borealis*) [73].

Neutral Interactions

The biocenotic interaction involving endophytes that do not apparently exert any particular effect on host plants can be defined as neutral, or based on a commensalitic aptitude. Awaiting further investigations which may eventually disclose unknown aspects concerning their effective role, this condition is inherent to the majority of the endophytic *Penicillium* strains recovered so far.

The available data aggregated for species (Table **1**) are not indicative of a host specialization or preference. Adaptation to a particular plant species might be conceived at some extent for strains that have resulted to produce secondary metabolites originally characterized from their host, in a relationship which possibly reflects a horizontal gene transfer between the two bionts [74]. Within a recently consolidated research trend aimed at identifying fungal endophytes expressing this particular aptitude to be exploited as an alternative and sustainable source, a number of *Penicillium* strains have been reported for the production of important plant-derived drugs. In fact, this is the case of the taxol-producing strains of *P. raistrickii* from the Pacific yew (*Taxus brevifolia*) [75], and *Penicillium* sp. from the Mexican yew (*Taxus globosa*) [76], of two unidentified isolates from *Cinchona ledgeriana* producing cinchonin and related alkaloids [77], and of the above-mentioned strain of *P. parvum* from *A. indica* producing azadirachtins [47]. Moreover, an endophytic *Penicillium* sp. from another azadirachtin source, the chinaberry tree (*Melia azedarach*), has been reported to produce the structurally related austins [78], indicating their possible derivation from a common biosynthetic pathway. It is also interesting to mention the finding of an endophytic strain of *P. griseoroseum* from coffee seeds able to synthesize a benzylated flavanoid when the compound pentamethoxyflavanone was added to the growth medium [79], which demonstrates that endophytes may exert their biosynthetic potential by modifying plant metabolites to generate products that are not ordinarily produced by the plants themselves.

In the field of biosynthetic affinities, there are also examples of known plant metabolites reported from endophytes of unrelated plants. This is the case of bergapten, occurring in bergamot essential oil and in grapefruit juice, that has been recently found as a product of a mangrove endophytic *Penicillium* strain [80]. Likewise asperphenamate, an anticancer compound reported from plants belonging to several unrelated families, is produced by the mentioned industrious and versatile strain H10BA2 of *P. raistrickii* from *T. brevifolia* [81], and is part of the pattern of extrolites characterizing *Penicillium* species in the section *Brevicompacta* [82], some of which are also known with reference to a facultative endophytic occurrence.

References for 66 *Penicillium* species and many unidentified strains recovered as endophytes are listed in Tables **1** and **2**. Within the identified strains, not surprisingly a higher number of records pertain to ubiquitous species, such as *P. brevicompactum, P. chrysogenum, P. citrinum* and *P. glabrum*, which confirm their ability to virtually colonize any kind of environment on earth. However, species identification has not been accomplished in as much as 43% of the findings, reflecting both the difficulty to get to a reliable ascription through the conventional methods, and the likely existence of novel species awaiting to be classified. According to the new taxonomic scheme, a good proportion of these isolates could actually belong to *Talaromyces*. Unfortunately, this possibility cannot be further investigated for the majority of such material, which introduces the opportunity to define appropriate description standards to be followed in reports concerning novel isolates of problematic taxonomic placement. Undoubtedly, more detailed investigations on the role and properties of endophytic strains cannot overlook a thorough taxonomic referencing.

