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Fungal quinones: Diversity, producers and applications of quinones from *Aspergillus*, *Penicillium*, *Talaromyces*, *Fusarium* and *Arthrinium*

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Abstract

Quinones represent an important group of highly structurally diverse, mainly polyketide derived secondary metabolites widely distributed among filamentous fungi. Many quinones have been reported to have important biological functions such as inhibition of bacteria, or repression of the immune response in insects. Other quinones, such as ubiquinones are known to be essential molecules in cellular respiration, and many quinones are known to protect their producing organisms from exposure to sunlight.

Most recently, quinones have also attracted a lot of industrial interest, since their electron donating and accepting properties makes them good candidates as electrolytes in redox flow batteries, like their often highly conjugated double bond systems make them attractive as pigments. On an industrial level, quinones are mainly synthesized from raw components in coal tar. However, the possibility of producing quinones by fungal cultivation has great prospects, since fungi can often be grown in industrially scaled bioreactors, producing valuable metabolites on cheap substrates.

In order to give a better overview of the secondary metabolite quinones produced by and shared between various fungi, mainly belonging to the genera *Aspergillus*, *Penicillium*, *Talaromyces*, *Fusarium* and *Arthrinium*, this review categorizes quinones into families such as emodins, fumigatins, sorbicillinoids, yanuthones and xanthomegnins, depending on structural similarities and information about the biosynthetic pathway from which they are derived, whenever applicable. The production of these quinone families are compared between the different genera, based on recently revised taxonomy.

Key points:

Quinones represent an important group of secondary metabolites widely distributed in important fungal genera such as *Aspergillus*, *Penicillium*, *Talaromyces*, *Fusarium* and *Arthrinium*.

Quinones are of industrial interest and can be used in pharmacology, as colorants and pigments, and as electrolytes in redox flow batteries.

Quinones are grouped into families and compared between genera according to revised taxonomy.

Key words: quinones, benzoquinones, anthraquinones, naphthoquinones, *Aspergillus*, *Penicillium*, *Talaromyces*, *Fusarium*, *Arthrimum*

Introduction

Quinones and quinols are widespread natural products in invertebrates, plants, algae, fungi, and lichens (Nohl et al. 1986; Medentsev and Akimenko 1998; Donner 2015; Futuro et al. 2018; García et al. 2018, Sunasse et al. 2018; Feng and Wang 2020). They are of interest to mankind because of their redox characteristics and they can be used as antioxidants, antibacterials, antifungals and battery components among other things (Ito et al. 1973, Kawai et al. 1978; Kawai and Nozawa 1979; Kawai and Cowger 1981; Xu et al. 2019; Kristensen et al. 2020; Masi and Evidente 2020). Quinones are present as ubiquinones (coenzyme Q, **6**) in mitochondria of all fungi, where they are considered primary metabolites (Kurasihi, 1985; Nohl et al. 1986; Sugiyama et al. 1988; Kurasihi et al. 1990), but other quinones are typical secondary metabolites, being small molecules produced during chemical differentiation of organisms and of restricted taxonomical distribution.

The main purpose of this review is to investigate whether quinones and quinols are widespread in the chemical arsenal of filamentous fungi, focusing on the genera *Aspergillus*, *Penicillium* and *Talaromyces* and to a lesser extent *Fusarium*, *Arthrimum* and *Alternaria*. The genera *Aspergillus*, *Penicillium* and *Talaromyces* have recently been revised and subdivided into formal sections, and for *Aspergillus* and *Penicillium* also into formal series based on phylogeny (cladification) and taxonomy (classification) (Houbraken et al. 2020). *Aspergillus* contains 446 species, *Penicillium* contains 483 species, and *Talaromyces* contains 171 species (Houbraken et al. 2020) and we follow this taxonomy, and have revised species designations accordingly when deciding on the species name of quinone producers. In *Fusarium* there is still a debate on whether to include most former species called *Fusarium* in that genus (O'Donnell et al. 2020; Geiser et al. 2021) or to subdivide *Fusarium* in *Fusarium sensu stricto* and other fusaroid genera such as *Neocosmospora*, *Bisifusarium* and others (Crous et al. 2021). We have chosen to mention both options, when mentioning these species, for example by mentioning both *Neocosmospora solani* and *Fusarium solani*.

Structural diversity of quinones

Quinones are an important class of small molecules that are widely distributed in nature and possess various natural functions as well as biotechnological applications. The most basic quinoid structure is the benzoquinone (BQ, **1**) structure, which consists of a fully conjugated six carbon ring with two keto-groups in *ortho*- or *para*-position. Other frequently observed core structures are naphthoquinones (NQ, **2**) and anthraquinones (AQ, **3**) in which the quinoid ring is merged with one or two benzene rings, respectively (Thomson 1971) (Fig. 1). Most often, fungal quinones are *para*-quinones, but *ortho*-quinones are also observed, such as spathullin C (**55**) (Thomson 1971, Nord et al. 2019). While BQs, NQs and AQs constitute the

most commonly observed quinone core structures in biological samples, several other core structures exist. Notable examples include the four ring tetracenequinone (**4**) carbon skeleton of the several anthracyclines produced by *Streptomyces* (Thomson 1971) and the highly aromatic perylenequinones (**5**) produced by some fungi, such as *Cercospora* and *Alternaria* sp. (Wu et al. 1989; Daub et al. 2013; Chagas et al. 2016).

Most fungal quinones such as xanthomegnin (**81**), terreic acid (**59**), fumigatin (**37**) and emodin (**98**) are biosynthesised by polyketide synthases (PKSs) (Turner 1971; Turner and Aldridge 1983; Frisvad et al. 2020). These are usually non-reducing or partially reducing, and their biosynthesis often involves several additional oxidation steps, resulting in highly oxygenated compounds. Interestingly, only a few examples of non-PKS derived fungal quinones exist. These include nonribosomal peptide synthetase (NRPS) derived BQs such as asterriquinone (**29**) and atromentin (**31**) which are dimers of modified amino acids, often with further modifications, such as prenylations, as is the case with terrequinone A (**30**) (Balibar et al. 2007).

Further structural diversity arises with modifications of the core structure of the quinone with functional groups. In addition to oxidations another common modification in naturally derived quinones are methylations as is the case with the AQ emodin (**98**). However, many other modifications occur, including prenylation (e.g. stemphone B, **56**), halogenation (e.g. nalgolaxin, **119**), amination (e.g. 2-aminoemodin, **110**) and acetylation (e.g. fumiquinone A, **42**) as well as almost any combination of these. Furthermore, some quinones are dimers (e.g. phoenicin (=phoenicine, phenicin, **47**) and skyrin (**95**) (Thomson 1971). Another example of quinone diversity is found in terreic acid (**59**), produced by *Aspergillus terreus*, which contains an epoxy-group on its core quinoid ring (Sheehan et al. 1958). It can be argued whether epoxy-containing quinone structures like this can be considered true quinones, however, for the purpose of this review, they are included. Thus, quinones possess a vast structural diversity based on the core carbon structure as well as the addition of a host of different functional groups.

Biological function of quinones

Quinones can undergo electron transfer reactions, resulting in three possible quinone states; the fully reduced hydroquinone (or quinol) state (QH₂), the fully oxidized quinone state (Q) and the intermediate semi-quinone radical state (QH[•]) (Uchimiya and Stone 2009; El-Najjar et al. 2011). Collectively, molecules in any of these states are occasionally referred to as quinones in the literature.

The vast diversity in structure enables quinones to have a broad spectrum of applicability in biological systems. The quinones involved in membrane bioenergetics, such as ubiquinone (**6**, Fig. 2), all possess a hydrophobic chain, which assist in membrane anchoring. The quinones involved in anaerobic respiration are primarily NQs, as these are more susceptible to reactions with oxygen compared to BQs, which have a higher standard reduction potential (Berry 2002). Some bacteria such as *Shewanella oneidensis* use quinols in electron transfer to reduce insoluble metal outside the cell in an anaerobic respiration process (Newman and Kolter 2000; Tikhonova and Popov 2014).

Some quinones are allelochemicals that inhibits or kills competing organisms (Uchimiya and Stone 2009). An example of such are the dimeric BQ oosporein (**48**), which increases virulence of the fungus *Beauveria bassiana*, by repressing the host immune response of insects (Feng et al. 2015; Mc Namara et al. 2019). In

addition, oosporein (**48**) shows anti-bacterial effect in insect cadavers indicating that it might help the fungus to avoid microbial competition after the insect host is dead (Fan et al. 2017). In fact, in an attempt to discover chemicals for pest controls, a total of 41 BQs (both synthetic and non-synthetic) were tested for their toxic effect on the subterranean termite *Coptotermes formosanus* (Mozaina et al. 2008). It was discovered that BQs with no substitutions, or only methyl or methoxy substitutions, showed none to very low termiticidal activity, while BQs which had one or two hydrophobic substitutions on one side of the ring, and one to two electron donating substitutions on the other side of the ring showed the highest toxicity (Mozaina et al. 2008). Similar experiments against *C. formosanus* with 17 natural NQs showed that NQs with no or a non-polar substitution in the quinoid ring, e.g. juglone (**75**), showed higher activity than the other NQs. The 24 natural AQs studied, generally had little activity against the termites (Osbrink et al. 2005). Mozaina et al. (2008) lists several references in which quinones are tested for the toxicity towards other agricultural pests.

Another example of allelochemical quinones are the perylenequinones (**5**) made by some plant-pathogenic fungi. These quinones act as photosensitizers, generating reactive oxygen species by reactions with sunlight, which causes cellular damage of the target plant (Daub et al. 2013). Few studies have investigated the mode of action of allelochemical quinones, but it is known that some BQs and AQs disrupt electron transfer in plants. A notable example is the plant derived BQ sorgoleone (**7**), which have a long acyl chain resembling the terpenoid chain seen in ubiquinones and plastoquinones. It is produced by sorghum and have been shown to inhibit photosystem II of other plants (Czarnota et al. 2001; Vyvyan 2002). Another example is juglone (**75**), produced by black walnut, which have been shown to affect both photosynthesis and respiration of plants (Hejl et al. 1993).

Some fungal bis-naphthopyrones have been shown to repel arthropod predation on fungal tissue, but the quinones involved did not show any particular toxicity towards the insects. This was also the case for aurofusarin (**145**), produced by several *Fusarium* species. Likewise, activity was shown for the structurally related quinones xanthomegnin (**81**) and viomellein (**83**) which have been observed in other ascomycetes, e.g. *Penicillium* and *Aspergillus* species (Xu et al. 2019).

Some AQs have been proposed to protect organisms from exposure to sunlight. An evolutionary study, showing that lichens, which have evolved to live in habitats with high sun exposure, were more likely to produce AQs, compared to lichen evolved to live in other, less exposed niches (Gaya et al. 2015). It has also been shown that synthesis of physcion (**102**), which is produced by many fungal species, is induced under UV-B radiation (app. 280-320 nm) in some lichens (Solhaug et al. 2003; Solhaug and Gauslaa 2004).

Quinones produced by basidiomycetes have been shown to be involved in the degradation of plant material by generating reactive oxygen species through a process called quinone redox cycling (Kerem et al. 1999; Jensen et al. 2002; Baldrian and Valášková 2008). Kerem et al. (1999) found that 2,5-dimethoxy-1,4-benzoquinone (DMBQ, **8**) produced by brown rot fungus *Gloeophyllum trabeum*, is used to degrade polyethylene glycol (PEG), a model for wood polymers: DMBQ (**8**) is reduced by the fungus to its hydroquinone-form, 2,5-dimethoxyhydroquinone (DMHQ, **9**), which in turn reduces iron(III) to iron(II). The resulting semi-quinone radical reacts with oxygen, producing reactive oxygen species such as

hydrogenperoxide. Hydrogenperoxide and iron(II) then function as Fenton reagents in the depolymerization of PEG (Kerem et al. 1999).

Biotechnological uses of quinones

Quinones can be used in many aspects of technology, including in supramolecular chemistry (Fang et al. 2020), in microbial fuel cells (Kracke et al. 2015; Kisieliute et al. 2019), in pest control (Segaran and Sathivelu 2019), as dyes and colorants (Hyde et al. 2019), as drugs (Nweze et al. 2020) and even as electrolytes in redox flow batteries (Huskinson et al. 2014; Kristensen et al. 2020). On an industrial level, quinones such as AQs and NQs are synthesized from raw components in coal tar (Vogel 2000; Collin et al. 2003), but the possibility of producing them by fungal cultivation has great prospects as a more environmentally viable alternative. Many filamentous fungi and yeasts can grow in industrially scaled bioreactors, producing valuable metabolites on cheap substrates (Sen et al. 2019). Additionally, the high structural diversity of fungal quinones is desirable for industries where chemical diversity is an advantage, for example in the search of new antibiotics, cancer drugs, food colorants and textile dyes. Below, the prospects of using quinones as pigments and drugs on an industrial level, are highlighted. When possible, examples of fungal quinones are used, but also studies where quinones are plant-derived are referenced.

Quinones as dyes and colorants

Pigment production from natural sources is increasing in popularity with concerns of the adverse effects of synthetic dyes (Oplatowska-Stachowiak and Elliott 2017). Traditionally, naturally occurring pigments are derived from insects and plants but production is limited on an industrial scale due to factors such as seasonal variability (Mapari et al. 2005; Sen et al. 2019). In contrast, microorganisms such as fungi can grow in industrially scaled bioreactors with relatively cheap substrates and industrial waste products (Panesar et al. 2015). Additionally, many fungal pigments are secreted under submerged fermentation, improving downstream processing compared to traditional pigment sources such as plants (da Costa Souza et al. 2016; Hernández et al. 2019; Suwannarach et al. 2019).

Fungal pigments are very diverse in structure, and besides quinones, include chemical classes such as carotenoids, melanins, flavins, phenazines and azaphilones (Dufossé et al. 2014; Dufossé 2018). When considering the quinoid class, AQs are the most investigated for food colorants and textile dyes (Mapari et al. 2005; Dufossé 2018; Räisänen 2019; Suwannarach et al. 2019) with the industrially available fungal pigment Arpink Red™ as an often cited example. Arpink Red™ is pH- and heat stable and is assumedly produced by *Penicillium oxalicum*, although this identification has been miscredited by Mapari et al. (2005) (Dufossé et al. 2005; Mapari et al. 2005). Another example is bostrycin (**148**), produced by *Nigrospora aurantiaca* (Suwannarach et al. 2019) and *Arthrimum phaeospermum* (van Eijk 1975). This NQ was found to be very promising as a textile dye and showed no toxicity towards human embryonic kidney cell (HEK 293T) (Suwannarach et al. 2019).

Microbial pigments still present challenges that needs to be addressed before they can completely outcompete synthetic alternatives. Most notably are issues regarding toxicity, production cost and chemical stability. There are many ways to improve pigment production and thus reduce the cost of microbial pigments and a lot of work is put into strategies such as growth condition optimization, effective downstream

processing and genetic engineering, all substantially increasing the potential of fungal derived quinoid pigments for industrial use (Sen et al. 2019). For example, the low chemical stability of some fungal quinones in the food colorant industry have been addressed by innovative solutions such as micro- and nano-emulsions (Özkan and Bilek 2014; Gupta et al. 2016).

Quinones as pharmaceuticals

Quinones have found their use as important pharmaceuticals most noticeably as laxative agents, cancer-therapy drugs and microbials.

Laxative agents: AQs have been widely used as laxative agents. Especially plant-derived glycosylated ones are preferred as they are non-active in the small intestine, but upon deglycosylation by bacterial activity in the large intestine, they become active and induce diarrhea by altering the excretion by epithelial cells (Gorkom et al. 1999). A well documented example is emodin (**98**) which is produced by many plant and fungal species (Srinivas et al. 2007).

Anti-cancer: Much research have been made on the anti-tumor effects of quinones and the effects have been shown for both NQs and AQs (Malik and Müller 2016; Futuro et al. 2018; Pereyra et al. 2019). These quinones target cancer cells by a host of different mechanisms, for example by generating reactive oxygen species (ROS), which damages proteins, lipids, DNA as well as RNA. Both NQs and anthracyclines have also shown to interfere with the function of topoisomerase II, which is required for DNA synthesis and repair in mammalian cells (Malik and Müller 2016; Pereyra et al. 2019). As in the case of laxative agents, emodin (**98**) is also a well studied anti-cancer agent (Srinivas et al. 2007). Some quinones have shown promise as photosensitizers in photodynamic light therapy. Here, the quinone is injected intravenously into the patient before being excited by a laser directed at the area of the tumor. The excited quinones react with oxygen to generate ROS, leading to tumor cell necrosis (Diwu and Lown 1994; Diwu et al. 1996; Rajendran 2016).

Anti-microbial: Many quinones have anti-bacterial, anti-fungal and/or anti-parasitocidal effects. When regarding *Penicillium* and *Aspergillus*-derived quinones, especially AQs have been investigated for their anti-microbial effects against gram-positive and gram-negative bacteria (Masi and Evidente 2020). Examples include iso-rhodoptilometrin-1-methyl ether (**10**), averantin (**134**) and nidurufin (**133**) isolated from *A. versicolor*, which all showed anti-bacterial activity against gram-positive bacteria (Lee et al. 2010; Hawas et al. 2012). Other examples include juglanthraquinone A triglycoside (**116**) from *A. fumigatus* and versicolorin C (**130**) and isoversicolorin C from *A. nidulans*, which targets both gram-positive and gram-negative bacteria (Abdel-Aziz et al. 2018; Yang et al. 2018). AQs from *Penicillium* with anti-bacterial effect include 2'-acetoxy-7-chlorocitreosein (**109**) from *P. citrinum* which showed effect against *Vibrio parahaemolyticus* (He et al. 2017) and penicillanthranin A (**113**) (also from *P. citrinum*) which showed activity against *Staphylococcus aureus* (Khamthong et al. 2012). Additionally, the AQ dimers 6,6'-oxybis(1,3,8-trihydroxy-2-((S)-1-methoxyhexyl)-anthracene-9,10-dione (**122**) and 6,6'-oxybis(1,3,8-trihydroxy-2-((S)-1-hydroxyhexyl)-anthracene-9,10-dione (**123**) isolated from *A. versicolor* and rugulosin A (**11**) isolated from *P. radicum* (= *Talaromyces radicus*) showed activity against *S. aureus* (Yamazaki et al. 2010; Li et al. 2019). Mostly, AQs have been tested for their antibacterial effects, but there are examples of other types of quinones: stemphone C (**57**) isolated from an *Aspergillus* species, showed strong synergistic effects with other

antibiotics in the inhibition of methicillin-resistant *S. aureus* (Koyama et al. 2005). From *P. spathulatum*, spathullin A (**53**), an 1,2-hydrobenzoquinol, showed activity against several bacteria, including *S. aureus* (Nord et al. 2019). Quinones from *Fusarium* with antibiotic effects include aurofusarin (**145**) and bivakerin (**146**) (Sondergaard et al. 2016). Furthermore, several BQs isolated from plants have been shown to have antibacterial effects (Guntern et al. 2001; Yang et al. 2001; Drewes et al. 2005).

Few studies have tested the anti-fungal activity of quinones from *Penicillium* and *Aspergillus* but there are some. Examples include the AQs 6,8,1'-tri-*O*-methyl averantin (**135**), aversin (**131**) and 6,8-di-*O*-methyl versiconol (**12**) from a fungus identified as *Penicillium purpurogenum* which showed moderate inhibitory activity towards *Botrytis cinerea* (Li et al. 2014) and juglanthraquinone A triglycoside (**116**) from *A. fumigatus*, which showed activity against yeast and filamentous fungi (*Candida albicans* and *A. niger*) (Abdel-Aziz et al. 2018). Quinones isolated from plants also showed to have anti-fungal activity, including both BQs (Suzuku et al. 1998; Guntern et al. 2001; Drewes et al. 2005) and NQs (Sasaki et al. 2002).

Several quinones have anti-viral effects. Ióca et al. (2016) found that naphthoquinoneimine (**13**) isolated from an *Aspergillus* strain and emodin (**98**) and ω -hydroxyemodin (=citreorosein) (**104**) isolated from *Penicillium* strains had moderate to strong activity against several vira (Avian metapneumovirus (AMPV), Bovine diarrhoea virus (BVDV), Herpes Simplex Virus Type 1 (HSV-1)). Additionally, Huang et al. (2017) found anti-viral effect against HSV-1 with the AQs aspergilol H (**137**) and I (**138**) isolated from *A. versicolor*.

Some fungal derived quinones have also been shown to be effective against parasites. Although not isolated from *Aspergillus* or *Penicillium* sp., anti-malarial effects have been shown from fungal AQs and BQs (Tansuwan et al. 2007; Kornsakulkarn et al. 2012). Furthermore, emodin (**98**) has been shown to possess inhibitory effect against the gut-parasite *Giardia lamblia* (Chabra et al. 2019).

Emodin (**98**) has also been cited as a mycotoxin (Wells et al. 1975; Hasan, 1998), but most data indicated that it is only marginally toxic (Izkaki, 2002; Gruber-Dorninger et al. 2017). However, other quinones such as the NQs xanthomegnin (**81**) and viomellein (**83**) have been shown to be toxic (Carlton et al. 1973, Carlton et al. 1976, Zimmermann 1977, Hald et al. 1983, Scudamore 1986, Mills et al. 1995).

Taxonomic distribution of quinones and hydroquinones

Ubiquinones

Ubiquinones (**6**) are present in the mitochondria in all eukaryotic organisms, but also in bacteria, as an essential part of the electron transport chain and are examples of primary metabolites (Nohl et al. 1986). Despite being primary metabolites, the type of ubiquinone present in fungi has a certain taxonomical value in *Aspergillus* classification (Kurasihi 1985; Sugiyama et al. 1988; Kurasihi et al. 1990; Chang et al. 1991; Kuraishi et al. 2000) and *Penicillium* classification (Kurasihi et al. 1991). Ubiquinones are named by the number of isoprene units and whether one or more isoprene units have had a double bond reduced, e.g. Q-10(2H) denotes a ubiquinone with 10 isoprene units, where one isoprene unit is reduced (Itoh et al. 1988). In Table 1, where species of *Aspergillus* have been re-classified according to an updated taxonomy and phylogeny (corrected according to Houbraken et al. (2020)), it can be seen that ubiquinone isoprenoid number and type

is section specific to a certain extent and in most cases follow the phylogeny of the large genus *Aspergillus*. An interesting exception is *Aspergillus* subgenus *Circumdati* section *Nigri* that is different from the other sections in subgenus *Circumdati* having ubiquinone Q-9. According to phylogenomic analysis of *Aspergillus* by Steenwyk et al. (2019), section *Nigri* is a sister section to subgenus *Nidulantes* in contrast to the phylogeny presented by Kocsubé et al. (2016) and Houbraken et al. (2020), but also in contrast to phenotypic characters in the classification of *Aspergillus* (Frisvad and Larsen 2015; Chen et al. 2016b; Vesth et al. 2018; Barrett et al. 2020). A comparison of mitochondrial and nuclear genome data may help solving this taxonomic and phylogenetic dilemma.

In the large genus *Penicillium*, all species have ubiquinone Q-9 as the main mitochondrial quinone (Kurasih et al. 1991; Kreisel and Schubert (1990), taxon names corrected according to Houbraken et al. 2020). However, depending on the chemical analytical method used, the profiles of ubiquinones may be more complex containing also some Q-10(H₂), Q-12 and traces of Q-10 (Paterson and Buddie 1991; Paterson 1993). The main ubiquinone system in *Talaromyces* and *Trichocoma* is Q-10(H₂) sometimes with a relative smaller amount of Q-10(H₄), while the dominant ubiquinone system in *Evansstolkia*, *Hamigera*, *Monascus*, *Pseudohamigera*, *Pseudopenicillium*, *Warcupiella* and *Xeromyces* is Q-10 and the dominant ubiquinone system in *Ascospirella*, *Penicillioptis*, *Phialomyces*, *Sclerocleista*, and *Thermoascus* is Q-9 (Kuraishi et al. 1985; Kuraishi et al. 1990; Kuraishi et al. 1991; Kuraishi et al. 2000; Ogawa et al. 1997).

Quinones involved in conidium and sclerotium formation

Most dark coloured fungi are protected by melanin, including black yeasts, *Alternaria*, *Cladosporium*, *Curvularia*, and other dematiaceous filamentous fungi (Bell and Wheeler 1986). In dematiaceous fungi, and many species of *Aspergillus*, *Penicillium* and *Talaromyces* with dark green conidia, melanin is derived from a pathway involving 1,8-dihydroxynaphthol (DHN, **14**) (Wheeler and Stipanovic 1985; Bell and Wheeler 1986; Wheeler and Hocking 1995; Sappak et al. 2015; Perez-Cuesta et al. 2020). Certain groups of species within the genus *Aspergillus*, however, have another type of melanin, or even two types of melanin. For example, in addition to DHN-derived melanin, *A. nidulans* produces melanin derived from the tyrosine-derived DOPA-pathway that involves the quinol L-3,4-dihydroxyphenylalanine (L-DOPA, **15**) and the corresponding BQ DOPA quinone (**16**) as intermediates. *A. fumigatus* (and other species from section *Fumigati*) has both DHN-derived melanin and the tyrosine-derived pyromelanin, which involves the BQ benzoquinooacetate (**17**) as intermediate (Geib et al. 2016; Chang et al. 2019; Blachowicz et al. 2020; Chang et al. 2020; Perez-Cuesta et al. 2020). In *Aspergillus* section *Flavi* with yellow green conidia, the DHN-derived melanins are not present, but the melanin produced is based on the AQ asparasone A (**18**) which after dehydration and being processed with laccases is converted into melanin (Chang et al. 2020). In *Aspergillus* section *Terrei*, melanin (called Asp-melanin) is also derived from tyrosine, but in that case quinones do not seem to be involved, but rather aspulvinone E (**19**) (Chang et al. 2020).

In most *Aspergillus* and *Penicillium* species with green conidia, DHN-derived melanins are involved, where flaviolin (**151**) is a shunt product, however some Aspergilli with green conidia have an additional pathway in order to produce DOPA-derived melanin (Chang et al. 2020). In *Aspergillus* section *Circumdati* with yellow conidia, melanin is based on the NQ viomellein (**83**) and the non-quinone vioxanthin (**20**), while in section

Candidi, melanin is only present in the black sclerotia (Varga et al. 2007). The conidia of the *Candidi* species are protected by terphenyllin (**21**) and similar secondary metabolites (Rahbæk et al. 2000; Varga et al. 2007; Kjærboelling et al. 2018; Houbraken et al. 2020). In general, most filamentous fungi and some yeasts can produce melanin, if not always in the conidia or the mycelium, then in sclerotia and ascomata (Butler et al. 2009; Chang et al. 2020). Therefore quinones may be produced by most melanin producing fungi, but it may require genetic manipulation in order to have the quinones accumulated in sufficient amounts.

Secondary metabolite quinones in *Aspergillus*, *Penicillium* and *Talaromyces*

In the following part of this review, we investigate the quinones produced as secondary metabolites in the genera *Aspergillus*, *Penicillium* and *Talaromyces*. In Table 2, 3 and 4, quinones observed in these genera are listed. The genera is organized into formal sections based on recently revised phylogeny and taxonomy (Houbraken et al. 2020). To better compare quinone production within and between genera, we have grouped quinones in what we describe as quinone families. Quinone families are based on structural similarity, as argued below, occasionally including information from known biosynthetic pathways, when applicable. In cases where only one quinone is present in a family, the quinone name is also used as the family name. Representative structures are shown for the BQ, NQ and AQ families (Fig. 3, Fig. 4 and Fig. 5).