On the plant side, a total number of 195 species are reported as hosts of endophytic *Penicillium* strains. Most of these trees and shrubs harbor just one or two species, but it is evident that more systematic investigations might disclose more composed assemblages, as happened for coffee. Occasionally the plant source has not been specified, such as in a few papers considering groups of medicinal and mangrove plants whose authors missed to relate the isolated strains to the pertinent botanical species [83-87]. Medicinal plants are more and more considered in view of the possible involvement of fungal endophytes in the expression of their favourable pharmacological effects [88]. Indeed, the search for novel pharmaceuticals has stimulated a huge investigational activity aiming at the exploitation of microbial sources, the reason why an increasing number of reports come from tropical habitats such as the mangrove forests [89, 90]. As inferable by a number of pertinent citations, the occurrence of endophytic manglicolous fungi has been intensively investigated in China and South-east Asia; unfortunately, additional data published on local journals could not be accessed, hence not considered in this manuscript. The context of temperate forests has been also diffusely examined in a number of studies, disclosing a few interesting cases of mutualistic interactions as mentioned above [91]. Conversely, reports concerning crop plants are quite fragmentary. Apart, the already mentioned exception of coffee, and a couple of plantation species such as cocoa and rubber tree (*Hevea brasiliensis*), the few occasional citations from grapevine (*Vitis vinifera*), kiwifruit (*Actinidia chinensis*), olive and pomegranate (Tables **1** and **2**) are indicative of an underestimation of the role of endophytes in crops, which is awaiting to be reconsidered particularly in view of a more thorough appreciation of the concept of defensive mutalism. Indeed, appropriate investigations on the ability to release bioactive metabolites *in vivo* could disclose interesting effects on the host plant, and foster additional applications of *Penicillium* strains in plant protection.

APPLICATIVE ISSUES OF BIOACTIVE SECONDARY METABOLITES

Directly or indirectly, a substantial part of the work carried out worldwide concerning endophytism in *Penicillium* aimed at the characterization of secondary metabolites, and their bioactivity. This has resulted in a huge