Benzoquinones

Aculeatusquinones are a relatively small family of BQs. They are characterized by a *para*-dimethylated BQ moiety fused to a polysubstituted benzene ring. They have been observed in both *Penicillium* section *Citrina* and *Aspergillus* section *Nigri* and include aculeatusquinone A (**22**), B (**23**) and D (**24**).

Anserinones have been isolated from species in *Penicillium* section *Citrina*. The family includes anserinone A (**25**), anserinone B (**26**), formylanserinone B (**27**) and hydroxymethylanserinone B (**28**), all sharing a unique carbon scaffold consisting of an *O*-methylated BQ ring, attached to an oxygenated three-carbon side chain.

Asterriquinones are an unusual family of BQs in that they are derived from single module NRPS enzymes, rather than from a non reducing PKS (Balibar et al. 2007). They are derived from fusion of two de-aminated tryptophan molecules and consist of a dihydroxybenzoquinone fused to two prenylated indoles and are observed in *Aspergillus* sections *Terrei* and *Nidulantes*. It is a large family with many known quinones and include at least 25 asterriquinone derivatives, such as asterriquinone A-D, isoasterriquinone, and asterriquinone monoacetate, as well as terrequinone A. Asterriquinone (**29**) and terrequinone A (**30**) are shown as examples of the family.

Atromentins are, like asterriquinones, derived from NRPS enzymes but uses two tyrosine molecules as starter units (Geib et al. 2019), and differ by the lack of prenylation. They are produced by both *Aspergillus* section *Nigri* as well as *Penicillium* section *Chrysogena* and includes atromentin (**31**) and cycloleucomelone (**32**).

Citrinoids are BQs associated with the citrinin (**33**) biosynthetic pathway and includes citrinin H1 (**34**) and its stereoisomer 1-epi-citrinin H1. Citrinin (**33**) itself is not a quinone, but citrinin H1 (**34**) can be synthesized by

heating molecules of citrinin in water (Trivedi et al. 1993), and has also been discovered in *P. citrinum* (section *Citrina*) along with 1-epi-citrinin H1 (Wang et al. 2019).

Citriquinones consists of the structurally similar BQs citriquinone A (**35**) and B (**36**), isolated from *P. citrinum* (Ranji et al. 2013) (Section *Citrina*), and contain a characteristic butan-2-yl formate side chain. Citriquinone A (**35**) has shown antibacterial and anticancer activity (Ranji et al. 2013).

Fumigatins consists of a large group of BQs observed in *Aspergillus* section *Fumigati* and *Penicillium* sections *Aspergilloides*, *Exilicaulis*, *Gracilenta* and *Canescentia*. They appear heavily decorated, from several oxidation steps and are all *O*-methylated. They include fumigatin (**37**), spinulosin (**38**), 3,6-dihydroxytoluquinone (**39**), fumigatin oxide (**40**), fumigatin chlorohydrin (**41**), fumiquinone A (**42**), fumiquinone B (**43**), and potentially many others. Frisvad et al. (2009) defined the fumigatin family to also include less decorated BQs such as toluquinone (**61**). In this work however, we argue that fumigatins and toluquinones are kept as separate families, as members of the toluquinone family have been observed in other biosynthetic pathways as well, such as the patulin and yanuthone pathways (Ali et al. 2017; Frisvad et al. 2020).

Macrophorinquinones include 4'-oxo-macrophorin A (**45**) and D (**46**) due to their structural similarity to macrophorin D (**44**), which itself is not a quinone (Fujimoto et al. 2001). Their prenylation makes them highly similar to yanuthones (see below), although macrophorinquinones distinguish themselves by having cyclized terpenoid moieties rather than the linear one observed for yanuthones. Macrophorinquinones are observed in *Penicillium* section *Chrysogena*. The quinones in this family further carries an epoxy group in the quinoid moiety and have shown immunosuppressive effects (Fujimoto et al. 2001; Marcos et al. 2010).

Phoenicin (**47**) is a BQ dimer constructed from two 2-hydroxy-6-methyl-benzoquinones. It is structurally related to the even more oxygenated oosporein (**48**), which has been shown to act immunosuppressive towards insects (Feng et al. 2015). Phoenicin (**47**) is observed in *Penicillium* sections *Charlesia*, *Citrina* and *Exilicaulis*, while oosporein (**48**) has been observed in *Beuveria* and never in *Penicillium* (Posternak 1938; Reilly et al. 1940; Feng et al. 2015).

Sorbicillinoids are a large family of molecules structurally related to sorbicillin (**49**). Sorbicillin itself is not a quinone, however several derivatives are. These include 3-acetonyl-2,6-dimethyl-5-hydroxy-1,4-benzoquinone (ADH-BQ, **50**), 2-(2',3'-dihydrosorbyl)-3,6-dimethyl-5-hydroxy-1,4-benzoquinone (DDH-BQ, **51**) and sorrentanone (**52**) produced by *P. chrysogenum*.

Spathullins appear in *Penicillium* section *Brevicompacta* and were isolated from *P. spathulatum* (Nord et al. 2019). Spathullin A (**53**) and spathullin B (**54**) are both quinols, while spathullin C (**55**) is an *ortho*-quinone. Spathullin A (**53**) and B (**54**) has shown antibacterial activity, and the compounds in the family is are proposed to be NRPS derived, originating from tyrosine and cysteine (Nord et al. 2019).

Stemphones include stemphone B (**56**), stemphone C (**57**) and cochlioquinone D (**58**), isolated from an unknown *Aspergillus* sp. These meroterpenoid BQs all share a unique cyclised sesquiterpenoid moiety as well as a five-carbon side chain, both with various modifications, on either side of the quinoid part.

Terreic acid (**59**) is a BQ with an epoxy group in the quinoid ring. It is produced by *Aspergillus* sections *Terrei* and *Cervini*. Its biosynthetic pathway begins from 6-MSA (Turner 1971; Frisvad et al. 2020).

Toluquinones are simple BQs which appear in several biosynthetic pathways, including the patulin and yanuthone pathways (Ali et al. 2017; Frisvad et al. 2020). They include toluquinone (**61**), gentisylquinone (**62**) and chlorogentisylquinone (**63**). As toluquinones are known precursors/shunt products of the patulin pathway (Ali et al. 2017), in the context of this review, sections able to produce patulin were deduced to also have the capacity to produce toluquinones. Thus, toluquinones are observed in *Aspergillus* sections *Cremeri* and *Clavati* and *Penicillium* sections *Gracilentia*, *Lanata-Divaricata*, *Canescentia*, *Fasciculata*, *Formosana*, *Osmophila*, *Penicillium*, *Robsamsonia* and *Roquefortorum*.

Variecolorquinone B (**64**) is an *O*-methylated BQ merged to a substituted benzoic acid moiety via a methylene bridge. It does not appear to be related to its namesake variecolorquinone A (**115**) which is an AQ belonging to the emodin family (see below). Variecolorquinone B (**64**) is observed in *Aspergillus* section *Aspergillus*.

Violaceoids include violaceoid A-C (**65**, **66**, **67**) observed in *Aspergillus* section *Nigri*. They consist of a gentisylquinone (**62**) in its quinol form, substituted with a seven-carbon chain with various degrees of oxidation.

Yanuthones are a large family of polyketide derived molecules fused to terpenoid moieties (Holm et al. 2014; Frisvad et al. 2020). While not all yanuthones are quinones, some examples from this family includes yanuthone B (**68**) and yanuthone D (**69**) produced by *Aspergillus* section *Nigri* and peniginsengin B (**70**) and 5-farnesyl-methylquinone (**71**) and produced by *Penicillium* section *Chrysogena*.

Naphthoquinones

Aspetritones includes aspetritone A (**72**) and aspetritone B (**73**), which are produced by species in *Aspergillus* section *Candidi* (Wang et al. 2017). They are both tricyclic NQs containing two *O*-methyl groups on the naphthoquinoid part, which is attached to a cyclohexanol carrying two hydroxyl and a methyl group. The quinoid moiety is on opposite rings between aspetritone A (**72**) and B (**73**).

Griseusins are a family of NQs having a 20-carbon backbone and includes many members and some of them have shown antibacterial and anticancer activity (Tsuji et al. 1975, He et al. 2007, Li et al. 2007). Although most griseusins have been isolated from bacteria, Li et al. (2006) discovered griseusin C (**74**) from an unknown *Penicillium* sp.

Juglones are simple, scarcely decorated NQs. They include 6-ethyl-7-methoxy-juglone (**76**) observed in *Aspergillus* section *Cervini*, 2-hydroxy-3-methyl-1,4-naphthoquinone (**77**) from *Penicillium* section *Chrysogena* and juglone (**75**) from *Talaromyces* section *Talaromyces*. They might not be in the same biosynthetic pathway, but as their structures are so similar, we choose to group these as one family in the context of this review.

Naphthgeranines includes naphthgeranines A-D and others as well as naphthoquinone C (**78**). They all contain a 20-carbon backbone, including two distinct methyl groups. While most of the naphthgeranines have been

isolated from *Streptomyces* sp., naphthoquinone C (**78**) have been observed in an unknown *Penicillium* sp. (Wessels et al. 1991; Li et al. 2006).

Purpurogenone (**79**) is a naphthoquinone observed in *Talaromyces* section *Trachyspermi*.

Thysanone (**80**) is a naphthopyrone with a NQ fused to a pyrone. Unlike the xanthomegnins, the pyrone is fused to the quinoid rather than the benzene ring in thysanone (**80**). It is produced by *Penicillium* section *Thysanophora*.

Xanthomegnins are a large group of naphthopyranones and include xanthomegnin (**81**), semixanthomegnin (**82**) viomellein (**83**), rubrosulphin (**84**) and viopurpurin (**85**). With the exception of semixanthomegnin (**82**), these compounds are dimers, consisting of two naphthopyrones, with at least one being a quinone. They are produced in *Aspergillus* section *Circumdati*, *Penicillium* sections *Fasciculata* and *Penicillium* and *Talaromyces* section *Islandici*.

Xanthoviridicatin is structurally similar to xanthomegnins but instead of two naphthopyrones, they consist of a naphthopyrone coupled to a NQ. They include xanthoviridicatin D-G (**86**, **87**, **88**, **89**) and xanthoradone A-C (**90**, **91**, **92**), which differ by the orientation of the NQ. Xanthoviridicatin D-G (**86**, **87**, **88**, **89**) has been observed in *Penicillium* sections *Chrysogena* and *Fasciculata*, while xanthoradone A-C (**90**, **91**, **92**) has been observed in *Talaromyces* section *Talaromyces*.

Anthraquinones

1,3-dihydroxy-6-hydroxymethyl-7-methoxyanthraquinone (DHM-AQ) (**93**) is an AQ closely related to the emodins (see below). However, while the emodins have an OH or OMe group at position 8, this position is non-substituted in DHM-AQ (**93**), suggesting that the polyketide backbone is reduced at this position, and thus that the PKS related to this biosynthetic pathway of DHM-AQ (**93**) is different from the one for emodins, by being partly reducing. DHM-AQ (**93**) is produced by *Penicillium* section *Citrina*.

Bimodins are composed of two AQs related to the emodin pathway, fused together via a likely radical coupling. In this review, we have decided to keep bimodins separate from what we call the *O*-bimodins, which are also composed of two emodins, but fused with an ether bond (see below). Besides the method of fusion, the bimodins are observed in *Talaromyces* sections *Islandici* and *Talaromyces*, while the *O*-bimodins are observed in *Aspergillus* section *Nidulantes*. Examples of the bimodins flavoskyrin (**94**), skyrin (**95**), dicatenarin (**96**) and rhodoislandin (**97**) are shown in Fig. 5., but many other known bimodins exist, including aurantioskyrin, auroskyrin, deoxyluteoskyrin, deoxyrubroskyrin, iridoskyrin, luteoskyrin, 4a-oxyluteoskyrin, oxyskyrin, punicoskyrin, roseoskyrin, rubroskyrin, skyrinol and rugulosin A (**11**).

Emodins are a large AQ family with a core structure similar to emodin (**98**). Besides emodin, this family includes many compounds, such as catenarin (**99**), erythroglaucon (**100**), fallacinol (**101**), physcion (**102**), questin (**103**), chrysophanol (**105**), rubrocristin (**106**), carviolin (**107**) and others (**108**, **109**, **110**, **111**, **112**, **139**, **140**, **113**, **114**, **115**). In this family we also include penicillanthranins A (**113**) and B (**114**) which are emodins attached to citrinin moieties. Emodins are produced in *Aspergillus*, *Penicillium* and *Talaromyces* across multiple sections and have also been observed in *Arthrinium* sp. (Elissawy et al. 2017).

Juglanthraquinone A triglycoside (**116**) is an AQ isolated from *A. fumigatus* (section *Fumigati*). It is interesting as it is fused with three glycoside units (Abdel-Aziz et al. 2018).

MT81 (**117**) is an AQ resembling the emodins, however as was the case for DHM-AQ (**93**), the polyketide backbone is reduced differently in MT81 (**117**) than in the emodins (position 3). This suggests that the biosynthetic pathway is different from that of the emodins. The molecule is decorated with a unique patulin-like moiety through an acetal. It is observed in *Penicillium* section *Canescentia*.

Nalgiovensins are AQs with similar structures to the emodins, although with a key difference in that they contain an additional two carbon atoms in the polyketide backbone. Nalgiovensins are observed in *Penicillium* sections *Brevicompacta* and *Chrysogena* and in *Aspergillus* section *Flavi* and include nalgiovensin (**118**), as well as the two chlorinated compounds nalgiolaxin (**119**) and 2-chloro-6-[2'(S)-hydroxypropyl]-1,3,8-trihydroxyanthraquinone (CHT-AQ, **120**).

O-biemodins are dimers of emodin-like AQs that include ascoquinone A (**121**), 6,6'-oxybis(1,3,8-trihydroxy-2-((S)-1-methoxyhexyl) anthracene-9,10-dione (**122**) and 6,6'-oxybis(1,3,8-trihydroxy-2-((S)-1-hydroxyhexyl) anthracene-9,10-dione (**123**). They differ from the biemodins (see above) by being fused via an ether bond, rather than a C-C bond. They are observed in *Aspergillus* section *Nidulantes*.

Pachybasin (**124**) is a heavily reduced AQ, compared to the emodins, that only contains a single phenol group. It is observed in *Penicillium* section *Paradoxa*.

Talaromannins are oxidised AQ derivatives of the dimeric non-quinone flavomannin (**125**). They include talaromannin A and B (**126**) that are observed in *Talaromyces* section *Islandici*.

Topopyrones are AQs fused with a 1,4-pyrone ring. Topopyrone C (**127**) and D (**128**) were discovered in an unknown *Penicillium* sp.

Versicolorins include the AQ precursors of aflatoxin and sterigmatocystine such as versicolorin A (**129**), versicolorin C (**130**), aversin (**131**), averufin (**132**), nidurufin (**133**) and averantin (**134**) (Caceres et al. 2020). Aspergilol A (**136**), B, G, H (**137**) and I (**138**), observed in *Aspergillus versicolor* are also included in this family due to structural similarity (Wu et al. 2016; Huang et al. 2017). Aspergilol A (**136**) and B have been proposed to use averantin (**134**) as a precursor (Wu et al. 2016). Although the end products of the versicolorins, the aflatoxins are very toxic, some of the precursors, such as versicolorin A (**129**) have also shown toxicity to humans (Gauthier et al. 2020).

Viocristins are the only 1,4-AQs among the AQs described in this review, and include viocristin (**139**) and isoviocristin (**140**), that only differ by the position of a single *O*-methylation. The viocristins have been observed in *Aspergillus* section *Aspergillus*.

Quinone families in *Aspergillus*

Table 2 lists the secondary metabolite quinones observed in the genus of *Aspergillus*, which is composed of 446 species in total divided across 26 known sections. The quinones from one unknown *Aspergillus* spp. are

also listed. Eighteen quinone families are produced by this genus. Of the five subgenera, *Polypaecilum* is not known to produce any quinones, although only three species from this subgenus have been investigated. The other four subgenera all include quinone-producers. In those subgenera, emodins are present in all. Subgenus *Aspergillus* is the only section able to produce variegolorquinone B (**64**) and viocristins, while *Nidulantes* is the only subgenus to produce *O*-biemodins. Subgenus *Circumdati* is most varied in its production, and is able to produce 12 quinone families, seven of them only observed within that subgenus, namely aspetritones, xanthomegnins, aculeatusquinones, atromentins, violaceoids, yanuthones and nalgiovensins. In *Fumigati* the quinone families shared with other subgenera are emodins, toluquinones and terreic acid (**59**), while juglones, fumigatins and juglanthraquinone A triglycoside (**116**) are unique for this subgenus. *Nidulantes* produces emodins, versicolorins, asterriquinones and *O*-biemodins which are unique for the subgenus. An *Aspergillus* sp. from an unknown section is able to produce stemphones.

There is a high variability in quinone production at the section level. Of the 26 examined sections, 16 are known quinone producers. It must be said, however, that for most non-producing sections, only few species have been investigated. The sections able to produce the most quinone families are *Nigri*, *Terrei* and *Nidulantes*, producing five, four and four families, respectively.

Most quinone families are observed within one section only and include variegolorquinone B (**64**), aspetritones, xanthomegnins, aculeatusquinones, atrometins, violaceoids, viocristins, yanuthones, juglones, fumigatins, *O*-biemodins, juglanthraquinone A triglycoside (**116**) and stemphones. Emodins are on the other hand observed across 11 out of the 26 investigated sections.

Quinone families in *Penicillium*

Table 3 lists the known secondary metabolites in *Penicillium*. The genus consists of 483 species. The analysis covers 28 sections from the subgenera *Aspergilloides* and *Penicillium*. Of the known sections, 18 are known to produce at least one quinone family. Across the genus, 24 quinone families are produced.

Toluquinones are the most frequently observed quinone family in *Penicillium*, observed in nine sections. The second largest family is emodins, which is observed in eight sections. Fumigatins, phoenicin (**47**), nalgiovensins, xanthomegnins and xanthoviridicatin also appear in more than one section, while the remaining 17 families appear in only one section each. Only three families are observed in both known subgenera (fumigatins, emodins and toluquinones), while the rest appear in either one subgenus or the other.

Ten of the known sections were able to produce more than one family, while eight sections were able to produce one family only. Sections *Chrysogena* and *Citrina* represent by far the most diverse quinone producers, able to make eight and seven families, respectively.

Quinone families in *Talaromyces*

Table 4 lists the known secondary metabolite quinones in *Talaromyces*. The genus includes 171 known species across 7 sections. Across the genus, seven quinone families are produced: emodins, xanthomegnins, xanthoviridicats, juglones, biemodins, purpurogenone (**79**) and talaromannins. This makes *Talaromyces* the genus with the least diversity in quinone production compared to *Aspergillus* and *Penicillium*. Emodins are observed in five different sections and biemodins are observed across two sections. The other families are observed in only one section each. The two sections *Islandici* and *Talaromyces* are the most diverse, able to produce five and three families, respectively. *Trachyspermi* produces two quinone families, while sections *Helici* and *Purpurei* each produce compounds from only one family.

Comparison of quinone families across *Aspergillus*, *Penicillium* and *Talaromyces*.

When comparing the secondary metabolite quinone production between the three genera *Aspergillus*, *Penicillium* and *Talaromyces*, some clear differences are apparent. Fig. 6 shows a Venn diagram comparing the quinone families observed across these genera. Only three quinone families are shared between all three genera: emodins, juglones and xanthomegnins. Six families are observed both in *Aspergillus* and *Penicillium*: aculeatusquinones, atromentins, fumigatins, nalgiovensins, toluquinones and yanuthones. Only xanthoviridicats are shared between *Penicillium* and *Talaromyces* and no families are shared only between *Aspergillus* and *Talaromyces*. The families that only appear in *Aspergillus* are *O*-biemodins, aspetritones, asterriquinones, terreic acid (**59**), varicolorquinone B (**64**), versicolorins and violaceoids, viocristins and juglanthraquinone A triglycoside (**116**). In *Penicillium* the unique families are DHM-AQ (**93**), anserinones, citrinoids, citriquinones, griusins, MT81 (**117**), macrophorinquinones, naphthgeranines, pachybasin (**124**), phoenicin (**47**), sorbicillinoids, spathullins, thysanone (**80**) and topopyrones. The only unique quinone families in *Talaromyces* are biemodins, purpurogenone (**79**) and talaromannins.

Quinone production and pigmentation of *Fusarium* and related fusaroid genera

The genus *Fusarium* and related fusaroid genera produce a large number of mycotoxins and other bioactive secondary metabolites, of which several are quinones (Nesic et al. 2014; Munkvold, 2017; Li et al. 2020; Wei and Wu, 2020). Most of the quinones from fusaroid taxa known are NQs.

Quinone pigmentation in the genera *Fusarium*, *Albonectria* and *Neocosmospora* is dictated by four polyketide gene clusters: fusarubins (**143**) (*PKS3*), bikaverin (**146**) (*PKS16*), aurofusarin (**145**) (*PKS12*) and an uncharacterized red pigment (*PKS35*) (Fig. 7). Members of *Fusarium* are capable of producing two of these non-reducing polyketide synthase (NR-PKS) derived pigments; one produced during mycelial growth and the other during perithecial development. *F. acuminatum* and *F. avenaceum* are the exception, each carrying four pigment biosynthetic gene clusters encoding the aurofusarin (**145**), fusarubin (**143**) and two bikaverin-like NR-PKSs (Brown & Proctor 2016; Hansen et al. 2015).

Aurofusarin (**145**) was originally described as a golden pigment in 1937 (Ashley et al. 1937), but was first structurally elucidated in 1966 (Baker and Roberts 1966; Shibata et al. 1966). The compound is produced by a cluster (*PKS12*) of at least ten genes of which the *PKS* shares high sequence similarity to *wA*, found in several *Aspergilli*. The two *PKS*s have also been shown to produce the same entry compound, *YWA1* (Watanabe et al. 1998; Frandsen et al. 2011). Aurofusarin (**145**) is a product of dimerization of the intermediary compound rubrofusarin (**142**), containing two naphthopyrones. It is structurally similar to xanthomegnin (**81**), using 4-pyrones instead of 2-pyrones. Despite the pigmented properties of aurofusarin (**145**), it has not been linked to UV-protection or, as other secondary metabolites, to pathogenicity, however it does affect the chemical composition of quail eggs (Brown et al. 2012a;b; Brown and Proctor, 2016; Coleman 2016). Rubrofusarin (**142**) can be converted into a quinone form. This quinone product is sometimes observed at higher concentrations than rubrofusarin (**142**) in grain (Wang et al. 2018).

Bikaverin (**146**) and norbikaverin (**147**) are heterotetracyclic quinones, which were originally isolated from *F. fujikuroi* as a red pigment (Kjaer et al. 1971). These compounds are produced primarily by members of the *F. fujikuroi*, *F. verticillioides*, *F. proliferatum*, *F. agapanthi* and *F. oxysporum* species (Edwards et al. 2016; Kohut et al. 2010; Lazarro et al. 2012), where the responsible gene cluster consists of at least six genes (Niehaus et al. 2016). Other related pigments can also be produced (Lebeau et al. 2019). The responsible *PKS* (*bik1* = *PKS16*) starts the biosynthetic pathway by producing prebikaverin which is subsequently oxygenated and *O*-methylated to yield bikaverin (**146**) (Wiemann et al. 2009). Interestingly, disruption of the terminal release domains of *bik1* and *aur1* results in production of the isocoumarins, bikisocoumarin (*SMA93*) and citreoisocoumarin, respectively (Ma et al. 2008; Sørensen et al. 2012). Bikaverin (**146**) has been shown to affect a wide variety of organisms, including various human cell lines (Fuska et al. 1975), nematodes (Kwon et al. 2007), protozoa (Balan et al. 1970), bacteria (Deshmukh et al. 2014; Sondergaard et al. 2016), and fungi (Cornforth et al. 1971).

The fusarubin (**143**) gene cluster is identified in all sequenced members of *Fusarium* and *Neocosmospora* and is associated with black/dark purple pigmentation of perithecia (Proctor et al. 2007, Brown 2012a,b, Frandsen et al. 2016), except for species within *Neocosmospora* (the *F. solani* species complex (FSSC)) where fusarubins and its derivative NQs accumulate in the mycelium (Medentsev and Akimenko 1998, Short 2013). The production of fusarubins in *Fusarium* spp., *Neocosmospora* (*N. solani*, *N. virguliformis* and *N. ambrosia*) and *Albonectria rigidiuscula* is therefore widespread, and the class of fusarubins also encompass a range of different compounds containing quinone-structures, such as anhydrofusarubin, bostrycoidin, 9-desmethylherbarine, javanicin, karuquinones, lucilactaenes, norjavanicin, novarubin, solaninaphthoquinones, and (+)-solaniol (Arnstein & Cook 1947; Arsenault 1968; Roos, 1977; Kimura et al. 1981; Kurobane et al. 1989; Kornsakulkarn et al. 2011; Takemoto et al. 2014; Tadpetch et al. 2015; Kehelpannala et al. 2018; Choi et al. 2020; Maharjan et al. 2020). All exhibit the hallmark red pigmentation and are a result of the same heptaketide scaffold-compound from *PKS3*, but differentiates between the many *Fusarium* species due to the large genetic variation found within the *PKS3* gene-cluster (Harvey 2018; Kim 2019; Proctor 2007; Short et al. 2013).

In addition, members of the FSSC carry the *PKS35* gene cluster that is not present in other *Fusaria* (Coleman 2016). *PKS35* contribute to the red/orange pigmentation of perithecia in FSSC. This conclusion is based on the

fact that deletion of *pksN* in *N. pisi* (= *F. solani* f. *pisi*) (Graziani et al. 2004) and *PKS35* in *N. vasinfecta* (= *F. neocosmosporiellum*) (Kim 2019) resulted in albino perithecia. Five genes within the *PKS35* gene cluster have homologs in the *Penicillium herquei* gene cluster responsible for the formation of herqueinone (**141**) (Gao et al. 2017). Another homologous gene cluster, *pks23* from the lichen-forming *Endocarpon pusillum*, produces the herqueinone precursor prephenalenone when expressing the cluster in *Saccharomyces cerevisiae* (Harvey et al. 2018). Thus, herqueinone (**141**) or a closely reassembling molecule likely causes the red pigmentation in perithecia in members of the FSSC. The related NQ marticin (**144**) is an octaketide and produced by *Neocosmospora cucurbitae*, *N. martii*, *N. pisi* and *N. vasinfecta* (Pfiffner 1963; Ross 1977; Kurobane et al. 1980; Holenstein et al. 1983).

Quinone production in *Arthrinium*

The genus *Arthrinium* has been reported in various environments worldwide including terrestrial and marine ecosystems (Crous and Groenewald 2013; Heo et al. 2018). It exists as an endophyte in different plant (Sharma et al. 2014; Pansanit and Pripdeevech 2018; Astuti et al. 2021) and lichen species (Yunzhe 2012) but also as a plant pathogen (Martinez-Cano 1992; Mavragani et al. 2007). The literature contains several examples of cutaneous infections in humans caused by *A. phaeospermum* (Hoog et al. 2021; Rai 1989; Zhao, Deng, and Chen 1990) and food poisoning with fatal outcome caused by *A. saccharicola* (Birkelund et al. 2021). Furthermore, many natural products are produced by *Arthrinium* spp., which possess a variety of industrial and pharmacological applications (Tsukada et al. 2011; Bao et al. 2018).

The NQ bostrycin (**148**) was first isolated from *A. phaeospermum* in 1975 as a red pigment (van Eijk 1975) (Fig. 6). Morushita et al. (2019) proposed that bostrycin (**148**) is biosynthesized via emodin (**98**) through an *O*-methylation step and multiple steps of oxidation in *A. sacchari*. Emodin has also been extracted from a marine *Arthrinium* sp. along with endocrocin (**112**) and chrysophanol (**105**) (Elissawy et al. 2017).

A. saccharicola KUC21221 and *Arthrinium* sp. 10 KUC21332 are both marine *Arthrinium* spp., reported to produce gentisyl alcohol (**152**) (Heo et al. 2018), the quinol form of gentisylquinone (**62**). In addition, arthrinone (**149**) extracted from *Arthrinium* sp. FA 1744 (Qian-Cutrone et al. 1994) is structurally related to the quinone cerdarin (**150**) (Uchiyama et al 2000).

Three genome sequences from the *Arthrinium* genus are available in NCBI: *A. phaeospermum* (ASM650353v1) (Li et al. 2020), *A. malaysianum* (ASM650811v1), and *Arthrinium* sp. KUC21332. (ASM1716395v1) (Heo et al. 2018). Four, six, and ten gene clusters containing NR-PKSs were found in *A. phaeospermum*, *A. malaysianum*, and *Arthrinium* sp. KUC21332, respectively, when analyzed by antiSMASH. These might potentially encode different kinds of known or novel quinones. For example, the gene cluster encoding 1,3,6,8-tetrahydroxynaphthalene (**153**) was found in all three genomes and the compound can be converted to the NQ flaviolin (**151**) by a monooxygenation step (Funa et al. 2005). Even though the *Arthrinium* genus is less studied compared to other filamentous fungi, it definitely has a vast biosynthetic potential for secondary metabolites including quinones.

Quinone production in *Alternaria* and other dematiaceous fungi
Alternaria (incl. *Ulocladium*), *Cercospora*, *Nigrospora*, *Stemphylium*, *Phoma* and similar common genera
produce a large number of quinones, including altersolanols (**154**), dothistromin (**155**), alterporriols (**156**),
astropaquinone (**157**), macrosporin (**158**), lentiquinone A, nigrisporin, neoanthraquinone, phomarin,
stemphylin, cercosporins and many other AQs and NQs (Fig. 6) (Turner, 1971; Turner and Aldridge, 1983;
Dalinova et al. 2020; Xu et al. 2021). Some of them are toxic to both animals and plants, but are in some
cases interesting candidates for production of biotechnologically relevant secondary metabolites.

Widely observed quinones

While many quinones appear to be uniquely associated with a certain species or section, some appear across
many. A well studied example is emodin (**98**), which is produced cross-kingdom in both fungi and plants. In a
review, Izhaki (2002) argues that the reason this quinone is observed broadly in plants is because it is
multifunctional. It provides the plant with several benefits such as antipredation towards both vertebrates
and invertebrates, inhibition of growth of competing plants, decreasing the availability of certain nutrients in
soil, broad antimicrobial effects and protection from free radicals due to UV exposure. It is likely that a
metabolite with such varied functionality would be beneficial across kingdoms. It is also interesting to note
that the many derivatives of emodin (**98**) are often observed together with the AQ (Table 2, 3 and 4), similarly
to what is observed in plants (Izhaki 2002).

While emodin (**98**) is a purposeful metabolite, it is also an intermediate of a host of other metabolites. In
fungi, it is associated with the production of secalonic acid A, geodin and tryptacidin to name a few (Frisvad
and Larsen 2015). In this review, we have also reported that emodin-like AQs can be dimerized by certain
fungi, like the ether bond linking the two monomers of the *O*-biemodins observed in *Aspergillus* section
Nidulantes and the C-C bonds observed in the biemodins of *Talaromyces*. All of this reinforces the notion that
the emodins are very purposeful metabolites, both by themselves and as intermediates, thereby having many
functions in the producing organism.

Another often observed quinone structure is the NQ dimer xanthomegnin (**81**), which is present in both
Aspergillus, *Talaromyces* and *Penicillium* (Table 2, 3 and 4). Like the emodin family, xanthomegnin (**81**) is part
of a large biosynthetic family with NQ dimers such as viomellein (**83**), rubrosulphin (**84**) and viopurpurin (**85**).

Quinone methides

Quinone methides are analogous to quinones with the exception that one of the carbonyl groups have been
substituted with a methyldene group. Certain quinone methides may be useful for some of the applications
discussed in this review, however, for other applications, such as in quinone redox flow batteries, they might
be too reactive. For example hydroxycylavatul ortho-quinone methide from *Penicillium crustosum* is very
reactive (Fan et al., 2019) and other quinone methides, both in their citrinin para-quinone methide and
citrinin ortho-quinone methide forms, have also been reported to be very reactive and are furthermore
considered mycotoxins (Appell et al., 2021; Silva et al., 2021; Zhang et al., 2021). In the citrinin biosynthetic

pathway there are also traditional quinones present such as citrinin H1 (**34**) (Silva et al. 2021), but because of potential toxicity they might not be suited in many applications as well. Some other azaphilones may also possess quinone-like properties, potentially applicable to some or more of the applications mentioned in this review (Pavesi et al., 2021; Williams et al., 2021).

Production of fungal quinones

Because of their vast structural diversity and the many different examples of biological uses of quinones, it is reasonable to assume that they do not serve one unifying biological purpose. As a result, it is impossible to propose a fermentation strategy that favors general quinone production, and production parameters must be fine tuned based on the fungus and the quinone. A large difference between quinones is whether they are secreted into the environment or accumulated inside fungal structures. For example, phoenicin (**47**) is readily secreted, darkening the growth media (Reilly et al. 1940) while fusarubin (**143**) has been shown to accumulate intracellularly (Medentsev and Akimenko 1998, Short 2013). For most production purposes, it would be of most benefit if the target quinone was secreted. This potentially narrows down the choice of fungal hosts and quinones available for production.

If a biological purpose of a quinone is suspected, it can help guide the production optimization. For example if the quinone of interest is hypothesized to protect the organism against sunlight, using UV-light radiation might trigger production, as is the case with the AQ phycion (**102**) (Solhaug and Gauslaa 2004). Likewise, if the quinone is assumed to have allelochemical action, co-cultivating the fungus with another organism can trigger quinone production (Khalid and Keller 2021). For example, exposing *Fusarium fujikuroi* to ralsolamycin, produced by the bacterium *Ralstonia solanacearum* induced production of bikaverin (**146**), which is known to have antimicrobial effects (Deshmukh et al. 2014; Spraker et al. 2018).

Many quinones are intermediates or shunt products of a pathway producing non-quinones, e.g. the toluquinones (Frisvad et al. 2020). Thus, if production of one of these intermediary quinones is desired, the discovery of a strain which stops the pathway mid-way is of great benefit. Alternatively, one could try to delete later parts of the biosynthetic pathway by genetic engineering.

Even though a large number of fungi and plants can produce quinones, it is important that filamentous fungi, such as species of *Aspergillus*, *Penicillium*, *Talaromyces* and *Fusarium*, are often well suited for fermentation and these fungi have been used for production of secondary metabolites in numerous applications. The diversity of quinones in those genera shows that a number of species are potential candidates for production of large amounts of quinones. Several quinones from these genera are secreted, but those that are cell-wall bound may be produced heterologously, if a suitable host is used and manipulated to secrete such quinones. For many quinone applications, such as as electrolytes in batteries, bulk production is necessary, and some species of the large genera mentioned above have been shown to be efficient producers of large amounts of at least some secondary metabolites. Optimization of secondary metabolite biosynthesis in the fungi, of fungal growth media and of physiological and technical fermentation conditions will probably allow bulk production, especially in *Aspergillus*, *Penicillium*, *Talaromyces* and *Fusarium*. (van der Beek and Roels 1984; Barrios-González and Miranda 2010; Zhai et al. 2016).

Author contributions

JVC planned the review with JCF, TOL and TI, wrote a major part of the text, and corrected and added to the tables and prepared some of the figures. JCF made the tables, and wrote parts of the text. TI wrote a major part of text on chemistry of the quinones and made a major part of the figures, TOL added to the text throughout the manuscript. JLS, TBP and MRN wrote a major part of the *Fusarium* part and added to the remaining text. TES and CP wrote the *Arthrinium* text and added to the remaining text. All authors read and approved the manuscript.

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Data availability statement

All data analysed during this study is included in this published article.

Software used for making the figures

Fig. 1 was created with a combination of Inkscape and ChemDraw Professional. Fig. 2, Fig. 3, Fig. 4, Fig. 5 and Fig. 7 were created with ChemDraw Professional. Fig. 6 was created with Python 3.

References:

- Abdel-Aziz MS, Ghareep MA, Saad AM, Refahy LA, Hamed AA (2018) Chromatographic isolation and structure elucidation of secondary metabolites from soil-inhabiting fungus *Aspergillus fumigatus* 3T-EGY. *Acta Chromatographica* 30: 243-249.
- Abdelwahab MF, Fouad MA, Mamel MS, Özkaya FC, Kalscheur R, Müller WEG, Lin W, Liu Z, Ebrahim W, Daletos G, Proksch P (2018) Tanzawaic acid derivatives from freshwater sediment-derived fungus *Penicillium* sp. *Fitoterapia* 128: 258-264.
- Ali T, Inagaki M, Chai H-B, Wieboldt T, Rapplye C, Rakotondraibe LH (2017) Halogenated compounds from directed fermentation of *Penicillium concentricum*, an endophytic fungus of the liverwort *Trichocolea tomentella*. *J Nat Prod* 80: 1397-1403.

- 1 Aly AH, Debbab A, Clements C, Edrade-Ebel R, Orlikova B, Diederich M, Wray V, Lin WH, Proksch P (2011) NF
2 kappa B inhibitors and antitrypanosomal metabolites from the endophytic fungus *Penicillium* sp. Isolated
3 from *Limonium tubiflorum*. Bioorg Chem Med 19: 411-421.
- 4 Anslow WK, Raistrick H. 1938. Studies in the biochemistry of microorganisms LVII. Fumigatin (3-hydroxy-4-
5 methoxy-2:5-toluquinone) and spinulosin (3:6-dihydroxy-4-methoxy-2:5-toluquinone), metabolic products
6 respectively of *Aspergillus fumigatus* Fresenius and *Penicillium spinulosum* Thom. Biochem J 32: 687-696.
- 7 Appell M, Moravec D, Bosma WB (2021) Quantum chemical study of the structure and properties of citrinin.
8 Mol Simul 38: 284-292.
- 9 Arai K, Matsuda K, Kiriya N, Nitta K, Yamamoto Y, Shimizu S (1981) Metabolites of *Aspergillus terreus*. IV.
10 Metabolites of the strain IFO 8835 (2). The isolation and structure of indolyl benzoquinone pigments. Chem
11 Pharm Bull 29: 961-969.
- 12 Arai K, Shimizu S, Taguchi Y, Yamamoto Y (1981) Metabolic products of *Aspergillus terreus*. IV. Demethylation
13 of asterriquinones. Chem Pharm Bull 29: 991-999.
- 14 Arnstein HRV, Cook AH (1947) Production of antibiotics by fungi. 3. Javanicin – an antibacterial pigment from
15 *Fusarium javanicum*. J Chem Soc 1947: 1021-1028.
- 16 Arsenault GP (1968). Fungal metabolites. III. Quinones from *Fusarium solani* D2 purple and structure of (+)-
17 solaniol. Tetrahedron 24: 4745-4749.
- 18 Arzanlou M, Samadi, R, Frisvad, JC, Houbraken J, Ghosta Y (2016) Two novel *Aspergillus* species from
19 hypersaline soils of the national park of Lake Urmia, Iran. Myc Prog 15: 1081-1092.
- 20 Ashley JN, Hobbs BC, Raistrick H (1937) Studies in the biochemistry of micro-organisms. LII. The crystalline
21 colouring matter of *Fusarium culmorum* (W.G. Smith) Sacc. and related forms. Biochem J 31: 385-397.
- 22 Astuti P, Pratoko OK, Rollando R, Hertiani T, Wahyuono S, Narrochimad A (2021) Bioactivities of a major
23 compound from *Arthrimum rasikravindraae*, an endophytic fungus of *Coleus amboinicus* Lour. Fabad J Pharm
24 Sci 46: 23-30.
- 25 Awakawa T, Kaji T, Wakimoto T, Abe I (2012) A heptaketide naphthaldehyde produced by a polyketide
26 synthase from *Nectria haematococca*. Bioorg Chem Med Lett 22: 4338-4340.
- 27 Awakawa T, Yokota K, Funa N, Doi F, Mori N, Watanabe H, Horinouchi S (2009) Physically discrete beta-
28 lactamase-type thioesterase catalyzes product release in atrochrysone synthesis by iterative type I polyketide
29 synthase. Chem Biol 16: 613-623.
- 30 Baker PM; Roberts JC (1966) Studies in mycological chemistry. Part XXI. The structure of aurofusarin, a
31 metabolite of some *Fusarium* species. J Chem Soc C 1966: 2234–2237.
- 32 Balajee SA, Baddley JW, Peterson SW, Nickle D, Varga J, Boey A, Lass-Flörl C, Frisvad JC, Samson RA, and the
33 ISHAM Working group on *A. terreus* (2009) *Aspergillus alabamensis*, a new clinically relevant species in the
34 section *Terrei*. Eukaryot Cell 8: 713-722.

- 1 Balan J, Fuska J, Kuhr I, Kuhrová V (1970) Bikaverin, an antibiotic from *Gibberella fujikuroi*, effective against
2 *Leishmania brasiliensis*. Folia Microbiol 15: 479-484.
- 3 Baldrian P, Valášková V (2008) Degradation of cellulose by basidiomyceteous fungi. FEMS Microbiol Rev 32:
4 501-521.
- 5 Balibar CJ, Howard-Jones AR, Walsh CT (2007) Terrequinone A biosynthesis through L-tryptophan oxidation,
6 dimerization and bisprenylation. Nat Chem Biol 3:584–592.
- 7 Bara R, Zerfass I, Aly AH, Goldbach-Gecke H, Raghavan V, Sass P, Mándi A, Wray V, Polavarapu PL, Pretsch A,
8 Lin W, Kurtán T, Debbab A, Brötz-Oesterhelt H, Proksch P (2013) Atropisomeric dihydroanthracenones as
9 inhibitors of multiresistant *Staphylococcus aureus*. J Med Chem 56:3257–3272.
- 10 Bao J, He F, Yu J-H, Zhai H-J, Cheng Z-Q, Jiang C-S, Zhang Y-Y, Zhang Y, Zhang X-Y, Chen G-Y, Zhang H (2018)
11 New chromones from a marine-derived fungus, *Arthrimum* sp., and their biological activity. Molecules 23:
12 1982.
- 13 Bao J, Zhang XY, Dong JJ, Xu XY, Nong XH, Qi SH (2014) Cyclopentane-condensed chromones from marine-
14 derived fungus *Penicillium oxalicum*. Chem Lett 43: 837-839.
- 15 Barrett K, Jensen K, Meyer AS, Frisvad JC, Lange L (2020) Fungal secretome profile categorization of CAZymes
16 by function and family corresponds to the taxonomy and phylogeny of fungi: Example *Aspergillus* and
17 *Penicillium*. Sci Rep 10: 5158.
- 18 Barrios-González J, Miranda RU (2010) Biotechnological production and applications of statins. Appl Microbiol
19 Biotechnol 85:869–883.
- 20 Barros Correia ACR, Barbosa R, Frisvad JC, Houbraken J, Souza-Motta CM (2020) The polyphasic re-
21 identification of a Brazilian *Aspergillus* section *Terrei* collection led to the discovery of two new species. Myc
22 Progr 19: 885-903.
- 23 Bell AA, Wheeler MH (1986) Biosynthesis and function of fungal melanins. Ann Rev Phytopathol 24: 411-451.
- 24 Berry S (2002) The chemical basis of membrane bioenergetics. J Mol Evol 54: 595-613.
- 25 Birch AJ, Massy-Westropp RA. 1957. Studies in relation to biosynthesis. II. The structure of nalgiovensin. J
26 Chem Soc 1957: 2215-2217.
- 27 Birch AJ, Stapleford KSJ (1967) Structure of nalgiolaxin. J Chem Soc 1967: 2570-2571.
- 28 Birkelund T, Johansen RF, Illum DG, Dyrskog SE, Østergaard JA, Falconer TM, Andersen C, Fridholm H,
29 Overballe-Petersen S, Jensen JS (2021) Fatal 3-nitropropionic acid poisoning after consuming coconut ewater.
30 Emer Infect Dis 27: 278-280.
- 31 Blachowicz A, Nicholas R, Bok JW, Choera T, Knox B, Lim FY, Huttenlocher A, Wang CCC, Venkateswaran K,
32 Keller NP (2020) Contribution of spores secondary metabolites to UV-C protection and virulence vary in
33 different isolates of *Aspergillus fumigatus* strains. Mbio 11: e03415-19.

- 1 Breen J, Dacre JC, Raistrick H, Smith G (1955) Studies in the biochemistry of microorganisms. 95. Rugulosin, a
2 crystalline colouring matter of *Penicillium rugulosum* Thom. Biochem J 60: 618-626.
- 3 Brown DW, Butchko RAE, Baker BE, Proctor RH (2012a) Phylogenomic and functional domain analysis of
4 polyketide synthases in *Fusarium*. Fung Biol 116: 318-331.
- 5 Brown DW, Butchko RAE, Busman M, Proctor RH (2012b) Identification of gene clusters associated with
6 fusaric acid, fusarin, and perithecial pigment produced by *Fusarium verticillioides*. Fung Genet Biol 49: 521-
7 532.
- 8 Brown DW, Proctor RH (2016) Insights into natural products biosynthesis from analysis of 490 polyketide
9 synthases from *Fusarium*. Fung Genet Biol 89: 37-51.
- 10 Bugni TS, Abbanat D, Brnan VS, Maiese WM, Greenstain M, von Wagoner RM, Ireland CM (2000) Yanuthones:
11 novel inhibitors from a marine isolate of *Aspergillus niger*. J Org Chem 65: 7195-7200.
- 12 Burton HS (1949) Antibiotics from Penicillia. Brit J Exptl Pathol 30: 151-158.
- 13 Butler MJ, Gardiner RB, Day AW (2009) Melanin synthesis by *Sclerotinia sclerotiorum*. Mycologia 101:296–
14 304.
- 15 Caceres I, Khoury A Al, El Khoury R, Lorber S, Oswald IP, El Khoury A, Atoui A, Puel O, Bailly JD (2020) Aflatoxin
16 biosynthesis and genetic regulation: A review. Toxins 12: 150.
- 17 Carlton WW, Tuite J, Caldwell R (1973) *Penicillium viridicatum* toxins and mold nephrosis. J Am Vet Med
18 Assoc 163: 1295-1297.
- 19 Carlton WW, Stack ME, Eppley RM (1976) Hepatic alterations produced in mice by xanthomegnin and
20 viomellein, metabolites of *Penicillium viridicatum*. Toxicol Appl Pharmacol 38: 455-459.
- 21 Chabra A, Rahimi-Esboei B, Habibi E, Monadi T, Azadbakht M, Elmi T, Valian HK, Akhbari T, Fakhar M,
22 Naghshvar F. 2019. Effects of some natural products from fungal and herbal sources on *Giardia lamblia* in
23 vivo. Parasitol 146: 1188-1198.
- 24 Chagas FO, Dias LG, Pupo MT (2016) New perylenequinone derivatives from the endophytic fungus *Alternaria*
25 *tenuissima* SS77. Tetrahedron Lett 57:3185–3189.
- 26 Chang J-M, Oyaizu H, Sugiyama J (1991) Phylogenetic relationships among 11 selected species of *Aspergillus*
27 and selected teleomorph genera estimated from 18S ribosomal RNA partial sequences. J Gen Appl Microbiol
28 37: 289-308.
- 29 Chang P-K, Cary JW, Lebar MD (2020) Biosynthesis of conidial and sclerotial pigments in *Aspergillus* species.
30 Appl Microbiol Biotechnol 104: 2277-2286.
- 31 Chang P-K, Scharfenstein LL, Mack B, Wei Q, Gilbert M, Labar M, Cary JW (2019) Identification of a copper-
32 transporting ATPase involved in the biosynthesis conidial pigments in *Aspergillus flavus*. Appl Microbiol
33 Biotechnol 103: 4889-4897.

- 1 Chao PD, Schiff PL, Slatkin D, Knapp JE (1979) Metabolites as aspergilli. 4. New naphthalenones and 6-ethyl-7-
2 methoxyjuglone from *Aspergillus parvulus*. J Chem Res S 1979: 236.
- 3 Chen AJ, Varga J, Frisvad JC, Jiang XZ, Samson RA (2016a) Polyphasic taxonomy of *Aspergillus* section *Cervini*.
4 Stud Mycol 85: 65-89.
- 5 Chen AJ, Frisvad JC, Sun BD, Varga J, Kocsubé S, Dijksterhuis J, Kim DH, Hong SB, Houbraken J and Samson RA
6 (2016b) *Aspergillus* section *Nidulantes* (formerly *Emericella*). Polyphasic taxonomy, chemistry and biology.
7 Stud Mycol 84: 1-118.
- 8 Chen AJ, Sun BD, Houbraken J, Frisvad JC, Yilmaz N, Zhou YG, Samson RA (2016c) New *Talaromyces* species
9 from indoor environments in China. Stud Mycol 84: 119-144.
- 10 Chen AJ, Hubka V, Frisvad JC, Visagie CM, Houbraken J, Meijer M, Varga J, Rasine D, Jurjević Ž, Kubátová A,
11 Sklenář F, Samson RA (2017) Polyphasic taxonomy of *Aspergillus* section *Aspergillus* (formerly *Eurotium*) and
12 its occurrence in indoor environment and food. Stud Mycol 88: 37-135.
- 13 Chen L, Zhang WW, Zheng Q-H, Liu QY, Zheng P, Hu X, Fang ZX, Zhang QQ (2013) Aculeatusquinones A-D,
14 novel metabolites from the marine-derived fungus *Aspergillus aculeatus*. Heterocycles 87: 861-868.
- 15 Chen M, Shao CL, Kong CJ, She ZG, Wang CY (2014) A new anthraquinone derivative from a gorgonian-
16 derieved fungus *Aspergillus* sp. Chem Nat Comp 50: 67-620.
- 17 Cheng Z, Xu W, Liu LJ, Li SM, Yaun MJ, Luo ZH, Zhang JJ, Cheng YJ, Li Q (2018) Penigingensins B-E, new
18 farnesylcyclohexanones from the deep sea-derived fungus *Penicillium* sp YPGA11. Mar Drugs 16: 358.
- 19 Chiang Y-M, Szewczyk E, Davidson AD, Entwistle R, Keller NP, Wang CCC, Oakley BR (2010) Characterization of
20 the *Aspergillus nidulans* monodictyphenone gene cluster. Appl Environ Microbiol 76: 2067-2074.
- 21 Choi HG, Song JH, Park M, Kim S, Kim CE, Kang KS, Shim SH (2020) Neuroprotective gamma-pyrones from
22 *Fusarium solani* JS-0169: Cell-based identification of active compounds and an informatics approach to
23 predict the mechanim of action. Biomolecules 10: 91.
- 24 Christensen M, Frisvad JC, Tuthill DE (1998) Taxonomy of the *Penicillium miczynskii* group based on
25 morphology and secondary metabolites. Mycol Res 103: 527-541.
- 26 Coleman JJ (2016) The *Fusarium solani* species complex: ubiquitous pathogens of agricultural importance.
27 Mol Plant Pathol 17: 146-158.
- 28 Collin G, Höke H, Greim H (2003) Naphthalene and hydronaphthalenes. In Ullmann's Encyclopedia of
29 Industrial Chemistry 23. Wiley-VCH Verlag, Weinheim, pp 661-670.
- 30 Cornforth JW, Ryback G, Robinson PM, Park D (1971) Isolation and characterization of a fungal vacuolation
31 factor (bikaverin). J Chem Soc C: 1971: 2786-2788.
- 32 Crous PW, Groenewald JZ (2013) A phylogenetic re-evaluation of *Arthrinium*. IMA Fungus 4: 133-154.

- 1 Crous PW, Lombard L, Sandoval-Denis M, Seifert KA, Schroers H-J, Chaverri P, Gené J, Guarro J, Hirooka Y,
2 Bensch K, Kema GHJ, Lamprecht SC, Cai L, Rossman AY, Stadler M, Summerbell RC, Taylor JW, Ploch S, Visagie
3 CM, Yilmaz N, Frisvad JC, Abdel-Azeem AM, Abdollahzadeh J, Abdolrasouli A, Akulov A, Alberts JF, Araújo
4 JPM, Ariyawansa HA, Bakhshi M, Bendiksby M, Amor ABH, Bezerra JDP, Boekhout T, Câmara MPS, Carbia M,
5 Cardinali G, Castañeda-Ruiz RF, Celis A, Chaturvedi V, Collemare J, Croll D, Damm U, Decock CA, Vries RP de,
6 Ezekiel CN, Fan XL, Fernández NB, Gaya E, González CD, Gramaje D, Groenewald JZ, Grube M, Guevara-Suarez
7 M, Gupta VK, Guarnaccia V, Haddaji A, Hagen F, Hansen K, Hashimoto A, Haelewaters D, Hernández-Restrepo
8 M, Houbraken J, Hubk V, Hyde KD, Iturriaga T, Jeewon R, Johnston PR, Jurjević Ž, Karalti İ, Korsten L, Kuramae
9 EE, Kušan I, Labuda R, Lawrence DP, Lee HB, Lechat CLL, Li HY, Litovka YA, Maharachchikumbura SSN, Marin-
10 Felix Y, Kemkuignou BM, Matočec N, McTaggart AR, Mičoch P, Mugnai L, Nakashima C, Nilsson RH, Noumeur
11 SR, Pavlov IN, Peralta MP, Phillips AJL, Pitt JI, Polizzi G, Quaedvlieg W, Rajeshkumar KC, Restrepo S, Rhaïem A,
12 Robert J, Robert V, Rodrigues AM, Salgado-Salazar C, Samson RA, Santos ACS, Shivas RG, Souza-Motta CM,
13 Sun GY, Swart WJ, Szoke S, Tan YP, Taylor JE, Taylor PWJ, Tiago PV, Váczy KZ, van de Wiele N, van der Merwe
14 NA, Verkley GJM, Vieira WAS, Vizzini A, Weir BS, Wijayawardene NN, Xia JW, Yañez-Morales MJ, Yurkov A,
15 Zamora JC, Zare R, Zhang CL, Thines M (2021) *Fusarium*: more than a node or a foot-shaped basal cell. *Stud*
16 *Mycol* 98: 110116.
- 17 Curtin T, Fitzgerald G, Reilly J (1940) Production of phenicine on synthetic media - 1. *Penicillium phoenicum*
18 van Beyma - 2. *Penicillium rubrum* Grassberger Stoll. *Biochem J* 34: 1605-1610.
- 19 Czarnota MA, Paul RN, Dayan FE, Nimbal CI, Weston LA (2001) Mode of action, localization of production,
20 chemical nature and activity of sorgoleone: A potent PSII inhibitor in *Sorghum* spp. root exudates. *Weed*
21 *technol* 15: 813-825.
- 22 Da Costa Souza PN, Bim Grigoletto TL, Beraldo de Moraes LA, Abreau LM, Guimuraes LHS, Santos C, Galvao
23 LR, Cardoso PG (2016) Production and chemical characterization of pigments in fungi. *Microbiology (SGM)*
24 162: 12-22.
- 25 Dalonova AA, Salomova DR, Berestetskii AO (2020) Fungi of genera *Alternaria* as producers of biologically
26 active compounds and mycoherbicides. *Appl Biochem Microbiol* 56: 256-272.
- 27 Daub ME, Herrero S, Chung K-R (2013) Reactive oxygen species in plant pathogenesis: the role of
28 perylenequinone photosensitizers, *Antiox Redox Signal* 19: 970-989.
- 29 Hoog GS, Guarro J, Gené J, Ahmed SA, Al-Hatmi AMS, Figueras MJ, Vitale RG (2021) Atlas of clinical fungi 4th
30 ed. Westerdijk Fungal Biodiversity Institute, Utrecht.
- 31 Del Valle P, Martínez A-L, Figuera M, Raja HA, Mata R (2016) Alkaloids from the fungus *Penicillium*
32 *spatulatum* as α -glucosidase inhibitors. *Planta Med* 82: 1289-1294.
- 33 Deshmukh R, Mathew A, Purohit HJ (2014) Characterization of antibacterial activity of bikaverin from
34 *Fusarium* sp. HKF15. *J Biosci Bioeng* 117:443–448.