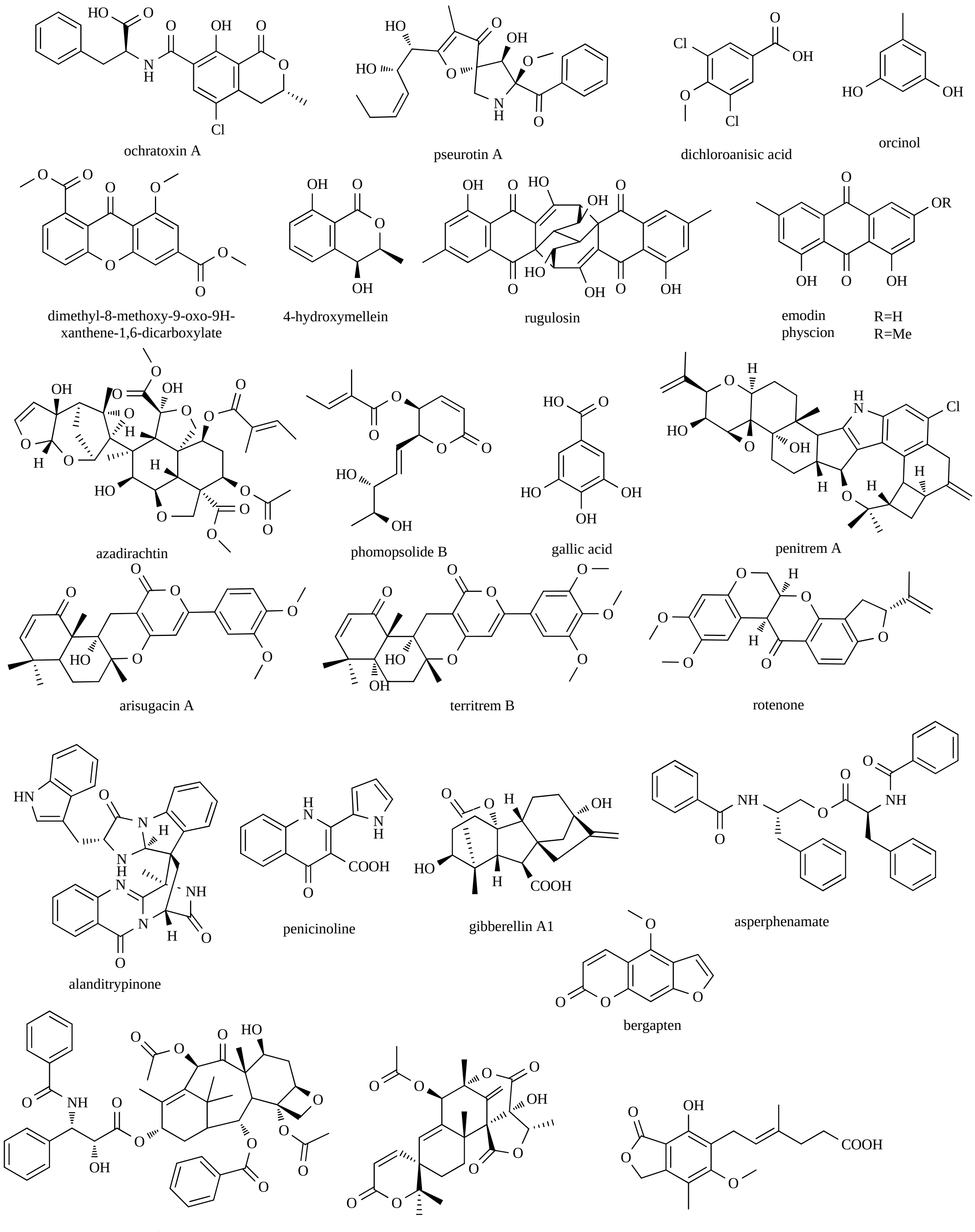

Fig. (1). Biodiversity of Secondary Metabolites Produced by Endophytic *Penicillium* Strains.

accumulation of novel knowledge in the field reflecting opportunities for a pharmaceutical exploitation, along the lines of a historical tradition of drugs derived from *Penicillium* strains which started in the 19th century with the discovery of mycophenolic acid [92], and continued with a number of blockbuster drugs, such as penicillin [93] and compactin [94, 95].

Very diverse in their molecular features (Fig. **1**), secondary metabolites produced by endophytic *Penicillia* are classified in more or less circumstantial structural groups, such as aldehydes, alkaloids, chromones, cyclohexanones, depsidones, diterpenes, ergochromes, esters, flavonoids, lactones, lignans, peptides and depsipeptides, phenols, polyketides, quinones, sesquiterpenes, steroids, xanthones, etc. [96, 97]. However, a grouping based on their functional and bioactive properties can be more useful for an applicative viewpoint. An alphabetic list is provided in Table **3**, including a relevant proportion of compounds, approximately 33%, first discovered from these strains. Their bioactivity has been assayed in multiple fields, disclosing antibiotic, cytostatic, insecticidal, and other miscellaneous properties, which of course are not intended to have been systematically investigated for each molecule. Thus, additional data are expected to be progressively integrated in view of a more thorough characterization of their biological effects. To this regard, readers should consider that this review covers endophytic *Penicillium* strains only; therefore, data summarized in Table **3** do not account for bioactivities resulting when these compounds were eventually extracted from other fungal strains or producing organisms.

CONCLUSION

The many and varied issues introduced with this overview announce future developments in studies concerning endophytic *Penicillium* strains. Indeed, quite intriguing aspects are involved covering diverse but interrelated disciplines, such as microbial ecology, plant pathology, biochemistry, food processing and pharmacology. A thorough knowledge of the state of the art is fundamental in order to enhance qualitative and quantitative detection of these fungi within endophytic communities, and to improve our ability to elucidate their ecological functions. Thus, data collected so far represent a valuable heritage to draw upon, both for the general purpose to expand the available information concerning *Penicillium* species, and for the more specific objective of exploiting these strains as a true microbial factory, yielding a largely untapped reservoir of chemically diverse natural products which have been optimized as effective bioactive agents by the pressure of evolutionary and environmental factors.

CONFLICT OF INTEREST

The authors confirm that this article content has no conflict of interest.

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