- 1 Diwu ZJ, Lown JW (1994) Photosensitization with anticancer agents 19 – EPR studies of photodynamic action
2 of calphostin C: Formation of semiquinones radical and activated oxygen on illumination with visible light.
3 Free Rad Bio Med 16: 645-652.
- 4 Diwu ZJJ, Haugland RP, Liu JX, Lown JW, Miller GG, Moore KB, Brown K, Tulip J, McPhee MS (1996)
5 Photosensitization by anticancer agents 21: New perylene- and aminonaphthoquinones. Free Rad Biol Med
6 20: 589-593.
- 7 Donner CD (2015) Naphthopyranones – isolation, bioactivity, biosynthesis and synthesis. Nat Prod Rep 32:
8 578-604.
- 9 Drewes SE, Khan F, Vuuren SF, Viljoen AM (2005) Simple 1,4-benzoquinones with antibacterial activity from
10 stems and leaves of *Gunnera perpensa*. Phytochem 66: 1812–1816.
- 11 Du F-Y, Li X-M, Somng J-Y, Li CS, Wang B-G (2014) Anthraquinone derivatives and an orsellinic acid ester from
12 the marine alga-derived endophytic fungus *Eurotium cristatum* EN-220. Helv Chim Acta 97: 973-978.
- 13 Du L, Zhu T-J, Fang Y-C, Liu H-B, Gu Q-Q, Zhu W-M (2007) Aspergiolide A, a novel anrhtaquinone derivative
14 with naphtho[1,2,3-de]chromene-2,7-dione skeleton isolated from a marine-derived fungus *Aspergillus*
15 *glaucus*. Tetrahedron 63: 1085-1088.
- 16 Dufossé, L, Galaup P, Yaron A, Arad SM (2005) Microorganisms and microalgae as sources of pigments for
17 food use: A scientific oddity or an industrial reality? Trends Food Sci Technol 16: 389–406.
- 18 Dufossé L, Fouillaud M, Caro Y, Mapari SAS, Sutthiwong N (2014) Filamentous fungi are large-scale producers
19 of pigments and colorants for the food industry, Curr Op Biotechnol, 26: 56–61.
- 20 Dufossé L (2018) Red colourants from filamentous fungi: Are they ready for the food industry?, J Food Comp
21 Anal 69:156–161.
- 22 Durley RC, MacMillan J, Simpson TJ, Glen AT, Turner WB (1975) Fungal products. Part XIII. Xanthomegnin,
23 viomellin, rubrosulphin, and viopurpurin, pigments from *Aspergillus sulphureus* and *Aspergillus melleus*. J
24 Chem Soc Perkin Trans 1 1975: 163-169.
- 25 Dvorska JE, Surai PF, Speake BK, Sparks NHC (2001) Effect of the mycotoxin aurofusarin on the antioxidant
26 composition and fatty acid profile of quail eggs. Br J Poult Sci 42: 643-649.
- 27 Edwards J, Auer D, de Alwis S-K, Summerell B, Aoki T, Proctor RH, Busman M, O'Donnell K (2016) *Fusarium*
28 *agapanthi* sp nov, a novel bikaverin and fusarubin-producing leaf and stem-rot pathogen of *Agapanthus*
29 *praecox* (African lily) from Australia and Italy. Mycologia 108: 981-992.
- 30 Elbanna AH, Khalil ZG, Bernhardt PV, Capon RJ (2021) Neobulgarones revisited: Anti and syn-bianthrone
31 from an Australian mud dauber wasp nest-associated fungus *Penicillium* sp. CMB-MD22. J Nat Prod 84: 762-
32 770.

- 1 Elissawy AM, Ebada SS, Ashour ML, Özkaya FC, Ebrahim W, Singab ANB, Proksch P (2017) Spiroarthrinols A
2 and B, two novel meroterpenoids isolated from the sponge-derived fungus *Arthrimum* sp. *Phytochem Lett* 20:
3 246-251.
- 4 El-Najjar N, Gali-Muhtasib H, Ketola RA, Vuorela P, Urtti A, Vuorela H (2011) The chemical and biological
5 activities of quinones: overview and implications in analytical detection. *Phytochem Rev* 10: 353–370.
- 6 Fan Y, Keyhani O, Tang GR, Pei Y, Zhang WW, Tong S (2017) Regulatory cascade and biological activity of
7 *Beauveria bassiana* oosporein that limits bacterial growth after host death. *Proc Natl Acad Sci USA* 114:
8 E1578–E1586.
- 9 Fan J, Liao G, Kindunger F, Ludwig-Radtke L, Yin W-B, Li S-M (2019) Peniphenone and penilactone formation
10 in *Penicillium crustosum* via 1,4-Michael additions of ortho-quinone methide from hydroxyclovatol to γ -
11 butyrolactones from crustosic acid. *J Amer Chem Soc* 141: 4225-4229.
- 12 Fang Y, Deng Y, Dehaen W (2020) Tailoring pillararene-based receptors for specific metal ion binding: From
13 recognition to supramolecular assembly. *Coord Chem Rev* 415: 213313.
- 14 Feng P, Shang Y, Cen K, Wang C (2015) Fungal biosynthesis of the bibenzoquinone oosporein to evade insect
15 immunity. *Proc Natl Acad Sci USA* 112: 11365-11370.
- 16 Feng S, Wang W (2020) Bioactivities and structure-activity relationships of natural tetrahydroanthraquinone
17 compounds: A review. *Front Pharmacol* 11: 299.
- 18 Frandsen RJN, Nielsen NJ, Maolanon, Sorensen JC, Olsson S, Nielsen J, Giese H (2006) The biosynthetic
19 pathway for aurofusarin in *Fusarium graminearum* reveals a close link between the naphthoquinones and
20 naphthopyrones. *Mol Biol* 61: 1069-1080.
- 21 Frandsen RJN, Rasmussen SA, Knudsen PB, Uhlig S, Petersen D, Lysøe E, Gotfredsen CH, Giese H, Larsen TO
22 (2016) Black perithecial pigmentation in *Fusarium* species is due to accumulation of 5-deoxybostrycoidin-
23 based melanin. *Sci Rep* 6: 26206.
- 24 Frandsen RJN, Schutt C, Lund BW, Staerk D, Nielsen J, Olsson S, Giese H (2011) Two novel classes of enzymes
25 are required for the biosynthesis of aurofusarin in *Fusarium graminearum*. *J Biol Chem* 286: 10419-10428.
- 26 Friedheim EAH (1938) Research of inferior fungi. I. Isolation of the red pigment of *Penicillium phoeniceum*
27 (phoenicine). *Helv Chim Acta* 21: 1464-1465.
- 28 Frisvad JC (2015) Taxonomy, chemodiversity, and chemoconsistency of *Aspergillus*, *Penicillium*, and
29 *Talaromyces* species. *Front Microbiol* 5: 773.
- 30 Frisvad JC (2018) A critical review of producers of small lactone mycotoxins: patulin, penicillic acid and
31 moniliformin. *World Mycotox J* 11: 73-100.
- 32 Frisvad JC, Filtenborg O (1990) Revision of *Penicillium* subgenus *Furcatum* based on secondary metabolites
33 and conventional characters. In: Samson RA, Pitt JI (eds): *Modern concepts in Penicillium and Aspergillus*
34 classification. Plenum Press, New York, pp 159-170.

- 1 Frisvad JC, Samson RA (2004) Polyphasic taxonomy of *Penicillium* subgenus *Penicillium*. A guide to
2 identification of the food and air-borne terverticillate *Penicillia* and their mycotoxins. *Stud Mycol* 49: 1-173.
- 3 Frisvad JC, Larsen TO (2015) Chemodiversity in the genus *Aspergillus*. *Appl Microbiol Biotechnol* 99: 7859-
4 7877.
- 5 Frisvad JC, Larsen TO (2016) Extrolites of *Aspergillus fumigatus* and other pathogenic species in *Aspergillus*
6 section *Fumigati*. *Front Microbiol* 6: 1485.
- 7 Frisvad JC, Filtenborg O, Samson RA, Stolk AC (1990) Chemotaxonomy of the genus *Talaromyces*. *Antonie van*
8 *Leeuwenhoek* 57: 179-189.
- 9 Frisvad JC, Frank JM, Houbraken JAMP, Kuijpers AFA, Samson RA (2004a) New ochratoxin producing species
10 of *Aspergillus* section *Circumdati*. *Stud Mycol* 50: 23-43.
- 11 Frisvad JC, Isbrandt T, Larsen TO (2020) Fungal partially reducing polyketides and related natural products
12 from *Aspergillus*, *Penicillium*, and *Talaromyces*. In *Comprehensive Natural Products III: Chemistry and Biology*.
13 Reference Module in Chemistry, Molecular Sciences and Engineering 3rd ed., H-W Liu, T Begley (eds), CH
14 14731, Elsevier, Amsterdam, pp 313-332.
- 15 Frisvad JC, Rank C, Nielsen KF, Larsen TO (2009) Metabolomics of *Aspergillus fumigatus*. *Med Mycol* 47: S53-
16 S71.
- 17 Frisvad JC, Seifert KA, Samson RA, Mills JT (1994) *Penicillium tricolor*, a new mold species from Canadian
18 wheat. *Can J Bot* 72: 933-939.
- 19 Frisvad JC, Hubka V, Ezekiel CN, Hong S-B, Nováková A, Chen AJ, Arzanlou M, Larsen TO, Sklenár F,
20 Mahakarnchanakul W, Samson RA, Houbraken J (2019) Taxonomy of *Aspergillus* section *Flavi* and their
21 production of aflatoxins, ochratoxins and other mycotoxins. *Stud Mycol* 93: 1-63.
- 22 Frisvad JC, Smedsgaard J, Larsen TO, Samson RA (2004b) Mycotoxins, drugs and other extrolites produced by
23 species in *Penicillium* subgenus *Penicillium*. *Stud Mycol* 49: 201-241.
- 24 Frisvad JC, Larsen TO, Dalsgaard PW, Seifert KA, Louis-Seize G, Lyhne EK, Jarvis BB, Fettingner JC, Overy DP
25 (2006) Four psychrotolerant species with high chemical diversity consistently producing cycloaspeptide A, *P.*
26 *jamesonlandense* sp. nov., *P. ribium* sp. nov., *P. soppii* and *P. lanosum*. *Int J Syst Evol Microbiol* 56: 1427-
27 1437.
- 28 Fuertges L, Obermaier L, Thiele W, Foegen S, Müller M (2019) Diversity in fungal intramolecular phenol
29 coupling of polyketides: Regioselective laccase-based systems. *ChemBioChem* 20: 1928-1932.
- 30 Fujimoto H, Nakamura E, Kim Y-P, Okuyama E, Ishibashi M, Sassa T (2001) Immunomodulatory constituents
31 of an ascomycete, *Eupenicillium crustaceum*, and revised structure of macrophorin D. *J Nat Prod* 64: 1234-
32 1237.
- 33 Fujimoto Y, Yokoyama E, Takahashi T, Uzawa J, Morroka N, Tsunoda H, Tatsuno T (1986) Studies on
34 metabolites of *Penicillium diversum* var. *aureum*.1. *Chem Pharm Bull* 34: 1497-1500.

- 1 Funa N, Funabashi M, Yoshimura E, Horinouchi S (2005) A novel quinone-forming monooxygenase family
2 involved in modification of aromatic polyketides. *J Biol Chem* 280: 14514-14523.
- 3 Fуска J, Proksa B, Fusková A (1975) New potential cytotoxic and antitumor substances. I. In vitro effect of
4 bikaverin and its derivatives on cells of certain tumors. *Neoplasma* 22: 335-338.
- 5 Fуска J, Proksa B, Uhrin D, Marvanova L, Sturdikova H (1991) Biosynthesis of dehydroaltenusin by
6 *Talaromyces flavus*. *Acta Biotechnol* 11: 73-76.
- 7 Futuro DO, Ferreira PG, Nicoletti CD, Borba-Santos LP, da Silva FC, Rozental SR, Ferreira VF (2018) The
8 antifungal activity of naphthoquinones: an integrative review. *An Acad Bras Ciênc* 90: 1187-1214.
- 9 Gao S-S, Garcia-Borras M, Barber JS, Hai Y, Duan A, Garg NK, Houk KN, Tang Y (2017) Enzyme catalyzed
10 intramolecular enantioselective hydroalkoxylation. *J Am Chem Soc* 139: 3639-3642.
- 11 García PA, Hernández ÁP, Feliciano AS, Castra MÁ (2018) Bioactive prenyl- and terphenyl-
12 quinones/hydroquinones of marine origins. *Mar Drugs* 16: 292.
- 13 Gauthier T, Duarte-Hospital C, Vignard J, Boutet-Robinet E, Sulyok M, Snini, SP, Alassane-Kpembi I, Lippi Y,
14 Puel S, Oswald IP, Puel O (2020) Versicolorin A, a precursor in aflatoxins biosynthesis, is a food contaminant
15 toxic for human intestinal cells. *Environ Int.* 137:105568.
- 16 Gautschi JT, Amagata T, Amagata FA, Valeriote SL, Mooberry SI, Crews P (2004) Expanding the strategies in
17 natural product studies of marine-derived fungi: a chemical investigation of *Penicillium* obtained from deep
18 water sediment. *J Nat Prod* 67: 362-367.
- 19 Gaya E, Fernández-Brime S, Vargas R, Lachlan RF, Gueidang C, Ramírez-Mejía M, Lutzoni F (2015) The
20 adaptive radiation of lichen-forming *Teloschistaceae* is associated with sunscreens pigments and a bark-to-
21 rock substrate shift. *Proc Natl Acad Sci USA*, 112: 11600–11605.
- 22 Geib E, Gressler M, Viedernikova I, Hillmann F, Jacobsen ID, Nietzsche S, Hertweck C, Brock M (2016) A non-
23 canonical melanin biosynthesis pathway protects *Aspergillus terreus* conidia from stress. *Cell Chem Biol* 23:
24 587-597
- 25 Geib E, Brock M (2017) Comment on: “Melanisation of *Aspergillus terreus* – is butyrolactone I involved in the
26 regulation of both DOPA and DHN types of pigments in submerged culture?” *Microorganisms* 5: 22”
27 *Microorganisms* 5: 34.
- 28 Geib E, Gressler M, Vieiernikova I, Hillman F, Jaconsen ID, Nietzsche S, Hertweck C, Brock M (2019) A non-
29 canonical melanin biosynthesis pathway protects *Aspergillus terreus* conidia from environmental stress. *Cell*
30 *Chem Biol* 23: 587-597.
- 31 Geiser DM, Al-Hatmi AMS, Aoki T, Arie T, Balmas V, Barnes I, Bergstrom GC, Bhattacharyya MK, Blomquist CL,
32 Bowden RL, Brankovics B, Brown DW, Burgess LW, Bushley K, Busman M, Cano-Lira JF, Carrillo JD, Chang H-X,
33 Chen C-Y, Chen W, Chilvers M, Chulze S, Coleman JJ, Cuomo CA, Beer ZW de, Hoog GS de, Castillo-Múnera J
34 Del, Ponte EM Del, Diéguez-Urbeondo J, Pietro A Di, Edel-Hermann V, Elmer WH, Epstein L, Eskalen A,

- 1 Esposto MC, Everts KL, Fernández-Pavía SP, Silva GF da, Foroud NA, Fourie G, Frandsen RJN, Freeman S,
2 Freitag M, Frenkel O, Fuller KK, Gagkaeva T, Gardiner DM, Glenn AE, Gold SE, Gordon TR, Gregory NF,
3 Gryzenhout M, Guarro J, Gugino BK, Gutierrez S, Hammond-Kosack KE, Harris LJ, Homa M, Hong C-F, Hornok
4 L, Huang J-W, Ilkit M, Jacobs A, Jacobs K, Jiang C, Jiménez-Gasco M del M, Kang S, Kasson MT, Kazan K,
5 Kennell JC, Kim H-S, Kistler HC, Kuldau GA, Kulik T, Kurzai O, Laraba I, Laurence MH, Lee T, Lee Y-W, Lee Y-H,
6 Leslie JF, Liew EY, Lofton LW, Logrieco AF, López-Berges MS, Luque AG, Lysøe E, Ma L-J, Marra RE, Martin
7 FN, May SR, McCormick SP, McGee C, Meis JF, Migheli Q, Nor NMIM, Monod M, Moretti A, Mostert D, Mulè
8 G, Munaut F, Munkvold GP, Nicholson P, Nucci M, O'Donnell K, Pasquali M, Pfenning LH, Prigitano A, Proctor
9 RH, Ranque S, Rehner SA, Rep M, Rodríguez-Alvarado G, Rose LJ, Roth MG, Ruiz-Roldán C, Saleh AA, Salleh B,
10 Sang H, Scandiani MM, Scauflaire J, III DGS, Short DPG, Šišić A, Smith JA, Smyth CW, Son H, Spahr E, Stajich JE,
11 Steenkamp E, Steinberg C, Subramaniam R, Suga H, Summerell BA, Susca A, Swett CL, Toomajian C, Torres-
12 Cruz TJ, Tortorano AM, Urban M, Vaillancourt LJ, Vallad GE, van der Lee TAJ, Vanderpool D, van Diepeningen
13 AD, Vaughan MM, Venter E, Vermeulen M, Verweij PE, Viljoen A, Waalwijk C, Wallace EC, Walther G, Wang J,
14 Ward TJ, Wickes BL, Wiederhold NP, Wingfield MJ, Wood AKM, Xu J-R, Yang X-B, Yli-Mattila T, Yun S-H,
15 Zakaria L, Zhang H, Zhang N, Zhang SX, Zhang X (2021) Phylogenomic analysis of a 55.1 kb 19-gene dataset
16 resolves a monophyletic *Fusarium* that includes the *Fusarium solani* Species complex. *Phytopathology*, in
17 press. <https://doi.org/10.1094/PHYTO-08-20-0330-LE>.
- 18 Graziani S, Pilar P, Daboussi M-J (2004) Bistability and hysteresis of the 'secteur' differentiation are controlled
19 by a two-gene locus in *Nectria haematococca*. *BMC Biology* 2: 18.
- 20 Gruber-Dorninger C, Novak B, Nagl V, Berthiller F (2017) Emerging mycotoxins: beyond traditionally
21 determined food contaminants. *J Agric Food Chem* 65: 7052-7070.
- 22 Guntern A, Ioset JR, Queiroz EF, Foggin CM, Hostettmann K (2001) Quinones from *Heliotropium ovalifolium*.
23 *Phytochem* 58:631–635.
- 24 Gupta A, Eral HB, Hatton TA, Doyle PS (2016) Nanoemulsions: Formation, properties and applications. *Soft*
25 *Matter* 12:2826–2841.
- 26 Gupta M, Majumder UK, Ray MR, Mukhopadhyay DK (1997) Inhibition of experimental murine tumors by
27 MT81, a new mycotoxin from *Penicillium nigricans*. *Neoplasma* 44: 329-333.
- 28 Gutarowska B, Skora J, Stephien L, Twaruček M, Blajet-Kosicka A, Otlewska A, Grajewski J (2014) Estimation
29 of fungal contamination and mycotoxin production at workplaces in composting plants, archives and
30 libraries. *World Mycotox J* 7: 345-355.
- 31 Hald B, Christensen DH, Krogh P (1983) On the mycotoxin viomellein in barley and the associated quinone-
32 producing *Penicillia*. *Appl Environ Microbiol* 46: 1311-1317.
- 33 Hallas-Møller M, Nielsen KF, Frisvad JC (2018) Secondary metabolite production by cereal-associated
34 penicillia during cultivation on cereal grains. *Appl Microbiol Biotechnol* 102: 8477-8491.

- 1 Hansen FT, Gardiner DM, Lysøe F, Fuertes PR, Tudzynski B, Wiemann P, Sondergaard TE, Giese H, Brodersen
2 DE, Sørensen JL (2015) An update to polyketide synthetases and non-ribosomal synthetase genes and
3 nomenclature in *Fusarium*. Fung Genet Biol 75: 20-29.
- 4 Harvey, CJB, Tang M, Schlecht U, Horecka J, Fischer CR, Lin HC, Li J, Naughton B, Cherry, J, Miranda M, Li YF,
5 Chu AM, Hennesy JR, Vandova GA, Inglis D, Aiyar RS, Steinmetz LM, Davis RN, Medema RH, Sattely E, Khosla
6 C, St Onge RP, Tang Y, Hillenmeyer ME (2018) HEx: A heterologous expression platform for the discovery of
7 fungal natural products. Science Adv 4: eaar5459.
- 8 Hasan HAH (1998) Studies on the toxigenic fungi in roasted foodstuffs (salted seed) and halotolerant activity
9 of emodin-producing *Aspergillus wentii*. Folia Microbiol 43: 383-391.
- 10 Hawas UW, Atef El-Beih A, El-Halawany AM (2013) Bioactive anthraquinones from the endophytic fungus
11 *Aspergillus versicolor* isolated from red sea algae. Arch Pharm Res 35: 1749-1756. (doi: 10.1007/s12272-012-
12 1006x)
- 13 Hayashi A, Fujioka S, Nukina M, Kawano T, Shimada A, Kimura Y (2007) Fumiquinones A and B, nematocidal
14 quinones produced by *Aspergillus fumigatus*. Biochem Biosci Biotechnol 71: 1697-1702.
- 15 Hawas UW, El-Halawany AM, Ahmed EF (2013) Hepatitis C virus NS3-NS4 protease inhibitors from the
16 endophytic *Penicillium chrysogenum* isolated from the red algae *Liagora viscida*. Z Naturforsch C68: 355-366.
- 17 He J, Roemer E, Lange C, Huang X, Maier A, Kelter G, Jiang Y, Xu LH, Menzel KD, Grabley S, Fiebig HH, Jiang CL,
18 Sattler I (2007) Structure, derivatization, and antitumor activity of new griseusins from *Nocardia* sp. J Med
19 Chem 50: 5168-5175.
- 20 He KY, Zhang C, Duan YR, Huang GL, Yang CY, Lu XR, Zheng CJ, Chen GY (2017) New chlorinated xanthone and
21 anthraquinone produced by a mangrove-derived fungus *Penicillium citrinum* HL-5126. J Antibiot 70:823-827.
- 22 Heathcote JG, Dutton MF (1969) New metabolites of *Aspergillus flavus*. Tetrahedron 25: 1497-1500.
- 23 Hejl AM, Einhellig FA, Rasmussen JA (1993) Effects of juglone on growth, photosynthesis and respiration. J
24 Chem Ecol 19: 559-568.
- 25 Heo YM, Kim K, Ryun SM, Kwon SL, Park MY, Kang JE, Homg JH, Lim YW, Kim C, Kim BS, Lee D, Kim JJ (2018)
26 Diversity and ecology of marine algicolous *Arthrionium* species as a source of bioactive natural products. Mar
27 Drugs 16: 508.
- 28 Hernández VA, Machuca Á, Saavedra I, Chavez D, Astuya A, Barriga C (2019) *Talaromyces australis* and
29 *Penicillium murcianum* pigment production in optimized liquid cultures and evaluation of their cytotoxicity in
30 textile applications. World J Microbiol Biotechnol 35:1–9.
- 31 Hind HG (1940) The constitution of carviolin: A new colouring matter of *Penicillium carmino-violaceum*
32 Biourge. Biochem J 34: 577-579.

- 1 Holenstein JE, Kern H, Stoessl A, Stothers JB (1983) The marticins: Evidence for a mixed origin from the
2 polyketide and tricarboxylic acid pathway by [2-¹³C₁] and [1,2-¹³C₂]-acetate incorporation experiment.
3 *Tetrahedron Lett* 24: 4059-4061.
- 4 Holm DK, Petersen LM, Klitgaard A, Knudsen PB, Jarzynska ZD, Nielsen KF, Gotfredsen CH, Larsen TO,
5 Mortensen UH (2014) Molecular and chemical characterization of the biosynthesis of the 6-MSA-derived
6 meroterpenoid yanuthone D in *Aspergillus niger*. *Chem Biol* 21: 519-529.
- 7 Houbraken J, Due M, Varga J, Meijer M, Frisvad JC and Samson RA (2007) Polyphasic taxonomy of *Aspergillus*
8 section *Usti*. *Stud Mycol* 59: 107-128.
- 9 Houbraken J, Frisvad JC, Samson RA (2010a) Taxonomy of *Penicillium citrinum* and related species. *Fungal*
10 *Diversity* 44: 117-133.
- 11 Houbraken J, Frisvad JC, Samson RA (2010b) Sex in *Penicillium* series *Roqueforti*. *IMA Fungus* 1: 171-180.
- 12 Houbraken J, Frisvad JC, Samson RA (2011) Taxonomy of *Penicillium* section *Citrina*. *Studies in Mycology* 70:
13 53-138.
- 14 Houbraken J, Visagie CM, Meijer M, Frisvad JC, Busby PE, Pitt JI, Seifert KA, Louis-Seize G, Demirel R, Yilmaz N,
15 Jacobs K, Christensen M, Samson RA (2014) A taxonomic and phylogenetic revision of *Penicillium* section
16 *Aspergilloides*. *Stud Mycol* 78: 373-451.
- 17 Houbraken J, Wang L, Lee HB, Frisvad JC (2016) New sections in *Penicillium* containing novel species
18 producing patulin, pyripyropens or other bioactive compounds. *Persoonia* 36: 299-314.
- 19 Houbraken J, Kocsubé S, Visagie CM, Yilmaz N, Wang X-C, Meijer M, Kraak B, Hubka V, Samson RA, Frisvad JC
20 (2020) Classification of *Aspergillus*, *Penicillium*, *Talaromyces* and related genera (*Eurotiales*), an overview of
21 families, genera, subgenera, sections, series and species. *Stud Mycol* 95: 5-169.
- 22 Howard BH, Raistrick H (1954) Studies in the biochemistry of microorganisms. 91. The colouring matters of
23 *Penicillium islandicum* Sopp. *Biochem J* 56; 56-65.
- 24 Huang Z, Nong X, Ren Z, Wang J, Zhang X, Qi S (2017) Anti-HSV-1, antioxidant and antifouling phenolic
25 compounds from the deep-sea-derived fungus *Aspergillus versicolor* SCSIO 41502. *Bioorg Med Chem Lett*
26 27:787–791.
- 27 Hubka V, Nováková A, Kolařík M, Jurjevic Ž, Peterson SW (2015) Revision of *Aspergillus* section *Flavipedes*:
28 seven new species and proposal of section *Jani* sect. nov. *Mycologia* 107: 169-208.
- 29 Hubka V, Nováková A, Samson RA, Houbraken J, Frisvad J.C., Sklenár F, Varga J, Kolařík M (2016a) *Aspergillus*
30 *europaeus* sp. nov. a widely distributed soil-borne species related to *Aspergillus wentii*. *Plant Syst Evol* 302:
31 641-650.
- 32 Hubka V, Peterson SW, Frisvad JC, Yaguchi T, Kubátová A, Kolařík M (2013) *Aspergillus waksmanii* sp. nov. and
33 *Aspergillus marvanovae* sp. nov., two new closely related species in section *Fumigati*. *Int J Syst Evol Microbiol*
34 63: 763-789.

- 1 Hubka V, Dudová Z, Kubátová A, Yaguchi T, Horie Y, Jurjevic Z, Frisvad JC, Hong S-B, Kolarik M (2017)
- 2 Taxonomic novelties in *Aspergillus* section *Fumigati*: *A. tasmanicus* sp. nov., induction of a sexual state in *A.*
- 3 *turcosus* and overview of related species. *Plant Syst Evol* 303: 787-806.
- 4 Hubka V, Nováková A, Jurjević Ž, Sklenar F, Frisvad JC, Houbaken J, Arendrup MC, Jørgensen KM, Siqueira
- 5 JPZ, Gené J, Kolařík M (2018a) Polyphasic data support the splitting of *Aspergillus candidus* into two species:
- 6 proposal of *A. dobrogensis* sp. nov. *Int J Syst Evol Microbiol* 68: 995-1011.
- 7 Hubka V, Barrs V, Dudová Z, Sklenář F, Kubátová A, Matsuzawa T, Yaguchi T, Horie Y, Nováková A, Frisvad JC,
- 8 Talbot JJ, Kolařík M (2018b) Unravelling species boundaries in the *Aspergillus viridinutans* complex (section
- 9 *Fumigati*): opportunistic human and animals pathogens capable of interspecific hybridization. *Persoonia* 41:
- 10 142-174.
- 11 Hubka V, Nováková A, Peterson SW, Frisvad JC, Sklenář F, Matsusawa T, Kubátová A, Kolařík M (2016b) A
- 12 reappraisal of *Aspergillus* section *Nidulantes* with descriptions of two new sterigmatocystin-producing
- 13 species. *Plant Syst Evol* 302: 1267-1299.
- 14 Huskinson B, Marshak MP, Suh C, Er S, Gerhardt MR, Galvin CJ, Chen X, Aspuru-Guzik A, Gordon RG, Aziz MJ
- 15 (2014) A metal-free organic-inorganic aqueous flow battery. *Nature* 505:195-198.
- 16 Hussain H, Al-Harrasi A, Green IR, Abbas G, Ahmed I (2015) Recent advances in natural dimeric quinones.
- 17 *Studies in Natural Products Chemistry* 46: 447-517.
- 18 Hyde KD, Xu J, Rapior S, Jeewon R, Lumyong S, Grace Niego AT, Abeywickrama PD, S Aluthmuhandiram J V,
- 19 Brahamanage RS, Brooks S, Chaiyasen A, Thilini Chethana KW, Chomnunti P, Chepkirui C, Chuankid B, de Silva
- 20 NI, Doilom M, Faulds C, Gentekaki E, Gopalan V, Kakumyan P, Harishchandra D, Hemachandran H, Hongsanan
- 21 S, Karunarathna A, Karunarathna SC, Khan S, Kumla J, Jayawardena RS, Liu J-K, Liu N, Luangharn T, Patrick
- 22 Macabeo AG, Marasinghe DS, Meeks D, Mortimer PE, Mueller P, Nadir S, Nataraja KN, Nontachaiyapoom S,
- 23 Penkhrue W, Phukhamsakda C, Shaanker Ramanan U, Rathnayaka AR, Sadaba RB, Sandargo B, Samarakoon
- 24 BC, Tennakoon DS, Siva R, Suwunwong T, Thongbai B, Thongklang N, Wei D, Nuwanthika Wijesinghe S,
- 25 Winiski J, Yan J, Yasanthika E, Stadler M (2019) The amazing potential of fungi: 50 ways we can exploit fungi
- 26 industrially. *Fungal Divers* 97:1–136.
- 27 Ióca LP, Romminger S, Santos MFC, Bandeira KF, Rodrigues FT, Kossuga MH, Nicacio KJ, Ferreira ELF, Morais-
- 28 Urano RP, Passos MS, Kohn LK, Arns CW, Sette LD, Berlinck RGS (2016) A strategy for the rapid identification
- 29 of fungal metabolites and the discovery of the antiviral activity of pyrenocine a and harzianopyridone. *Quim*
- 30 *Nova* 39:720–731.
- 31 Ito Y, Kawai K, Nozawa Y (1973) Biochemical studies of pigments from pathogenic fungus *Microsporum cookei*
- 32 - effect of 1,4-naphthoquinone pigment, xanthomegnin on oxidative phosphorylation in rat-liver. *J Biochem*
- 33 74: 805-810.
- 34 Itoh M, Katayama Y, Kuraishi H, Sugiyama J (1988) Isolation and Structure Elucidation of a
- 35 Tetrahydrogenated Isoprenoid Side-Chain Ubiquinone with ten isoprene units isolated from
- 36 *Chaetomium funicola* JS 525. *Agric Biol Chem* 52: 1195-1201

- 1 Izhaki I (2002) Emodin - A secondary metabolite with multiple ecological functions in higher plants. New
2 Phytol 155:205–217.
- 3 Janso JE, Bernan VS, Greenstein M (2005) *Penicillium dravuni*, a new marine-derived species from an alga in
4 Fiji. Mycologia 97: 444-453.
- 5 Jensen KA, Ryan ZC, Wymelenberg A Vanden, Cullen D, Hammel KE (2002) An NADH: Quinone oxidoreductase
6 active during biodegradation by the brown-rot basidiomycete *Gloeophyllum trabeum*. Appl Environ Microbiol
7 68:2699–2703.
- 8 Johnson BC, Cohen P, Polonsky J, Lederer E (1963) Piloquinone: A new phenanthrene-o-quinone isolated
9 from the mycelium of *Streptomyces pilosus*. Nature 199:285–286 .
- 10 Jørgensen TR, Park J, Arentshorst M, van Welzen AM, Lamers G, vanKuyk PA, Damveld RA, van den Hondel
11 CAM, Nielsen KF, Frisvad JC, Ram AFJ (2011) The molecular and genetic basis of conidial pigmentation in
12 *Aspergillus niger*. Fung Genet Biol 48: 544-553.
- 13 Jurjevic Z, Kubatova A, Kolarik M, Hubka V (2015) Taxonomy of *Aspergillus* section *Petersonii* sect. nov.
14 encompassing indoor and soil-borne species with predominant tropical distribution. Plant Syst Evol 301:
15 2441-2462.
- 16 Kaji A, Iwata T, Kiriya N, Wakusawa S, Miyamoto K (1994) 4 new metabolites of *Aspergillus terreus*. Chem
17 Pharm Bull 42: 1682-1684.
- 18 Kalansuriya P, Khalil ZG, Salim AA, Capon RJ (2019) Talarophenol sulfate and talarophilones from the
19 Australian mud dauber wasp-associated fungus, *Talaromyces* sp. CMB-WO45. Tetrahedron Lett 60: 151157.
- 20 Kanai Y, Ishiyama D, Senda H, Iwatani W, Takahashi H, Konno H, Tokumasu S, Kanazawa S (2000) Novel
21 human topoisomerase I inhibitors, topopyrones A, B, C and D. I. Producing strain, fermentation, isolation,
22 physico-chemical properties and biological activity. J Antibiot 53: 863-872.
- 23 Kawai K, Akita T, Nozawa Y (1978) Biochemical studies of pigments from pathogenic fungus *Microsporium*
24 *cookei*. 5 Evidence for transmembrane permeability of xanthomegnin across phospholipid bilayer
25 membranes. Experientia 34: 977-978.
- 26 Kawai K, Nozawa Y (1979) Biochemical studies of pigments from pathogenic fungus *Microsporium cookei*. 6.
27 Formation of a xanthomegnin-bypass to the mitochondrial electron transport system. Experientia 35: 721-
28 722.
- 29 Kawai K, Cowger ML (1981) The interaction of quinone pigment, xanthomegnin, with the mitochondrial
30 respiratory chain. Res Commun Chem Pathol Pharmacol 32: 499-514.
- 31 Kehelpannala C, Kumar NS, Jayasinghe L, Araya H, Fujimoto Y (2018) Naphthoquinone metabolites produced
32 by *Monacrosporium ambrosium*, the ectosymbiont fungus of tea shot-hole borer, *Euwallacea fornicates* in
33 stems of tea, *Camellia sinensis*. J Chem Ecol 44: 95-101.

- 1 Kerem Z, Jensen KA, Hammel KE (1999) Biodegradative mechanism of the brown rot basidiomycete
2 *Gloeophyllum trabeum*: evidence for an extracellular hydroquinone-driven fenton reaction. FEBS Lett 446:
3 49–54.
- 4 Khalid S, Keller NP (2021) Chemical signals driving bacterial-fungal interactions. Environ Microbiol 23: 1334-
5 1347.
- 6 Khamthong N, Rukachaisirikul V, Phongpaichit S, Preedanon S, Sakayaroj J (2012) Bioactive polyketides from
7 the sea fan-derived fungus *Penicillium citrinum* PSU-F51. Tetrahedron 68: 8245-8250.
- 8 Kim W, Cavinder B, Proctor RH, O'Donnell K, Townsend JP, Trail F (2019) Comparative genomics and
9 transcriptomics during sexual development gives insight into the life history of the cosmopolitan fungus
10 *Fusarium neocosmosporiellum*. Front Microbiol 10: 1247.
- 11 Kimura Y, Hamasaki T, Nakajima H (1981) Isolation, identification and biological activities of 8-O-methyl
12 javanicin produced by *Fusarium solani*. Agric Biol Chem 45: 2653-2654.
- 13 Kiriyaama N, Nitta K, Sakaguchi Y, Taguchi Y, Yamamoto Y (1977) Studies in metabolic products of *Aspergillus*
14 *terreus*. 3. Metabolites of strain IFO 8835. Chem Pharm Bull 25: 2593-2601.
- 15 Kisieliute A, Popov A, Apetrei RM, Cârâc G, Morkvenaite-Vilkonciene I, Ramanaviciene A, Ramanavicius A
16 (2019) Towards microbial biofuel cells: Improvement of charge transfer by self-modification of
17 microorganisms with conducting polymer – polypyrrole. Chem Eng J 356:1014–1021.
- 18 Kjaer D, Kjaer A, Pedersen C, Bullock JD, Smith JR (1971) Bikaverin and norbikaverin, benzoxanthentrione
19 pigments of *Gibberella fujikuroi*. J Chem Soc C 1971: 2792-2797.
- 20 Kjærboelling I, Vesth TC, Frisvad JC, Nybo JL, Theobald S, Kuo A, Bowyer P, Matsuda Y, Mondo S, Lyhne EK,
21 Kogle ME, Clum A, Lipzen A, Salamov A, Ngan CY, Daum C, Chiniy J, Barry K, LaButti K, Haridas S, Simmons
22 BA, Magnuson JK, Mortensen UH, Larsen TO, Grigoriev I V., Baker SE, Andersen MR (2018) Linking secondary
23 metabolites to gene clusters through genome sequencing of six diverse *Aspergillus* species. Proc Natl Acad Sci
24 U S A 115:E753–E761.
- 25 Kjærboelling I, Vesth TC, Frisvad JC, Nybo JL, Theobald S, Kildgaard S, Petersen TI, Kuo A, Sato A, Lyhne EK,
26 Kogle ME, Wiebenga A, Kun RS, Lubbers RJM, Mäkälä MR, Barry K, Chovatia M, Clum A, Daum C, Haridas S,
27 He G, LaButti K, Lipzen A, Mondo S, Pangilinan J, Riley R, Salamov A, Simmons BA, Magnuson JK, Henrissat B,
28 Mortensen UH, Larsen TO, de Vries RP, Grigoriev IV, Machida M, Baker SE, Andersen MR (2020) A
29 comparative genomics study of 23 *Aspergillus* species from section *Flavi*. Nat Commun 11: 1106.
- 30 Kocsubé S, Perrone G, Magistà D, Houbraeken J, Varga J, Szigeti G, Hubka V, Hong S-B, Frisvad JC and Samson
31 RA (2016) *Aspergillus* is monophyletic: evidence from multiple gene phylogenies and extrolite profiles. Stud
32 Mycol 85: 199-213.
- 33 Kohut G, Olah B, Adam AL, Garcia-Martinez J, Hornok L (2010) Adenyl cyclase regulates heavy metal
34 sensitivity, bikaverin production and plant tissue colonization in *Fusarium proliferatum*. J Basic Microbiol 50:
35 59-71.

- 1 Kornsakulkarn J, Dolsophan K, Boonyen N, Boonruangprapa T, Rachtawee P, Prabpai S, Kanasaeree P,
2 Thongpanchang C (2011) Dihydronaphthalenones from endophytic fungus *Fusarium* sp. BCC14842.
3 Tetrahedron 67: 7540-7547.
- 4 Kornsakulkarn J, Saepua S, Srichomthong K, Supothina S, Thongpanchang C (2012) New mycotoxins from the
5 scale insect fungus *Aschersonia coffeae* Henn. BCC 28712. Tetrahedron 68: 8480–8486.
- 6 Koyama N, Nagahiro T, Yamaguchi Y, Masuma R, Tomoda H, Omura S (2005) Stemphones, novel potentiators
7 of imipenem activity against methicillin-resistant *Staphylococcus aureus*, produced by *Aspergillus* sp. FKI-
8 2136. J Antibiot 58:695–703.
- 9 Kracke F, Vassilev I, Krömer JO (2015) Microbial electron transport and energy conservation - The foundation
10 for optimizing bioelectrochemical systems. Front Microbiol 6: 1–18.
- 11 Kreisel H, Schubert M (1990) Ubiquinone in einigen filamentöse Pilzen. Zentralb Mikrobiol 145: 91-94.
- 12 Kristensen SB, van Mourik T, Pedersen TB, Sørensen JL, Muff J (2020) Simulation of electrochemical
13 properties of natural occurring quinones. Sci Rep 10: 13571.
- 14 Kurashi H, Katayama-Fujimura Y, Sugiyama J, Yokoyama T (1985) Ubiquinone systems in fungi. I. Distribution
15 of ubiquinones in major families of ascomycetes, basidiomycetes and deuteromycetes, and their taxonomic
16 implications. Trans Mycol Soc Jpn 26: 383-395.
- 17 Kuraishi H, Itoh M, Tsuzaki N, Katayama Y, Yokoyama T, Sugiyama J (1990) Ubiquinone systems in fungi. 3.
18 The ubiquinone system as a taxonomic aid in *Aspergillus* and its teleomorphs. In: Samson RA and Pitt JI (eds.).
19 *Modern concepts in Penicillium and Aspergillus classification*. Nato Advanced Science Institute Series, Series
20 A, Life Sciences 185: 407-421. Plenum Press, New York.
- 21 Kuraishi H, Aoki M, Itoh M, Katayama Y, Suguyama J, Pitt JI (1991) Distribution of ubiquinones on *Penicillium*
22 and related genera. Mycol Res 95: 705-711.
- 23 Kuraishi H, Itoh M, Katayama Y, Ito T, Hasegawa A, Sugiyama J (2000) Ubiquinone systems in fungi. V.
24 Distribution and taxonomic implications of ubiquinone in *Eurotiales*, *Onygenales* and related plectomycete
25 genera, except for *Aspergillus*, *Paecilomyces*, *Penicillium*, and their related teleomorphs. Antonie van
26 Leuwenhoek 77: 179-186.
- 27 Kurobane I, Vining LC, Mcinnes AG, Gerber NN (1980). Metabolites of *Fusarium solani* related to
28 dihydrofusarubin. J Antibiot 33: 1376–1379.
- 29 Kwon HR, Son SW, Han HR, Choi GJ, Jang KS, Choi YH, Lee S, Do Sung N, Kim JC (2007) Nematicidal activity of
30 bikaverin and fusaric acid isolated from *Fusarium oxysporum* against pine wood nematode, *Bursaphelenchus*
31 *xylophilus*. Plant Pathol J 23: 318-321.
- 32 Laatsch H, Anke H (1982) Metabolic products of microorganisms. 24. Viocristin, isoviocristin and
33 hydroxyviocristin – Structure and synthesis of naturally occurring 1,4-anthraquinones. Liebigs Ann Chem
34 1982: 2189-2215.

- 1 Lan S, Wu B (2020) Chemistry and bioactivities of secondary metabolites from the genus *Talaromyces*. Chem
2 Biodiv 17: e2000229.
- 3 Larsen TO, Smedsgaard J, Nielsen KF, Hansen ME, Samson RA and Frisvad JC (2007) Production of mycotoxins
4 by *Aspergillus lentulus* and other medically important and closely related species in section *Fumigati*. Med
5 Mycol 45: 225-232.
- 6 Lazarro I, Busma N, Battilani P, Butchko RAE (2012) FUM and BIK gene expression contributes to describe
7 fumonisin and bikaverin synthesis in *Fusarium verticillioides*. Int J Food Microbiol 160: 94-98.
- 8 Lebeau J, Petit T, Clerc P, Dufosse L, Caro Y (2019) Isolation of two new purple naphthoquinone pigments
9 concomitant with the bioactive red bikaverin and derivatives thereof produce by *Fusarium oxysporum*.
10 Biotechnol Prog 35: e2738.
- 11 Lee YM, Li H, Hong J, Cho HY, Bae KS, Kim MA, Kim D-K, Jung JH (2010) Bioactive metabolites from the
12 sponge-derived fungus *Aspergillus versicolor*. Arch Pharm Res 33:231-235.
- 13 Li H, Wei J, Pan SY, Gao JM, Tian JM (2014) Antifungal, phytotoxic and toxic metabolites produced by
14 *Penicillium purpurogenum*. Nat Prod Res 28:2358-2361.
- 15 Li JL, Jiang X, Liu X, He C, Di Y, Lu S, Huang H, Lin B, Wang D, Fan B (2019) Antibacterial anthraquinone dimers
16 from marine derived fungus *Aspergillus* sp. Fitoterapia 133: 1–4.
- 17 Li M-Z, Yu R-L, Bai X-L, Wang H, Zhang X-W (2020) *Fusarium*: a treasure trove of bioactive secondary
18 metabolites. Nat Prod Rep 37: 1568–1588.
- 19 Li Q, Zhy RY, Yi WW, Chai WY, Zhang ZZ, Lian XY (2018) Peniciphenalins A-F from the culture of a marine-
20 associated fungus *Penicillium* sp ZZX901. Phytochem 152: 53-60.
- 21 Li S, Tang Y, Fang X-M, Qiao T, Han S, Zhu T-H (2020) Whole genome sequencing of *Arthrinium*
22 *phaeospermum*, a globally distributed pathogenic fungus. Genomics 112: 919-929.
- 23 Li X, Zheng Y, Sattler I, Lin WH (2006) Griseusin C, a novel quinone derivative from a marine-derived
24 *Penicillium* sp. Arch Pharm Res 29: 942-945.
- 25 Li YQ, Li MG, Li W, Zhao JY, Ding ZG, Cui XL, Wen ML (2007) Griseusin D, a New Pyranonaphthoquinone
26 Derivative from a Alkaphilic Nocardiosis sp. J Antibiot 60: 757–761.
- 27 Li XF, Choi HD, Kang JS, Lee CO, Son BW (2003) New polyoxygenated farnesylcyclohexanones,
28 deacetoxyanuthone A and its hydro derivative from the marine-derived fungus *Penicillium* sp. J Nat Prod 66:
29 1499-1500.
- 30 Lim FY, Hoo Y-P, Chen Y-M, Oh J-H, Lee I, Bugni TS, Keller NP (2012) Genome-based cluster reveals an
31 endocrocin biosynthetic pathway in *Aspergillus fumigatus*. Appl Environ Microbiol 78: 4117-4125.
- 32 Limón MC, Rodriguez-Ortiz, Avalos J (2010) Bikaverin production and applications. Appl Microbiol Biotechnol
33 87: 21-29.

- 1 Liu FA, Lin X, Zhou X, Chen M, Huang X, Yang B, Tao H (2017) Xanthonenes and quinolones derivatives produced
2 by the deep-sea-derived fungus *Penicillium* sp. SCSIO Ind16F01. *Molecules* 22:10–16.
- 3 Liu W-Z, Gu Q-Q, Zhu W-M, Cui C-B, Fang T (2005) Two new benzoquinone derivatives and two new
4 bisorbicillinoids were isolated from a marine-derived fungus *Penicillium terrestre*. *J Antibiot* 58: 441-446.
- 5 Lund F, Frisvad JC (1994) Chemotaxonomy of *Penicillium aurantiogriseum* and related species. *Mycol Res* 98:
6 481-492.
- 7 Luo H, Qing Z, Deng Y, Deng Z, Xia'an T, Feng B, Lin W (2019) Two polyketides produced by endophytic
8 *Penicillium citrinum* DBBR-9 from medicinal plant *Stephania kwangsiensis* and their antifungal activity against
9 plant pathogenic fungi. *Nat Prod Commun* 14: 1-6.
- 10 Malz S, Grell MN, Thrane C, Maier FJ, Rosaager P, Felk A, Albertsen KS, Salomon S, Pohn L, Schafer W, Giese
11 H (2005) Identification of a gene cluster responsible for the biosynthesis of aurofusarin in the *Fusarium*
12 *graminearum* species complex *Fung Genet Biol* 42: 420-433.
- 13 McNamara L, Dolan SK, Walsh JMD, Stephens JC, Glare TR, Kavanagh K, Griffin CT (2019) Oosporein, an
14 abundant metabolite in *Beauveria caledonica*, with a feedback induction mechanism and a role in insect
15 virulence. *Fungal Biol* 123:601-610.
- 16 Ma SM, Zhan JX, Xie XK, Watanabe KJ, Tang Y, Zhang WJ (2008) Redirection of the cyclization steps of fungal
17 polyketide synthase. *J Am Chem Soc* 130: 38-39.
- 18 Maharjan S, Lee SB, Kim GJ, Cho SJ, Nam JW, Chin J, Choi H (2020) Isolation of unstable isomers of
19 lucilactaene and evaluation of anti-inflammatory activity of secondary metabolites produced by the
20 endophytic fungus *Fusarium* sp. QF001 from the roots of *Scutellaria bicalensis*. *Molecules* 25: 923.
- 21 Mahmoodian A, Strickings CE (1964) 15 metabolites of *Penicillium frequentans* Westling. Isolation of
22 sulochrin, asteric acid, (+)-bisdechlorogedon + 2 new substituted anthraquinones questin and questinol.
23 *Biochem J* 92: 369-378.
- 24 Malik EM, Müller CE (2016) Anthraquinones as pharmacological tools and drugs. *Med Res Rev* 36:705–748.
- 25 Mandelare PE, Adpressa DA, Kaweesa EN, Zakharov LN, Loesgen S (2018) Coculture of Two Developmental
26 Stages of a Marine-Derived *Aspergillus alliaceus* Results in the Production of the Cytotoxic Bianthrone
27 Allanthrone A. *J Nat Prod* 81:1014-1022.
- 28 Mapari SAS, Nielsen KF, Larsen TO, Frisvad JC, Meyer AS, Thrane U (2005) Exploring fungal biodiversity for the
29 production of water-soluble pigments as potential natural food colorants. *Curr Opin Biotechnol* 16: 231-238.
- 30 Marcos IS, Conde A, Moro RF, Basabe P, Diez D, Urones JG (2010) Quinone/hydroquinone sesquiterpenes.
31 *Mini Rev Org Chem* 7: 230-254.
- 32 Martínez-Cano C, Grey WE, Sands DC (1992) 1st report of *Arthrinium arundinis* causing kernel blight on
33 barley. *Plant Dis* 76: 1077.

- 1 Masi, M., Evidente A (2020) Fungal bioactive anthraquinones and analogues. *Toxins* 12: 714.
- 2 Matsuda H, Kohno S, Maesaki S, Yamada H, Koga H, Tamuro M, Kuraishi H, Sugiyama J (1992) Application of
3 ubiquinone systems and electrophoretic comparison of enzymes to identification of clinical isolates of
4 *Aspergillus fumigatus* and several other species of *Aspergillus*. *J Clin Microbiol* 30: 1999-2005.
- 5 Mavragani DC, Abdel-Latif FB, McConkey B, Hanel C, Vujanovic V (2007) First report on damping-off of durum
6 wheat caused by *Arthrinium sacchari* in the semi-arid Saskatchewan fields. *Plant Dis* 91: 469.
- 7 Medentsev AG, Akimenko VK (1997). Effect of secondary metabolites and electron transfer inhibitors on
8 naphthoquinone synthesis in *Fusarium decemcellulare*. *Microbiol (Moscow)* 66: 647-651.
- 9 Medentsev AG, Akimeno VK (1998) Naphthoquinone metabolites of the fungi. *Phytochem* 47: 935-959.
- 10 Meng J, Wang X, Xu D, Fu X, Zhang X, Lai D, Zhou L, Zhang G (2016) Sorbicillinoids from fungi and their
11 bioactivities. *Molecules* 21: 715.
- 12 Miller RF, Huang S (1995) Isolation and structure of sorrentanone – a new tetrasubstituted quinone from
13 *Penicillium chrysogenum*. *J Antibiot* 48: 520-521.
- 14 Mills JT, Frisvad JC, Seifert KA, Abramson D (1995) Identification of nephrotoxic *Penicillium* species from
15 cereal grains. *Mycotox Res* 11: 25-36.
- 16 Mocek U, Schlultz L, Buchan T, Balk C, Fretto L, Nzerem J, Sehl L, Sinhu U (1996) Isolation and structure
17 elucidation of five new asterriquinones from *Aspergillus*, *Humicola* and *Botryotrichum* species. *J Antibiot* 49:
18 854-859.
- 19 Mondal A, Singh SK, Manna T, Husain SM (2020) Chemoenzymatic, biomimetic total synthesis of (-)-rugulosin
20 B, C and rugulin analogues and their biosynthetic implications. *Chem Commun* 56: 3337-3340.
- 21 Morehouse NJ, Flewelling AJ, Johnson JA, Gray CA (2020) Halogenated bianthrone from *Penicillium*
22 *roseopurpureum*, a fungal endophyte of the marine alga *Petalonia fascia*. *Nat Prod Commun* 15: 1-4.
- 23 Morishta Y, Okazaki Y, Luo YY, Nurioki J, Taniguchi T, Oshima Y, Asai T (2019) Use of plant hormones to
24 activate silent polyketide biosynthetic pathways in *Arthrinium sacchari*, a fungus isolated from a spider. *Org*
25 *Biomol Chem* 17: 780-784.
- 26 Mozaina K, Cantrell CL, Mims AB, Lax AR, Tellez MR, Osbrink WLA (2008) Activity of 1,4-benzoquinones
27 against Formosan subterranean termites (*Coptotermes formosanus*). *J Agric Food Chem* 56:4021-4026.
- 28 Munkvold GP (2017) *Fusarium* species and their associated mycotoxins. In Moretti A, Susca A (eds.).
29 *Mycotoxigenic fungi: methods and protocols. Methods in Molecular Biology* 1542: 51-106, Amsterdam:
30 Springer.
- 31 Myobatake Y, Takimoto K, Kamisuki S, Inoue N, Takasaki A, Takeuchi T, Mizushima Y, Sugawara T (2014)
32 Cytotoxic alkylated hydroquinone, phenol, and cyclohexanone derivatives from *Aspergillus brunneoviolaceus*
33 Gasperini. *J Nat Prod* 77: 1236-1240.

- 1 Nesic K, Ivanovic S, Nesic V (2014) Fusarial toxins: secondary metabolites of *Fusarium* fungi. Rev Environ
2 Contam Toxicol 228: 101–120.
- 3 Newman DK, Kolter R (2000) A role for excreted quinones in extracellular electron transfer. Nature 405:94-
4 97.
- 5 Ngan NTT, Quang TH, Kim KW, Kim HJ, Sohn JK, Kang DG, Lee HS, Kim YC, Oh H (2017) Anti-inflammatory
6 effects of secondary metabolites isolated from the marine-derived fungal strain *Penicillium* sp. SF-5629. Arch
7 Pharm Res 40: 328-337.
- 8 Nicolaisen M, Sandal T, Frisvad JC, Rossen L (1996) 2D-PAGE examination of mRNA populations from mutants
9 of *Penicillium freii* deficient in the production of xanthomegnin metabolites. Microbiol Res 151: 285-290.
- 10 Niehaus MR, Munsterkotter M, Proctor RH, Brown DW, Sharon A, Idan Y, Oren-Young L, Sieber CM, Novak O,
11 Pencik A, Tarkowska D, Hromadova K, Freeman S, Maymon M, Elazar M, Youssef SA, El-Shabrawy EM, Shalaby
12 ABA, Houterman P, Brock NL, Burkhardt I, Tsavkelova EA, Dickschat JS, Galuszka P, Guldener U, Tudzynski B
13 (2016) Comparative 'omics' of the *Fusarium fujikuroi* species complex highlights differences in genetic
14 potential and metabolite synthesis. Genome Biol Evol 8: 3574-3599.
- 15 Nielsen MR, Sondergaard TE, Giese H, Sørensen JL (2019) Advances in linking polyketides and non-ribosomal
16 peptides to their biosynthetic gene clusters in *Fusarium*. Cur Genet 65: 1263-1280.
- 17 Nielsen MR, Holwarth AKR, Brew E, Chrapkova N, Kanik SEK, Kastaniegaard K, Sorensen T, Westphal KR,
18 Wimmer R, Sondergaard TE, Sørensen JL (2019) A new vector system for targetted integration of genes in the
19 crop pathogen *Fusarium solani*. Fung Biol Biotechnol 6: 26.
- 20 Nohl H, Jordan W, Youngman RJ (1986) Quinones in biology: Functions in electron transfer and oxygen
21 activation. Adv Free Rad Biol Med 2: 211-279.
- 22 Nord C, Levenfoss JJ, Bjerketorp J, Sahlberg C, Guss B, Oberg B, Broberg A (2019) Antibacterial isoquinoline
23 alkaloids from the fungal *Penicillium spathulatum* Em19. Molecules 24: 4616.
- 24 Nweze JA, Mbaaji FN, Huang G, Li Y, Yang L, Zhang Y, Huang S, Pan L, Yang D (2020) Antibiotics development
25 and the potentials of marine-derived compounds to stem the tide of multidrug-resistant pathogenic bacteria,
26 fungi, and protozoa. Mar Drugs 18: 145.
- 27 O'Donnell K, Al-Hatmi AMS, Aoki T, Brankovics B, Cano-Lira JF, Coleman JJ, de Hoog GS, Di Pietro A, Frandsen
28 RJN, Geiser DM, Gibas CFC, Guarro J, Kim H-S, Kistler HC, Laraba I, Leslie JF, López-Berges MS, Lysøe E, Meis
29 JF, Monod M, Proctor RH, Rep M, Ruiz-Roldán C, Šišić A, Stajich JE, Steenkamp ET, Summerell BA, van der Lee
30 TAJ, van Diepeningen AD, Verweij PE, Waalwijk C, Ward TJ, Wickes BL, Wiederhold NP, Wingfield MJ, Zhang
31 N, Zhang SX (2020) No to *Neocosmospora* : Phylogenomic and Practical Reasons for Continued Inclusion of
32 the *Fusarium solani* Species Complex in the Genus *Fusarium*. mSphere 5:00810–20.
- 33 Ogawa H, Yoshimura A, Sugiyama J (1997) Polyphyletic origins of the anamorphic genus *Geosmithia* and the
34 relationships of the cleistothecial genera: Evidence from 18S, 5S and 28S rDNA sequence analysis. Mycologia
35 89: 756-771.

- 1 Oplatowska-Stachowiak M, Elliott CT (2017) Food colors: Existing and emerging food safety concerns. Crit Rev
2 Food Sci Nutr 57:524-548.
- 3 Osbrink WLA, Tellez MR, Kobaisy M, Lax AR (2005) Assessment of Natural Products for Control of Formosan
4 Subterranean Termites. In: Petroski RJ, Tellez M, Behle R (eds) Semiochemicals in Pest and Weed Control, 1st
5 edn. American Chemical Society, Washington DC, pp 73–87
- 6 Özkan G, Bilek SE (2014) Microencapsulation of natural food colourants. Int J Nutr Food Sci 3:145–156.
- 7 Palonen EK, Raina S, Brandt A, Meriluoto J, Kashavar ZT, Soine JT (2017) Melanisation of *Aspergillus terreus* –
8 is butyrolactone I involved in the regulation of both DOPA and DHN types of pigments in submerged culture?
9 Microorganisms 5: 22.
- 10 Panesar R, Kaur S, Panesar PS (2015) Production of microbial pigments utilizing agro-industrial waste: A
11 review. Curr Opin Food Sci 1:70–76.
- 12 Pansanit A, Pripdeevech P (2018) Antibacterial secondary metabolites from an endophytic fungus *Arthrinium*
13 sp. MFLUCC16-1053 isolated from *Zingiber cassumunar*. Mycology Int J Fung Biol 9: 264-272.
- 14 Paterson RRM, Buddie M (1991) Rapid determination of ubiquinone profiles in *Penicillium* by reversed phase
15 high performance thin-layer chromatography. Lett Appl Microbiol 13: 133-136.
- 16 Paterson RRM. (1993). Effect of growth on taxonomically useful ubiquinone/lipid profiles of *Penicillium*.
17 Mycol Res 97: 173-178.
- 18 Pavesi C, Flan V, Mann S, Leleu S, Prado S, Franck X (2021) Biosynthesis of azaphilones: a review. Nat Prod
19 Rep 38: 1058-1071.
- 20 Pedersen TB, Nielsen MR, Kristensen SB, Spedtsberg EML, Yasmine W, Matthiesen R, Kaniki SEK, Sorensen T,
21 Petersen C, Muff J, Sondergaard TE, Nielsen KL, Wimmer R, Sørensen JL (2020) Heterologous expression of
22 the core genes in the complex fusarubin gene cluster of *Fusarium solani*. Int J Mol Sci 21: 7601.
- 23 Pereyra CE, Dantas RF, Ferreira SB, Gomes LP, Silva FP (2019) The diverse mechanisms and anticancer
24 potential of naphthoquinones. Cancer Cell Int 19: 207.
- 25 Peterson SW, Jurjevics Z, Frisvad JC (2015) Expanding the species and chemical diversity of *Penicillium* section
26 *Cinnamopurpurea*. PLoS ONE 10: e0121987
- 27 Perez-Cuesta V, Aparicio-Fernandez L, Guruceaga X, Martin-Souto L, Abad-Diaz-de-Ceria A, Antaran A, Baldain
28 I, Hernandez FL, Ramirez-Garcia A, Rementeria A (2020) Melanin and pyomelanin in *Aspergillus fumigatus*:
29 From its genetics to host interaction. Int Microbiol 23: 55-63.
- 30 Perrone G, Stea G, Epifani F, Varga J, Frisvad JC, Samson RA (2011) *Aspergillus niger* contains the cryptic
31 phylogenetic species *A. awamori*. Fung Biol 115: 1138-1150.
- 32 Pfiffner A (1963) Isolierung und Konstitutionenermittlung von Marticin und Isomarticin, zwei neuen
33 Welketoxinen aus *Fusarium martii*. Dissertation No. 3666, Zürich: ETH.

- 1 Posternak T, Ruelius HW, Tcherniak J (1943) Research on the biochemistry of inferior mushrooms. V. New
2 synthesis of phoenicine and isophoenicine. *Helv Chim Acta* 26: 2031-2044.
- 3 Proctor RH, Butchko RAF, Brown DW, Moreth A (2007) Functional characterization, sequence comparison and
4 distribution of a polyketide synthase gene required for perithecial pigments of some *Fusarium* species. *Food*
5 *Addit Contam A* 24: 1076-1087.
- 6 Proksa B, Adamcova J, Fuska J (1994) Detection and assay of secondary metabolites of *Penicillium*
7 *vermiculatum* Dang. *J Chromatogr A* 665: 185-190.
- 8 Qian-Cutrone J-F, Gao Q, Huang S, Klohr SE, Veitsch JA, Bristol-Meyers Y-ZS (1994) Arthrinone, a novel fungal
9 metabolite from *Arthrinium* sp. FA1744. *J Nat Prod* 57: 1656-1660.
- 10 Rahbæk L, Frisvad JC, Christophersen C (2000) An amendment of *Aspergillus* section *Candidi* based on
11 chemotaxonomical evidence. *Phytochem* 53: 581-586.
- 12 Rai MK (1989) Mycosis in man due to *Arthrinium phaeospermum* var. *indicum*. First case report. *Mycoses* 32:
13 472-475.
- 14 Räisänen R (2019) Fungal colorants in applications – focus on *Cortinarius* species. *Color Technol* 135: 22-31.
- 15 Raistrick H, Ziffer J (1951) Studies in the biochemistry of microorganisms. 84. The colouring matters of
16 *Penicillium nalgiovense* Laxa. 1. Nalgiovensin and nalgisolaxin – isolation, derivatives and partial structure.
17 *Biochem J* 49: 563-574.
- 18 Rajendran M (2016) Quinones as photosensitizer for photodynamic therapy: ROS generation, mechanism and
19 detection methods. *Photodiagnosis Photodyn Ther* 13:175-187.
- 20 Ranji PKV, Wiewarath S, Chandrani S, Jayawardana KH, Gunakerata GMKB (2013) Citriquinones A and B, new
21 benzoquinones from *Penicillium citrinum*. *Nat Prod Commun* 8: 1431-1434.
- 22 Raper KB, Fennell DI (1965) The genus *Aspergillus*. Williams & Wilkins, Baltimore.
- 23 Reilly J, Curtin T, Fitzgerald G (1940) Production of phoenicine on synthetic media. *Biochem J* 34: 1605-1610.
- 24 Roberts JC, Thompson DJ (1971) Studies in mycological chemistry 27. Reinvestigation of purpurogenone,
25 metabolite of *Penicillium purpurogenum* Stoll. *J Chem Soc C* 1971: 3488-3492.
- 26 Roos A (1977) Physiology and pathogenicity of *Neocosmospora vasinfecta* EF Smith. PhD thesis, ETH Zurich,
27 Switzerland.
- 28 Samson RA, Visagie CM, Houbraken J, Hong S-B, Hubka V, Klaassen CHW, Perrone G, Seifert KA, Susca A,
29 Tanney JB, Varga J, Kocsubé S, Szigeti G, Yaguchi T, Frisvad JC (2014) Phylogeny, identification and
30 nomenclature of the genus *Aspergillus*. *Stud Mycol* 78: 141-173.
- 31 Samson RA, Houbraken JAMP, Kuijpers AFA, Frank JM and Frisvad JC (2004) New ochratoxin or sclerotium
32 producing species in *Aspergillus* section *Nigri*. *Stud Mycol* 50: 45-61.

- 1 Samson RA, Noonim P, Meijer M, Houbraken J, Frisvad JC and Varga J (2007a) Diagnostic tools to identify
2 black *Aspergilli*. *Stud Mycol* 59: 129-145.
- 3 Samson RA, Hong S-B, Peterson SW, Frisvad JC and Varga J (2007b) Polyphasic taxonomy of *Aspergillus*
4 section *Fumigati* and its teleomorph *Neosartorya*. *Stud Mycol* 59: 147-203.
- 5 Samson RA, Peterson SW, Frisvad JC, and Varga J (2011a) New species in *Aspergillus* section *Terrei*. *Stud*
6 *Mycol* 69: 39-55.
- 7 Samson RA, Stolk AC, Frisvad JC (1989) Two new synnematos species of *Penicillium*. *Stud Mycol* 31: 133-
8 0143.
- 9 Samson RA, Varga J, Meijer M and Frisvad JC (2011b) New species in *Aspergillus* section *Usti*. *Stud Mycol* 69:
10 81-97.
- 11 Samson RA, Yilmaz N, Houbraken J, Spierenburg H, Seifert KA, Peterson SW, Varga J, Frisvad JC (2011)
12 Phylogeny and nomenclature of the genus *Talaromyces* and taxa accommodated in *Penicillium* subgenus
13 *Biverticillium*. *Stud Mycol* 70: 159-184.
- 14 Sapmak A, Boyce KJ, Andrianopoulos A, Vanittanakom N (2015) The pbrB gene encodes a laccase required for
15 DHN-melanin synthesis in conidia of *Talaromyces (Penicillium) marneffe*. *PLoS ONE* 10: e0122728.
- 16 Sasaki K, Abe H, Yoshizaki F (2002) In vitro antifungal activity of naphthoquinone derivatives. *Biol Pharm Bull*
17 25:669–670
- 18 Scudamore KA, Atkin PM, Buckle AE (1986) Natural occurrence of the naphthoquinone mycotoxins,
19 xanthomegnin and viomellein and vioxanthin in cereals and animal feedstuffs. *J Stored Prod Res* 22: 81-84.
- 20 Sedmera P, Podojil M, Vokoun J, Betina V, Memec P (1978) 2,2'-dimethoxy-4a,4a'-dehydrorugulosin (rugulin),
21 a minor metabolite from *Penicillium rugulosum*. *Folia Microbiol* 23: 64-67.
- 22 Segaran G, Sathivelu M (2019) Fungal endophytes: A potent biocontrol agent and a bioactive metabolites
23 reservoir. *Biocatal Agric Biotechnol* 21: 101284.
- 24 Seifert KA, Hoekstra ES, Frisvad JC, Saosno RA (2004) *Penicillium cecidicola*, a new species on cynipid insect
25 galls on *Quercus pacifica* in the western United States. *Stud Mycol* 50: 517-523.
- 26 Sen T, Barrow CJ, Deshmukh SK (2019) Microbial pigments in the food industry - challenges and the way
27 forward. *Front Nutr* 6: 1-14.
- 28 Shang Z, Khalil Z, Li L, Salim AA, Quezada M, Kalansuriya P, Capon RJ (2016) Roseopurpurins: Chemical
29 diversity enhanced by convergent biosynthesis and forward and reverse Michael additions. *Org Lett* 18: 4340-
30 4343.
- 31 Sharma R, Kulkarni G, Sonawane MS, Shouche (2014) A new endophytic species of *Arthrinium*
32 (*Apiosporaceae*) from *Jatropha podagrica*. *Mycoscience* 55: 118-123.
- 33 Sheehan JC, Lawson WB, Gaul RJ (1958) The structure of terreic acid. *J Am Chem Soc* 80: 5536-5538.

- 1 Shibata S, Sankawa U, Taguchi H, Yamazaki K (1966) Biosynthesis of natural products. 3. Biosynthesis of
2 erythroskyrine, a coloring matter of *Penicillium islandicum* Sopp. Chem Pharm Bull 14: 474-478.
- 3 Short DPG, O'Donnell K, Thrane U, Nielsen KF, Zhang N, Juba JH, Geiser DM (2013) Phylogenetic relationships
4 among members of the *Fusarium solani* species complex in human infections and the description of *F.*
5 *keratinophilum* and *F. petrofilum*. stat. nov. Fung Genet Biol 53: 59-70.
- 6 Silva LPG, Pereira AMPT, Pena A, Lino CM (2021) Citrinin in foods and supplements: a review of occurrence
7 and analytical methodologies. Foods 10: 14.
- 8 Singh PD, Johnson JH, Aklonis CA, Bush K, Fisher SM, O'Sullivan J (1985) Two new inhibitors of phospholipase
9 A2 produced by *Penicillium chermesinum*, taxonomy, fermentation, isolation, structure determination and
10 biological properties. J Antibiot (Tokyo) 38: 706-712.
- 11 Singh SB, Cordingley MG, Ball RG, Smith JL, Dombrowski AW, Goetz MA (1991) Structure and stereochemistry
12 of thysanone: a novel human Rhinovirus 3C-protease inhibitor of *Thysanophora penicilloides*. Tetrahedron
13 Lett 32: 5279-5282.
- 14 Singh SB, Zink DI, Guan Z, Collado J, Palaez F, Felock PJ, Hazuda DJ (2003) Isolation, structure, and HIV-1
15 integrase inhibitor activity of xanthoviridicatin E and F, two novel fungal metabolites produced by *Penicillium*
16 *chrysogenum*. Helv Chim Acta 86: 3380-3385.
- 17 Sklenář F, Jurjević Ž, Zalar P, Frisvad JC, Visagie C, Kolařík M, Houbraken J, Chen AJ, Yilmaz N, Seifert KA,
18 Coton M, Deniel F, Gunde-Cimerman N, Samson RA, Peterson SW, Hubka V (2017) Phylogeny of xerophilic
19 aspergilli (subgenus *Aspergillus*) and taxonomic revision of section *Restricti*. Stud Mycol 88: 161-236.
- 20 Smetanina OF, Yurchenko AN, Ivanets EV, Kirichuk NN, Khudyakova YV, Yurchenko EA, Afyattullov SS (2016)
21 Metabolites of the marine fungus *Penicillium citrinum* associated with a brown alga *Podina* sp. Chem Nat
22 Comp 52: 111-112.
- 23 Solhaug KA, Gauslaa Y (2004) Photosynthates stimulate the UV-B induced fungal anthraquinone synthesis in
24 the foliose lichen *Xanthoria parietina*. Plant, Cell Environ 27:167-176.
- 25 Solhaug KA, Gauslaa Y, Nybakken L, Bilger W (2003) UV-induction of sun-screening pigments in lichens. New
26 Phytol 158: 91-100.
- 27 Sondergaard TE, Fredborg M, Christensen AMO, Damsgaard SK, Kramer NF, Giese H, Sørensen JL (2016)
28 Fast Screening of Antibacterial Compounds from Fusaria. Toxins 8:355.
- 29 Sørensen JL, Nielsen KF, Sondergaard TE (2012) Redirection of pigment biosynthesis to isocoumarins in
30 *Fusarium*. Fung Genet Biol 49: 413-418.
- 31 Spraker JE, Wiemann P, Baccile JA, Venkatesh N, Schumacher J, Schroeder FC, Sanchez LM, Keller NP (2018)
32 Conserved responses in a war of small molecules between a plant-pathogenic bacterium and fungi. MBio 9:
33 e00820.

- 1 Srinivas G, Babykutty S, Sathiadevan PP, Srinivas P (2007) Molecular mechanism of emodin action: Transition
2 from laxative ingredient to an antitumor agent. *Med Res Rev* 27: 591-608.
- 3 Stack ME, Mislivec PB (1978) Production of xanthomegnin and viomellein by isolates of *Aspergillus ochraceus*,
4 *Penicillium cyclopium*, and *Penicillium viridicatum*. *Appl Environ Microbiol* 36: 552-554.
- 5 Stack ME, Eppley RM, Dreifuss PA, Pohland AE (1977) Isolation and identification of xanthomegnin,
6 viomellein, rubrosulphin, and viopurpurin as metabolites of *Penicillium viridicatum*. *Appl Environ Microbiol*
7 33: 351-355.
- 8 Stack ME, Mazzola ES, Eppley RM (1979) Structures of xanthoviridicatin D and xanthoviridicatin G,
9 metabolites of *Penicillium viridicatum*: Application of proton and carbon-13 NMR spectroscopy. *Tetrahedron*
10 Lett 20: 4989-4992.
- 11 Steenwyk JL, Shen X-X, Lind AL, Goldman GH, Rokas A (2019) A robust phylogenetic time tree for
12 biotechnologically and medically important fungi in the genera *Aspergillus* and *Penicillium*. *Mbio* 10: e00925-
13 19.
- 14 Steenwyk JL, Mead ME, Knowles S, Raja H, Roberts CD, Bader O, Houbraken J, Goldman GH, Oberlies NH,
15 Rokas A (2020) Variation among biosynthetic gene clusters, secondary metabolite profiles and cards of
16 virulence across *Aspergillus* species. *Genetics* 216: 481-498.
- 17 Steyn PS, Vleggaar R (1974) Austocystins - 6 novel dihydro furo[3',2'-4,5]furo(3,2-b)xanthenones from
18 *Aspergillus ustus*. *J Chem Soc Perkin Trans. I* 1974: 2250-2256.
- 19 Studt L, Wiemann PK, Kleingrewe K, Humpf H, Tudzynski B (2012) Biosynthesis of fusarubins accounts for
20 pigmentation of *Fusarium fujikuroi* perithecia. *Appl Environ Microbiol* 78: 4468-4480.
- 21 Sugiyama J, Itoh M, Katayama Y, Yamaoka Y, Ando K, Kakishima M and Kuraishi H (1988) Ubiquinones in
22 fungi. II. Distribution of ubiquinones in smut and rust fungi. *Mycologia* 80: 115-120.
- 23 Sun B-C, Chen AJ, Houbraken J, Frisvad JC, Wu W-P, Wei H-L, Zhou Y-G, Jiang X-Z, Samson RA (2020) New
24 section and species in *Talaromyces*. *MycKeys* 68: 75-113.
- 25 Sun BD, Houbraken J, Frisvad JC, Jiang XZ, Chen AJ, Samson RA (2020) New species in *Aspergillus* section *Usti*
26 and an overview of *Aspergillus* section *Cavernicolarum*. *Int J Syst Evol Microbiol* 70: 5401-5416.
- 27 Sun Y-L, Zhang X-Y, Zhang Z-H, Xu X-Y, Qi S-H (2013) Three new polyketides from marine-derived fungus
28 *Penicillium citrinum* SCSGAFO167. *Nat Prod Res* 28: 239-244.
- 29 Sunasse SN, Davies-Coleman MT (2018) Cytotoxic and antioxidant marine prenylated quinones and
30 hydroquinones. *Nat Prod Rep* 29: 513-535.
- 31 Suwannarach N, Kumla J, Nishizaki Y, Sugimoto N, Meerak J, Matsui K, Lumyong S (2019) Optimization and
32 characterization of red pigment production from an endophytic fungus, *Nigrospora aurantiaca* CMU-ZY2045,
33 and its potential source of natural dye for use in textile dyeing. *Appl Microbiol Biotechnol* 103: 6973-6987.

- 1 Suzuki Y, Kono Y, Inoue T, Sakurai A (1998) A potent antifungal benzoquinone in etiolated sorghum seedlings
2 and its metabolites. *Phytochem* 47: 997-1001.
- 3 Tadpetch K, Chukong C, Jeanmard L, Thirapon A, Rukachaisirikul V, Phongpaichit S, Sakayaroj J (2015)
4 Cytotoxic naphthoquinones and new succinate esters from the soil fungus *Fusarium solani* PSU-RSPG227.
5 *Phytochem Lett* 11: 106-110.
- 6 Talbot JJ, Houbraken J, Frisvad JC, Samson RA, Kidd SWE, Pitt J, Lindsay S, Beatty JA, Barrs VR (2017) Discovery
7 of *Aspergillus frankstonensis* sp. nov. during environmental sampling for pathogens. *PLoS ONE* 12: e0181660.
- 8 Takeda N, Seo S, Ogihara Y, Sankawa U, Iitaka I, Kitagawa I, Shibata S (1973) Studies of fungal metabolites. 31.
9 Anthraquinone coloring matters of *Penicillium islandicum* Sopp, and some other fungi. *Tetrahedron* 29: 3703-
10 3719.
- 11 Takemoto K, Kamisuki S, Chio PT, Kuriyama I, Mizushima Y, Sugawara F (2014) Bioactive
12 dihydronaphthoquinone derivatives from *Fusarium solani*. *J Nat Prod* 77: 1992-1996.
- 13 Tanney JB, Visagie CM, Yilmaz N, Seifert KA (2017) *Aspergillus* subgenus *Polypaecilum* from the built
14 environment. *Stud Mycol* 88: 237-267.
- 15 Tansuwan S, Pornpakakul S, Roengsumran S, Petsom A, Muangsin N, Sihanonta P, Chaichit N (2007)
16 Antimalarial benzoquinones from an endophytic fungus, *Xylaria* sp. *J Nat Prod* 70: 1620-1623.
- 17 Theobald S, Vesth T, Rendsvig JK, Nielsen KF, Riley R, Magalhaes de Abreu L, Salamov A, Frisvad JC, Larsen
18 TO, Andersen MR, Hoof JB (2018) Uncovering secondary metabolite evolution and biosynthesis using gene
19 cluster networks and genetic dereplication. *Sci Rep* 8: 17957.
- 20 Thomson RH (1971) Naturally occurring quinones. Academic Press, London.
- 21 Thomson RH (1997) Naturally occurring quinones. IV. Recent Advances. Springer Science, London.
- 22 Tikhonova T V, Popov VO (2014) Structural and functional studies of multiheme cytochromes C involved in
23 extracellular electron transport in bacterial dissimilatory metal reduction. *Biochem* 79: 1584-1601.
- 24 Trivedi AB, Hirota M, Doi E, Kitabatake N (1993) Formation of a new toxic compound, citrinin H1, from citrinin
25 on mild heating in water. *J Chem Soc Perkin Trans I* 1993: 2167-2171.
- 26 Tsuji N, Kobayashi M, Wakisaka Y, Kawamura Y, Mayama M, Matsumoto K (1975) New antibiotics, griseusins
27 A and B isolation and characterization. *J Antibiot* 29: 7-9.
- 28 Tsukuda M, Fukai M, Miki K, Shiraishi T, Suzuki T, Kazuto N, Sugita T, Ishino M, Kinoshita K, Takahashi K, Shiro
29 M, Koyama K (2011) Chemical constituents of a marine fungus, *Arthrinium sacchari*. *J Nat Prod* 74: 1645-
30 1649.
- 31 Turner WB (1971) Fungal Metabolites. Academic Press, London.
- 32 Turner WB, Aldridge DC (1983) Fungal metabolites II. Academic Press, London.

- 1 Uchiyama M, Kimura Y, Ohta A (2000) Stereoselective total synthesis of (±)-arthrinone and related natural
2 compounds. *Tetrahedron Lett* 41: 10013-10017.
- 3 Uchimiya M, Stone AT (2009) Reversible redox chemistry of quinones: Impact on biogeochemical cycles.
4 *Chemosphere* 77: 451-458.
- 5 van der Beek CP, Roels JA (1984) Penicillin production: biotechnology at its best. *Antonie Van Leeuwenhoek*
6 50:625–639.
- 7 Van Eijk GW (1973) Anthraquinones in the fungus *Talaromyces stipitatus*. *Experientia* 29: 522-523.
- 8 Van Eijk GW (1975) Bostrycin, a tetrahydroanthraquinone pigment and some other metabolites from the
9 fungus *Arthrimum phaeospermum*. *Experientia* 31: 783-784.
- 10 Van Gorkom BAP, de Vries EGE, Karrenbeld A, Kleibucker JH (1999) Review article: anthranoid laxatives and
11 their potential carcinogenic effects. *Aliment Pharmacol Ther* 13: 443–452.
- 12 Van Reenen-Hoekstra ES, Frisvad JC, Samson RA, Stolk AC (1990) The *Penicillium funiculosum* complex - well
13 defined species and problematic taxa. In: Samson RA, Pitt JI (eds): *Modern concepts in Penicillium and*
14 *Aspergillus* classification. Plenum Press, New York. pp. 173-191
- 15 Varga J, Due M, Frisvad JC and Samson RA (2007) Taxonomic revision of *Aspergillus* section *Clavati* based on
16 molecular, morphological and physiological data. *Stud Mycol* 59: 89-106.
- 17 Varga J, Frisvad JC, Samson RA (2007) Polyphasic taxonomy of *Aspergillus* section *Candidi* based on
18 molecular, morphological and physiological data. *Stud Mycol* 59:75–88.
- 19 Varga J, Frisvad JC and Samson RA (2010a) *Aspergillus* sect. *Aenei* sect. nov., a new section of the genus for
20 *A. karnatakaensis* sp. nov. and some allied fungi. *IMA Fung* 1: 197-205.
- 21 Varga J, Frisvad JC and Samson RA (2011a) Two new aflatoxin producing species, and an overview of
22 *Aspergillus* section *Flavi*. *Stud Mycol* 69: 57-80.
- 23 Varga J, Frisvad JC, Kocsubé S, Brankovics B, Tóth B, Szigeti G and Samson RA (2011b) New and revisited
24 species in *Aspergillus* section *Nigri*. *Stud Mycol* 69: 1-17.
- 25 Vesth TC, Nybo JL, Theobald S, Frisvad JC, Larsen TO, Nielsen KF, Hoof JB, Brandl J, Salamov A, Ryley R,
26 Gladden JM, Phatale P, Nielsen MT, Lyhne EK, Kogle ME, Strasser K, McDonald E, Berrey K, Clun A, Chen C,
27 Nolan M, Sandor L, Kuo A, Lipzen A, Hainaut M, Drula E, Tsang A, Magnuson JK, Henrissat B, Wiebenga A,
28 Simmons BA, Mäkelä MR, de Vries RP, Grigoriev IV, Mortensen UH, Baker SE, Andersen MR (2018)
29 Investigation on inter- and intraspecies variation through genome sequencing of *Aspergillus* section *Nigri*. *Nat*
30 *Genet* 50: 1688-1695.
- 31 Vogel A (2000) Anthraquinones. In: *Ullmann's Encyclopedia of Industrial Chemistry*. Weinheim: Wiley-VCH,
32 pp 503-511.

- 1 Visagie CM, Renaud JB, Burgess KMN, Malloch DW, Clark D, Ketch L, Urb M, Louiz-Sieze G, Assabgui R,
2 Sumarah MW, Seifert KA (2016) Fifteen new species of *Penicillium*. *Persoonia* 36: 247-270.
- 3 Visagie CM, Houbraken J, Frisvad JC, Hong S-B, Klaassen CHW, Perrone G, Seifert KA, Varga J, Yaguchi T,
4 Samson RA (2014) Identification and nomenclature of the genus *Penicillium*. *Stud Mycol* 78: 343-371.
- 5 Visagie CM, Frisvad JC, Visagie A, Houbraken J, Seifert KA, Samson RA, Jacobs K (2021) A re-evaluation of
6 *Penicillium* section *Canescentia*, including the description of five new *Penicillium* species isolated from South
7 Africa and a phylogenetic. *Persoonia* 46: 163-187.
- 8 Visagie CM, Houbraken J (2020) Updating the taxonomy of *Aspergillus* in South Africa. *Stud Mycol* 95: 252-
9 292.
- 10 Visagie CM, Varga J, Houbraken J, Meijer M, Kocsubé S, Yilmaz N, Fotedar R, Seifert KA, Frisvad JC, Samson RA
11 (2014) Ochratoxin production and taxonomy of the yellow aspergilli (*Aspergillus* section *Circumdati*). *Stud*
12 *Mycol* 78: 1-61.
- 13 Vyvyan JR (2002) Allelochemicals as leads for new herbicides and agrochemicals. *Tetrahedron* 58: 1631-1646.
- 14 Wang W-L, Zhu T-J, Tao H-W, Lu Z-Y, Fang Y-C, Gu Q-Q, Zhu W-M (2007) Two new quinone type compounds
15 from the halotolerant fungus *Aspergillus variegatus*. *J Antibiot* 60: 603-607.
- 16 Wang H, Wang Y, Wang W, Fu P, Liu P, Zhu W (2011) Anti-influenza virus polyketides from the acid-tolerant
17 fungus *Penicillium purpurogenum* JS03-21. *J Nat Prod* 74: 2014-2108.
- 18 Wang PL, Li DY, Xie LR, Wu X, Hua HM, Li ZL (2014) Two new compounds from a marine-derived fungus
19 *Penicillium oxalicum*. *Nat Prod Res* 28: 290-293.
- 20 Wang W, Liao Y, Tang C, Huang X, Luo Z, Chen J, Cai P (2017) Cytotoxic and antibacterial compounds from the
21 coral-derived fungus *Aspergillus tritici* SP2-8-1. *Mar Drugs* 15:1-10.
- 22 Wang S-S, Cui H, Ye J, Wu J, Wang S-X, Yin W-B (2018). Identification and detection of rubrofusarin,
23 rubrofusarin isomer and their quinone forms in grains using high resolution mass spectrometry. *ACS Omega*
24 3: 15924-15932.
- 25 Wang W, Liao Y, Zhang B, Gao M, Ke W, Li F, Shao Z (2019) Citrinin monomer and dimer derivatives with
26 antibacterial and cytotoxic activities isolated from the deep sea-derived fungus *Penicillium citrinum* NLG-S01-
27 P1. *Mar Drugs* 17: 46.
- 28 Watanabe, A., Ono, Y., Fujii, I., Sankawa, U., Mayorga, M.E., Timberlake, W.E., Ebizuka, Y. (1998) Product
29 identification of polyketide synthase coded by *Aspergillus nidulans* wA gene. *Tetrahedron Lett* 39: 7733-7736.
- 30 Wei R, Li F, Song R, Qin S (2009) Comparison of two marine-sponge-associated *Penicillium* strains DQ25 and
31 SC10: differences in secondary metabolites and their bioactivities. *Ann Microbiol* 59: 579-585.
- 32 Wei J, Wu B. (2020) Chemistry and bioactivities of secondary metabolites from the genus *Fusarium*.
33 *Fitoterapia* 146: 104638.

- 1 Wells JM, Cole RJ, Kirksey JW (1975) Emodin, a toxic metabolite of *Aspergillus wentii* isolated from weevil-
2 damaged chestnuts. Appl Microbiol 30: 26-28.
- 3 Wessels P, Gohrt A, Zeeck A, Drautz H, Zahner H (1991) Metabolic Products of Microorganisms. 260.
4 Naphthgeranines, new naphtho-quinone antibiotics from *Streptomyces* sp. J Antibiot 44: 1013-1018.
- 5 Wheeler MH, Stipanovic RD (1985) Melanin biosynthesis and the metabolism of flaviolin and 2-
6 hydroxyjuglone in *Wangiella dermatitidis*. Arch Microbiol 142: 234-241.
- 7 Wheeler MH, Klich MA (1995) The effect of tricyclazole, pyroquilone, phthalide, and related fungicides on the
8 production of conidial wall pigments by *Penicillium* and *Aspergillus* species. Pesticide Biochem Physiol 52:
9 125-136.
- 10 Wheeler MH, Hocking AD (1995) The effect of tricyclazole, pyroquilone, phthalide, and related fungicides on
11 the production of conidial wall pigments. Pest Biochem Physiol 52: 125-136.
- 12 Wiemann P, Willmann A, Straeten M, Kleigrew K, Beyer M, Humpf HU, Tusdzynski B (2009) Biosynthesis of
13 the red pigment bikaverin in *Fusarium fujikuroi*: genes, their function and regulation. Mol Microbiol 72: 931-
14 946.
- 15 Williams K, Greco C, Bailey AM, Willis CL (2021) Core steps to the azaphilone family of fungal natural
16 products. ChemBioChem 22, in press. Doi: 10.1002/cbic.202100240.
- 17 Wu H, Lao X-F, Wang Q-W, Lu R-R, Shen C, Zhang F, Liu M, Jia L (1989) The Shriachromes: Novel fungal
18 perylenequinone pigments from *Shiraia bambusicola*. J Nat Prod 52:948–951.
- 19 Wu Z, Wang Y, Liu D, Proksch P, Yu S, Lin W (2016) Antioxidative phenolic compounds from a marine-derived
20 fungus *Aspergillus versicolor*. Tetrahedron 72:50–57.
- 21 Xu D, Xue M, Shen X, Jia X, Hou X, Lai D, Zhou L (2021) Phytotoxic secondary metabolites from fungi. Toxins
22 13: 261.
- 23 Xu Y, Vinas M, Alsarrag A, Su L, Pfohl K, Rohlf M, Schafer W, Chen W, Karlovsky P (2019) Bis-naphthopyrone
24 pigments protect filamentous ascomycetes from a wide range of predators. Nat Commun 10: 3579.
- 25 Yamamoto Y, Hirai T, Okada K, Saito K (1974) Studies on the metabolic products of a strain of *Aspergillus*
26 *fumigatus* DH413. 6. Metabolic position of 3,4-dihydroxytoluquinone and fumigatin chlorohydrin in fumigatin
27 biosynthesis. Chem Pharm Bull 22: 83-87.
- 28 Yamamoto Y, Kiriyama N, Arahata S (1968) Studies on products of *Aspergillus fumigatus* (J-4). Chemical
29 structure of metabolic products. Chem Pharm Bull 16; 304-310.
- 30 Yamamoto Y, Kiriyama N, Shimizu S, Koshimura S (1976) Antitumor activity of asterriquinone – metabolic
31 product of *Aspergillus terreus*. Gann 67: 623-624.
- 32 Yamazaki H, Koyama N, Ōmura S, Tomoda H (2010) New rugulosins, anti-MSRA antibiotics, produced by
33 *Penicillium radicum*. Org Lett 12: 1572-1575.

- 1 Yamazaki H, Nonaka H, Masuma R, Ōmura S, Tomoda H (2009) Xanthoradones, new potentiators of
2 imipenem activity against methicillin-resistant *Stahylococcus aureus*, produced by *Penicillium radicum* FKI-
3 3765-2: I. Taxonomy, fermentation, isolation and biological properties. J Antibiot 62: 431-434.
- 4 Yamazaki H, Ōmura S, Tomoda H (2010) Xanthoradone C, a new potentiator of imipenem activity against
5 methicillin-resistant *Stahylococcus aureus*, produced by *Penicillium radicum* FKI-3765-2: I. Taxonomy,
6 fermentation, isolation and biological properties. J Antibiot 63: 329-330.
- 7 Yang LK, Khoo-Beattie C, Goh KL, Chng BL, Yoganathan K, Lai YH, Butler MS (2001) Ardisiaquinones from
8 *Ardisia teysmanniana*. Phytochemistry 58: 1235-1238.
- 9 Yang SQ, Li XM, Xu GM, Li X, An CY, Wang BG (2018) Antibacterial anthraquinone derivatives isolated from a
10 mangrove-derived endophytic fungus *Aspergillus nidulans* by ethanol stress strategy. J Antibiot 71: 778-784.
- 11 Yang Y, Yan Y-M, Wei W, Luo J, Zhang L-S, Zhou X-J, Wang P-C, Yang Y-X, Cheng Y-X (2013) Anthraquinone
12 derivatives from *Rumex* plants and endophytic *Aspergillus fumigatus* and their effects on diabetic
13 nephropathy. Bioorg Med Chem Lett 23: 3905-3909.
- 14 Yang Y, Yang F, Zhao L, Duang R, Chen G, Li X, Li Q, Qin S, Ding Z (2016) A new polyoxygenated
15 farnesylhexenone from fungus *Penicillium* sp. Nat Prod Res 30: 65-68.
- 16 Yilmaz N, Visagie CM, Houbraken J, Frisvad JC, Samson RA (2014) Polyphasic taxonomy of the genus
17 *Talaromyces*. Stud Mycol 78: 175-341.
- 18 Yilmaz N, Visagie CM, Frisvad JC, Houbraken J, Seifert KA, Samson RA (2016) Taxonomic re-evaluation of
19 species in *Talaromyces* section *Islandici*, using a polyphasic approach. Persoonia 36: 37-56.
- 20 Yunzhe H (2012) Diversity in organism in the *Usnea longissimi* lichen. Afr J Microbiol Res 6: 4797-4804.
- 21 Zhai MM, Li J, Jiang CX, Shi YP, Di DL, Crews P, Wu QX (2016) The bioactive secondary metabolites from
22 *Talaromyces* species. Nat Prod Bioperspect 6: 1-24.
- 23 Zhan J, Wijeratne EMK, Seliga CJ, Zhang J, Pierson EE, Pierson III LS, Vanetten HD, Gunatilaka AL (2004) A new
24 anthraquinone and cytotoxic curvularins of a *Penicillium* sp. from the rhizosphere of *Fallugia paradoxa* of the
25 Sonoran desert. J Antibiot 57: 341-344.
- 26 Zhang H, Ahima J, Yang Q, Zhao L, Zhang X, Zheng X (2021) A review of citrinin: Its occurrence, risk
27 implication, analytical techniques, physiochemical properties and control. Food Res Int 141: 110075.
- 28 Zhao YM, Deng CR, Chen X (1990) *Arthriniium phaeospermum* causing dermatomycosis, a new record of
29 China. Acta Mycol Sin 9: 232-235.
- 30 Zimmermann JL, Carlton WW, Tuite J (1979) Mycotoxicosis produced in swine by cultural products of an
31 isolate of *Aspergillus ochraceus*. II. Clinicopathological changes. Vet Pathol 16: 702-709.

Figure captions

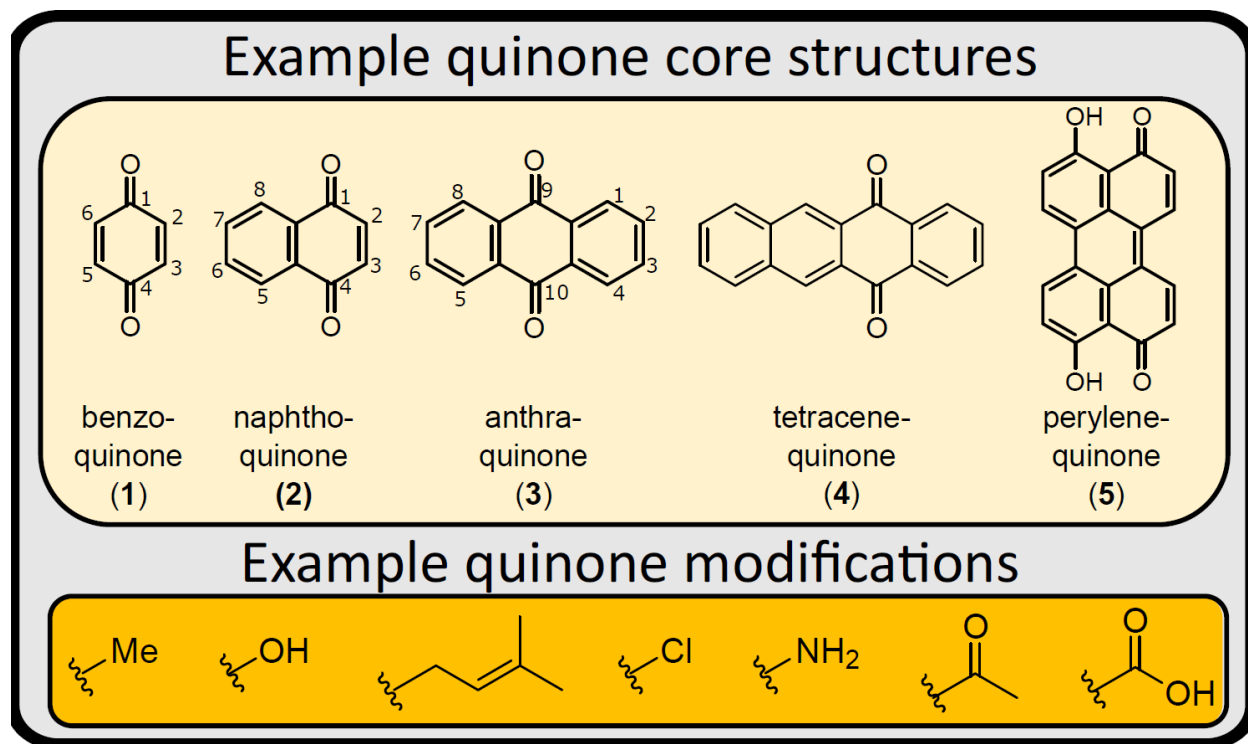


Fig. 1 Structural diversity of naturally occurring quinones. A quinone typically consist of one of several core structures, such as (1), (2), (3), (4) and (5) and a number of additional functional groups such as methylations, oxidations, prenylations, halogenations, aminations, acetylations and carboxylations

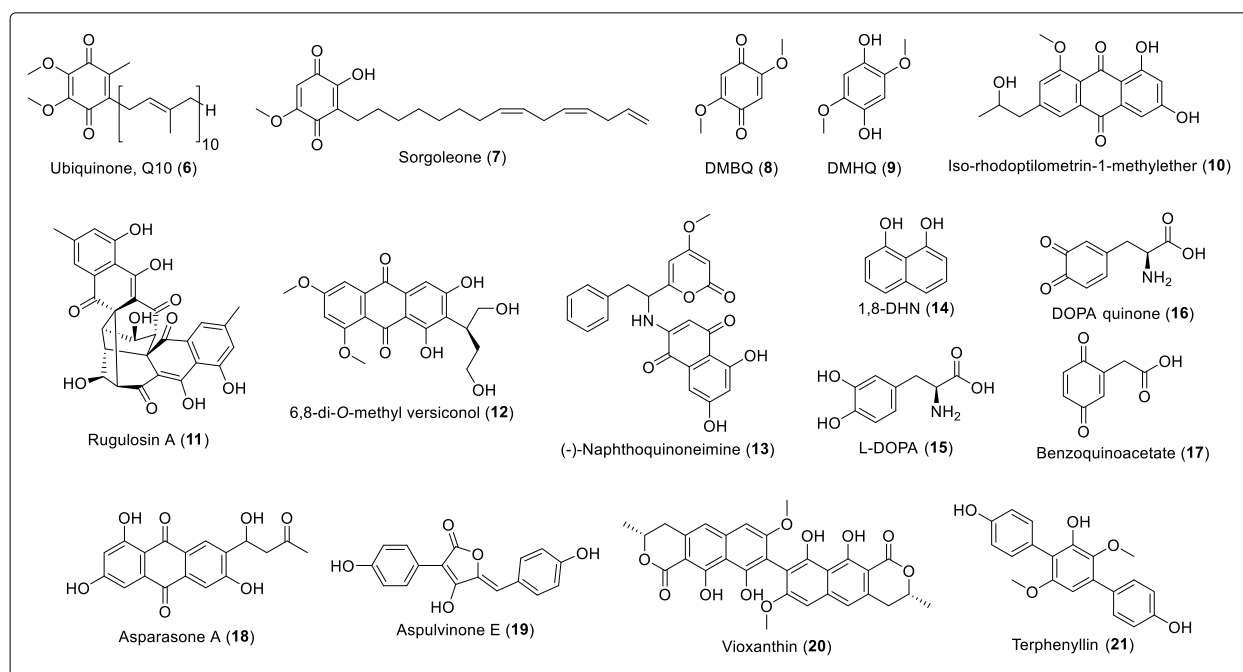


Fig. 2 Some of the quinones and related molecules mentioned in the introduction

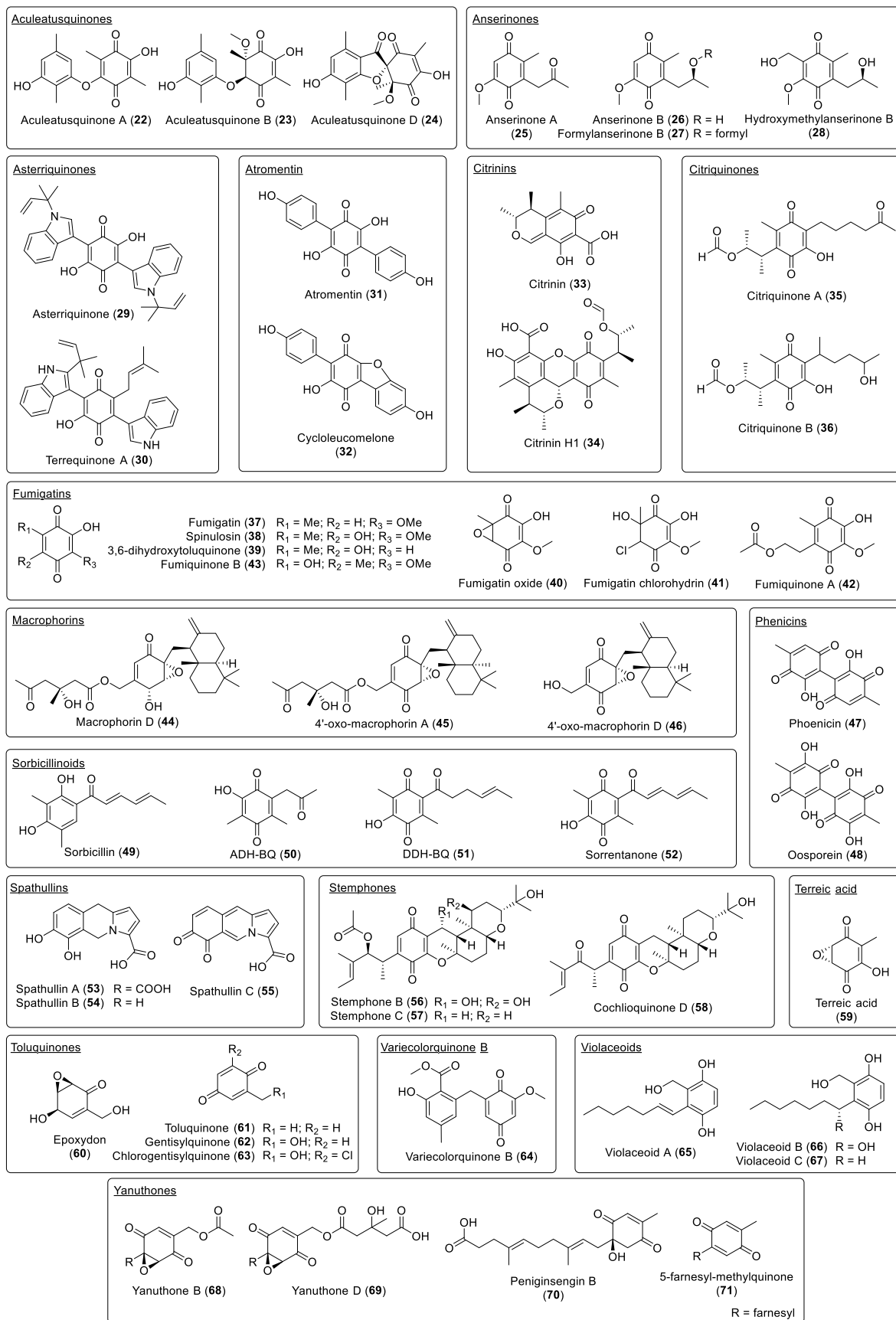


Fig. 3 Representative BQs and related molecules from the quinone families observed in *Aspergillus*,
Penicillium and *Talaromyces*

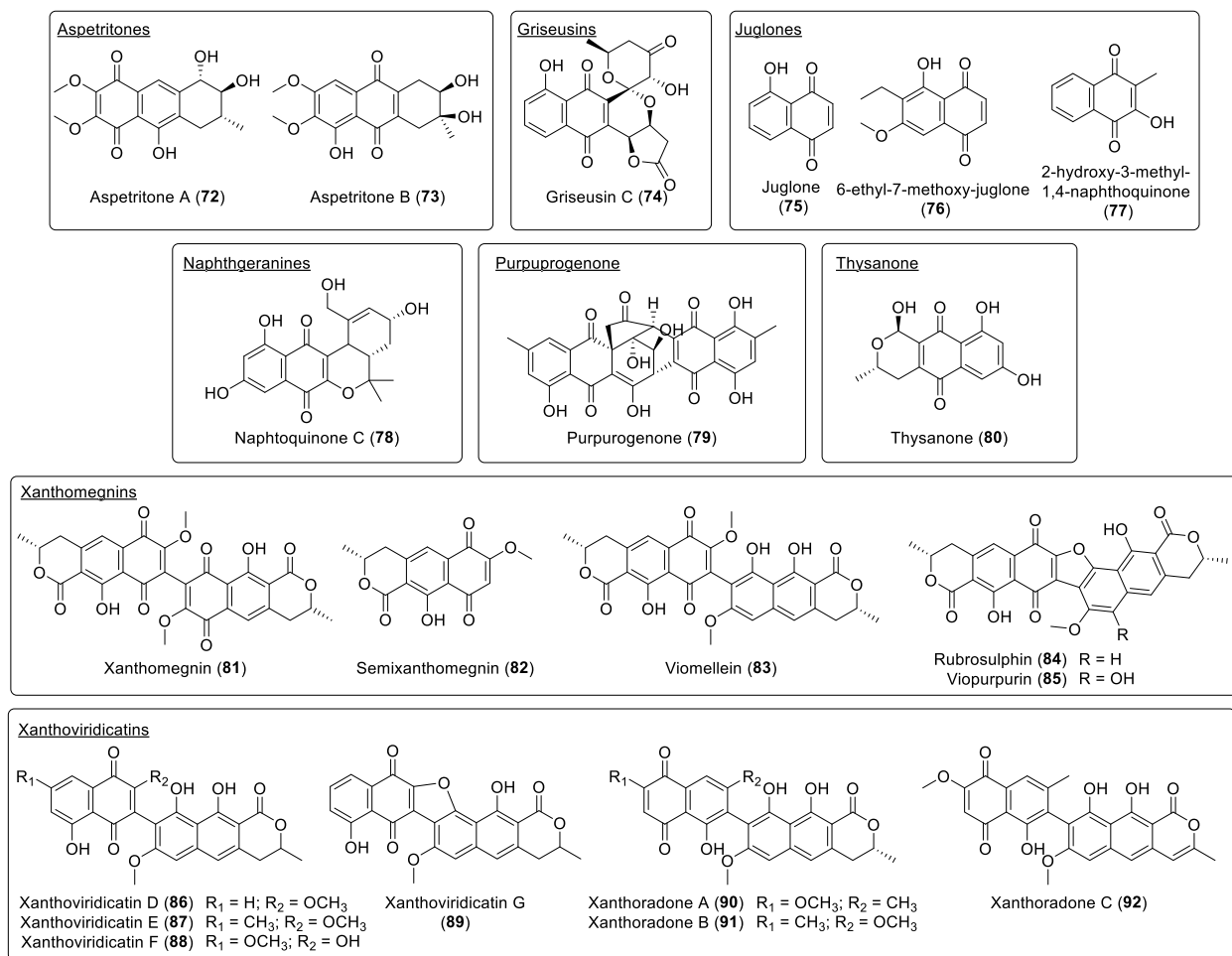
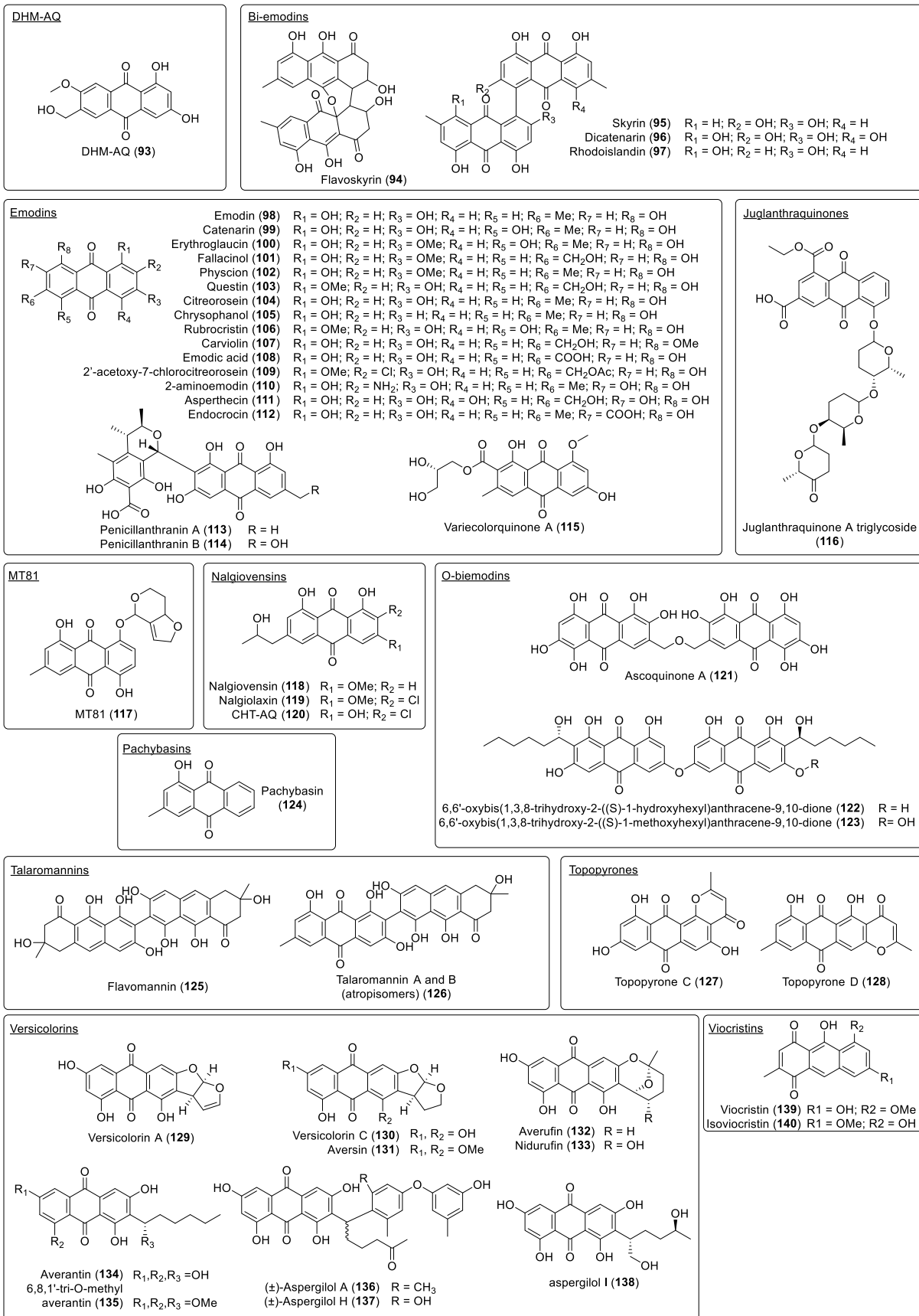
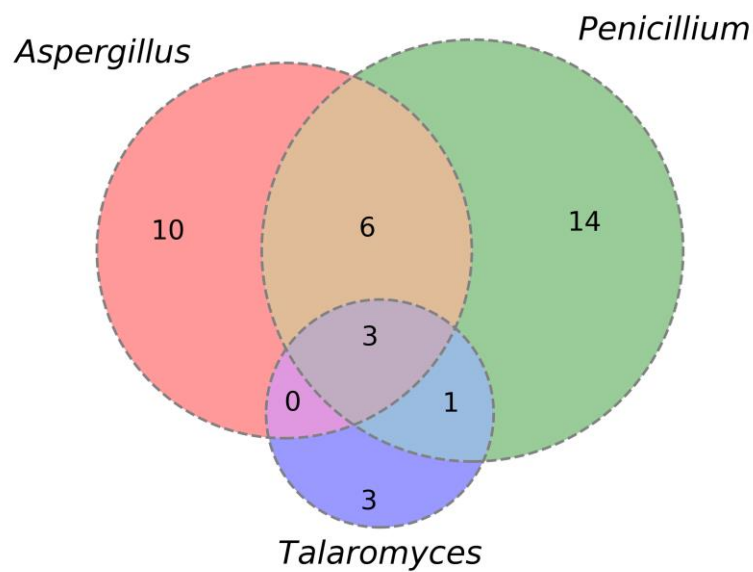


Fig. 4 Representative NQs and related molecules from the quinone families observed in *Aspergillus*,
Penicillium and *Talaromyces*

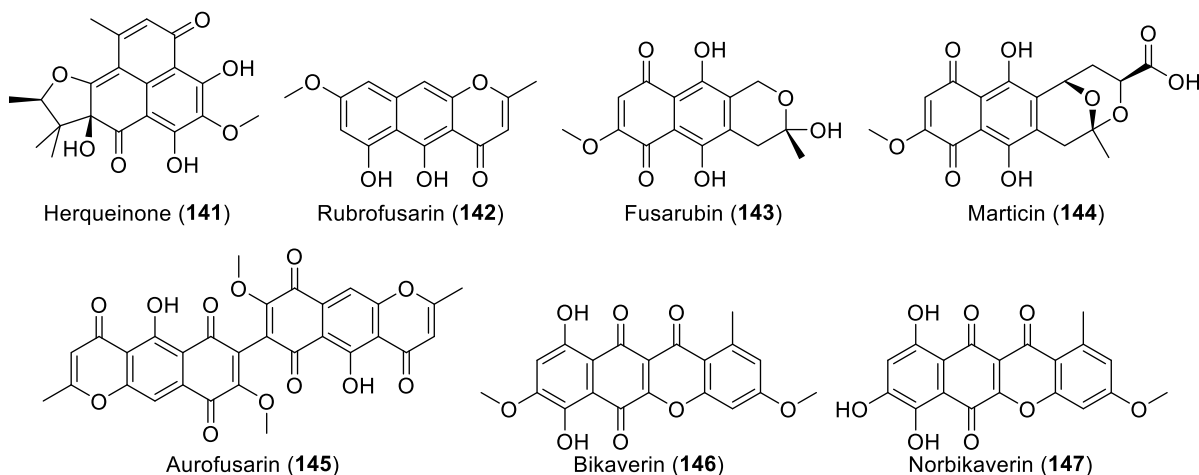


- 1 **Fig. 5** Representative AQs and related molecules from the quinone families observed in *Aspergillus*,
- 2 *Penicillium* and *Talaromyces*

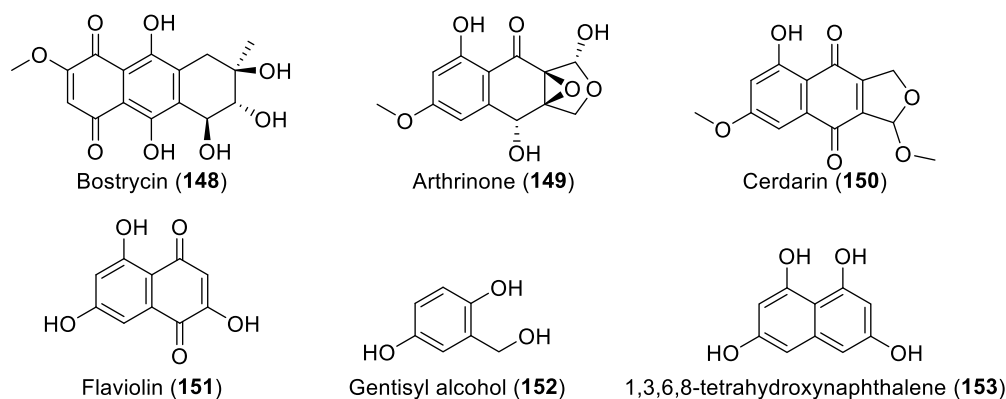


- 3
- 4 **Fig. 6** Venn-diagram showing the number of quinone families appearing in genera *Aspergillus*, *Penicillium* and
- 5 *Talaromyces*

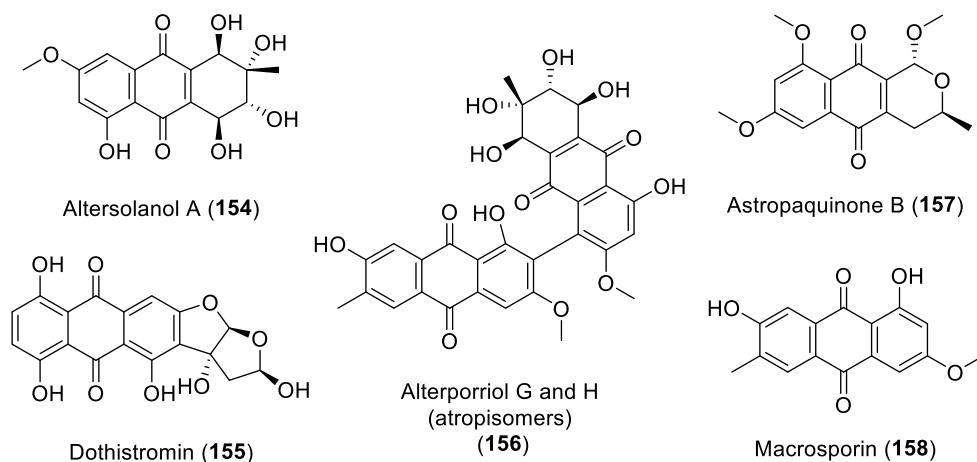
Fusarium quinones



Arthrinium quinones



Alternaria quinones



1
2 **Fig. 7** Quinones and related molecules associated with *Fusarium* and related fusaroid genera, *Arthrinium* and
3 *Alternaria*

Tables

Table 1. Distribution of ubiquinones in the genus *Aspergillus* (Kuraishi et al. 1990; Matsuda et al. 1992; Houbraeken et al. 2020: the species have been updated from Kuraishi et al. (1990); Chang et al. 1991) and listed in an order reflecting their phylogeny).

Subgenus	Section	Number of species examined	Ubiquinone system
<i>Circumdati</i>	<i>Candidi</i>	2	Q-10 (H2)
<i>Circumdati</i>	<i>Petersoniorum</i>	0	-
<i>Circumdati</i>	<i>Nigri</i>	7	Q-9
<i>Circumdati</i>	<i>Terrei</i>	5	Q-10 (H2)
<i>Circumdati</i>	<i>Flavipedes</i>	3	Q-10 (H2)
<i>Circumdati</i>	<i>Janorum</i>	1	Q-10 (H2)
<i>Circumdati</i>	<i>Circumdati</i>	9	Q-10 (H2)
<i>Circumdati</i>	<i>Tannerorum</i>	0	-
<i>Circumdati</i>	<i>Robusti</i>	1	Q-10 (H2)
<i>Circumdati</i>	<i>Flavi</i>	10	Q-10 (H2) (7 spp.), Q10 (3 spp.)
<i>Nidulantes</i>	<i>Nidulantes</i>	24	Q-10 (H2) (19 spp.) and mixed Q-10 (H2) and Q-10 (5 spp.)
<i>Nidulantes</i>	<i>Aenei</i>	2	Q-10 (H2)
<i>Nidulantes</i>	<i>Usti</i>	3	Q-10 (H2)
<i>Nidulantes</i>	<i>Cavernicolarum</i>	0	-
<i>Nidulantes</i>	<i>Raperorum</i>	2	Q-10 (H2)
<i>Nidulantes</i>	<i>Silvatici</i>	1	Q-10 (H2)
<i>Nidulantes</i>	<i>Bispori</i>	1	Q-10 (H2)
<i>Nidulantes</i>	<i>Ochraceorosei</i>	2	Q-10 (H2)
<i>Nidulantes</i>	<i>Sparsi</i>	3	Q-10 (H2)
<i>Fumigati</i>	<i>Fumigati</i>	12	Q-10
<i>Fumigati</i>	<i>Clavati</i>	5	Q-10 (one species Q10 and Q-9)
<i>Fumigati</i>	<i>Vargarum</i>	1	Q-10
<i>Fumigati</i>	<i>Cervini</i>	3	Q-9
<i>Aspergillus</i>	<i>Aspergillus</i>	14	Q-9
<i>Aspergillus</i>	<i>Restricti</i>	6	Q-9
<i>Cremeri</i>	<i>Cremeri</i>	8	Q-9
<i>Polypaecilum</i>	<i>Polypaecilum</i>	0	-

Table 2. Quinones in the genus *Aspergillus*¹⁻⁴ (Frisvad 2015¹; Frisvad and Larsen 2016²; Samson et al. 2014³; Houbraeken et al. 2020⁴; Chen et al. 2017⁵; Du et al. 2014^{5a}; Wang et al. 2007^{5b}; Du et al. 2007^{5c}; Laatsch et al. 1982^{5d}; Sklenář et al. 2017⁶; Rahbæk et al. 2000⁷; Varga et al. 2007⁸; Hubka et al. 2018a⁹; Frisvad et al. 2004¹⁰; Visagie et al. 2014¹¹; Varga et al. 2011a¹²; Frisvad et al. 2019¹³; Kjærboelling et al. 2020¹⁴; Heathcote and Dutton 1969^{14a}; Chen et al. 2014^{14b}; Caceres et al. 2020^{14c}; Mandelare et al. 2018; Samson et al. 2011¹⁵; Hubka et al. 2015¹⁶; Arzanlou et al. 2016¹⁷; Hubka et al. 2016a¹⁸; Varga et al. 2011b¹⁹; Samson et al. 2004²⁰; Samson et al. 2007a²¹; Perrone et al. 2011²²; Vesth et al. 2018²³; Theobald et al. 2018²⁴; Chen et al. 2013²⁵; Myobataka et al. 2014^{25a}; Holm et al. 2014^{25b}; Bugni, et al. 2000^{25c}; Jurjevics et al. 2015²⁶; Barros Correia et al. 2020²⁷; Samson et al. 2011a²⁸; Balajee et al. 2009²⁹; Kiriyaama et al. 1977^{29a}; Hubka et al. 2016a³⁰; Chen et al. 2016a³¹; Varga et al. 2007³²; Visagie and Houbraeken 2020³³; Anslow and Raistrick 1938³⁴; Samson et al. 2007b³⁵; Larsen et al. 2007³⁶; Frisvad et al. 2009³⁷; Frisvad and Larsen 2016³⁸; Hubka et al. 2013³⁹; Hubka et al. 2017⁴⁰; Talbot et al. 2017⁴¹; Hubka et al. 2018b⁴²; Yang et al. 2013^{42a}; Lim et al. 2012^{42b}; Yamamoto et al. 1974^{42c}; Hayashi et al. 2007^{42d}; Turner 1971^{42e}; Yamamoto et al. 1968^{42f}; Abdel-Aziz

- 1 et al. 2018; Steenwyk et al. 2020⁴³; Varga et al. 2010a⁴⁴; Sun et al. 2020b⁴⁵; Chen et al. 2016b⁴⁶; Hubka et al.
- 2 2016b⁴⁷; Wu et al. 2016^{47a}; Huang et al. 2017^{47b}; Chiang et al. 2010^{47c}; Brown and Salvo 1994^{47d}; Li et al.
- 3 2019^{47e}; Houbaken et al. 2007⁴⁸; Samson et al. 2011b⁴⁹; Steyn and Vleggaar, 1974^{49a}; Tanney et al. 2017⁵⁰;
- 4 Koyama et al. 2005.

Section	Subgenus	Number of species examined (number of species known in section)	Number of species producing quinone (percentage)	Quinones produced	Quinone families produced
<i>Aspergillus</i> ^{5, 5a, 5b, 5c, 5d}	<i>Aspergillus</i>	30 (31)	27 (90%)	Emodins including erythroglaucon (100), fallacinal (101), questin (103), questinol, rubrocristin (106), varicolorquinone A (115), viocristin (139), isoviocristin (140) and others*, varicolorquinone B (64)	Emodins (AQ), varicolorquinone B (BQ), viocristins (AQ)
<i>Restrictus</i> ⁶	<i>Aspergillus</i>	20 (21)	1 (5%)	Emodin (98)	Emodins
<i>Candidi</i> ^{7, 8, 9}	<i>Circumdati</i>	7	2 (29%)	Aspetritone A (72) and B (73), emodin	Aspetritones (NQ), emodins
<i>Circumdati</i> ^{10, 11}	<i>Circumdati</i>	27 (28)	21 (78%)	Emodin, xanthomegnins (81)	Emodins (AQ), xanthomegnins (NQ)
<i>Flavi</i> ^{12, 13, 14, 14a, 14b, 14c, 14d}	<i>Circumdati</i>	35 (37)	22 (63%)	Versicolorins**, nalgiovensin (118), nalgioaxin (119)	Versicolorins (AQ), nalgiovensins (AQ)
<i>Flavipedes</i> ^{15, 16, 17, 18}	<i>Circumdati</i>	15	4 (27%)	Emodin (98)	Emodins
<i>Janorum</i> ¹⁶	<i>Circumdati</i>	4	0 (0%)	-	-
<i>Nigri</i> ^{19, 20, 21, 22, 23, 23a, 24, 25, 25a, 25b, 25c}	<i>Circumdati</i>	28	24 (86%)	Aculeatusquinone B (23) and D (24), atromentin (31), emodin (98) (secalonic acid BF), violaceoid A-C (65 , 66 , 67), yanuthone B (68) and D (69)	Aculeatusquinones (BQ), atromentins (BQ), emodins, violaceoid (BQ), yanuthones (BQ)
<i>Petersoniorum</i> ²⁶	<i>Circumdati</i>	4	0 (0%)	-	-
<i>Robusti</i> ¹¹	<i>Circumdati</i>	1	0 (0%)	-	-
<i>Tannerorum</i> ¹¹	<i>Circumdati</i>	1	0 (0%)	-	-
<i>Terrei</i> ^{27, 28, 29, 29a}	<i>Circumdati</i>	17	5 (29%)	Asterriquinones***, 3,6-dihydroxytoluquinone (39), emodin (98), questin (103), terreic acid (59)	Asterriquinones (BQ), fumigatins (BQ), emodins, terreic acid (BQ)
<i>Cremeri</i> ³⁰	<i>Circumdati</i>	17	8 (47%)	Emodin (98) (bisanthrones are end-products), patulin****	Emodins, toluquinones (BQ)
<i>Cervini</i> ³¹	<i>Fumigati</i>	10	6 (60%)	Terreic acid (59), 6-ethyl-7-methoxy-juglone (76)	Terreic acid, juglones (NQ)
<i>Clavati</i> ^{32, 33}	<i>Fumigati</i>	6 (8)	3 (50%)	Patulin****	Toluquinones
<i>Fumigati</i> ^{34, 35, 36, 37, 38, 39, 40, 41, 42, 42a, 42b, 42c, 42d, 42e, 42f, 42g}	<i>Fumigati</i>	52 (59)	11 (21%)	3,4-dihydroxytoluquinone, emodin (98), 2-chloroemodin, (chloroanthrones are end products), emodin 1,6-dimethylether, endocrocin (112), fumigatin (37), fumigatin chlorhydrin, fumiquinone A (42) and B (43), 1-methylemodin, physcion (102), questin, spinulosin (38), juglanthraquinone A triglycoside (116)	Fumigatins, emodins, juglanthraquinone A triglycoside
<i>Vargarum</i> ⁴³	<i>Fumigati</i>	1	0 (0%)	-	-
<i>Aenei</i> ⁴⁴	<i>Nidulantes</i>	11	8 (73%)	Emodin (98), versicolorins**	Emodins, versicolorins
<i>Cavernicolarum</i> ⁴⁵	<i>Nidulantes</i>	5	0 (0%)	-	-

<i>Nidulantes</i> ^{46,47,47a,47b, 47c,47d,47e}	<i>Nidulantes</i>	71 (75)	59 (83%)	2-aminoemodin (110), 2-amino- ω -hydroxyemodin, ascoquinone A (121), asperthecin, emodic acid (108), emodin (98) (monodictyphenone BF), endocrocin (112), 2-hydroxyemodin, ω -hydroxyemodin (104), 2- ω -hydroxyemodin, methyl 2-hydroxyemodin, terrequinone (30), versicolorins** including aspergilol A (136), B, G, H (137) and I (138), 6,6'-oxybis(1,3,8-trihydroxy-2-((S)-1-methoxyhexyl)anthracene-9,10-dione (122), 6,6'-oxybis(1,3,8-trihydroxy-2-((S)-1-hydroxyhexyl) anthracene-9,10-dione (123))	Emodins, O-bi-emodins (AQ), asterriquinones, versicolorins
<i>Ochraceorosei</i> ⁴⁶	<i>Nidulantes</i>	3	2 (66%)	Versicolorins**	Versicolorins
<i>Raperorum</i> ⁴⁶	<i>Nidulantes</i>	2	1 (50%)	Unknown AQ	-
<i>Silvatici</i> ⁴⁶	<i>Nidulantes</i>	1	0 (0%)	-	-
<i>Sparsi</i> ⁴⁷	<i>Nidulantes</i>	9	0 (0%)	-	-
<i>Usti</i> ^{45,46,48,49,49a}	<i>Nidulantes</i>	25	5 (20%)	Versicolorins**	Versicolorins
<i>Polypaecilum</i> ⁵⁰	<i>Polypaecilum</i>	3 (16)	0 (0%)	-	-
Unknown section ⁵¹				Stemphone B (56) and C (57), cochlioquinone D (58)	Stemphones

*Emodins including emodin (**98**), 2- ω -hydroxyemodin, physcion (**102**), caternarin (**99**) and others (the biosynthetic end products can be derived secondary metabolites that are not quinones (i.e. aspergiolide A, bisanthrons, chloroanthraquinones, secalonc acids, tryptacidin, sulochrin).

Versicolorins and related decaketide precursors and end- or shunt-products of sterigmatocystins, aflatoxins or austocystins (averufin (132**), averantin (**134**), averantin-1'-butylether, aversin (**131**), averthrin, 7-chloroaverantin, (1'S)-7-chloroaverantin, deoxyversicolorin A, (1'S)-6,1'-O,O-dimethylaverantin, (1'S)-6,1'-O,O-dimethyl-7-bromoaverantin, (1'S)-6,1'-O,O-dimethyl-7-chloroaverantin, hydroxyaverufin, 1-O-methylaverantin, 6-O-methylaverantin, (1'S)-6-O-methyl-7-bromoaverantin, (1'S)-1'-O-methylchloroaverantin, (1'S)-1'-O-methyl-7-chloroaverantin, 6-O-methyl-7-chloroaverantin, 8-O-methylindurufin, norsolorinic acid, 1,3,6,8-tetrahydroxy-2,2'-(6'-methyltetrahydrofuran)anthraquinone, versicolorin A (**129**), B, C (**130**), versiconol, and others).

***Asterriquinones include asterriquinone (**29**), asterriquinone monoacetate, asterriquinone A, A-1, A-2, A-3, A-4, B-1, B-2, B-3, B-4, C-1, C-2, B, C, D, CT5, demethylasterriquinone B1, isoasterriquinone, neoasterriquinone, and terrequinone A (**30**) (Yamamoto et al. 1976; Arai et al. 1981a,b; Kaji et al. 1994; Mocek et al. 1996).

****Patulin is not itself a quinone but quinones such as toluquinone (**61**), gentisylquinone (**62**), chlorogentisyl quinone (**63**) and hydroxychlorogentisyl quinone have been reported from patulin producers, as precursors or shunt products in the biosynthetic pathway (Ali et al. 2017).

1 Table 3. Distribution of quinones in the genus *Penicillium* (¹Frisvad and Samson, 2004; ²Frisvad et al. 2004a;b;
2 ³Visagie et al. 2014; Houbraken et al. ⁴Houbraken et al. 2010a; ⁵Houbraken et al. 2011; ⁶Houbraken et al.
3 2014; ⁷Houbraken et al. 2020; ⁸Mahmoodian and Stickings, 1964; ⁹Anslo and Raistrick, 1938; ¹⁰Friedheim,
4 1938; ¹¹Curtin et al. 1940, ¹²Posternak et al. 1943; ¹³Peterson et al. 2015; ¹⁴Shang et al. 2016; ¹⁵Ranji et al.
5 2013; ¹⁶Abdelwahab et al. 2018; ¹⁷Gautschi et al. 2004; ¹⁸Smetanina et al. 2016; ¹⁹Sun et al. 2013; ²⁰Ngan et
6 al. 2017; ²¹Luo et al. 2019; ²²Zhan et al. 2004; ²³Aly et al. 2011; ²⁴Morehouse et al. 2020; ²⁵Hind, 1940;
7 ²⁶Elbanna et al. 2021; ²⁷Christensen et al. 1998; ²⁸Ngan et al. 2017; ^{28a}Khamthong et al. 2012; ^{28b}He et al.
8 2017; ²⁹Janso et al. 2005; ³⁰Visagie et al. 2016; ³¹Unpublished observations; ³²Frisvad and Filtenborg, 1990;
9 ³³Bao et al. 2014, ³⁴Wang et al. 2014; ³⁵Li et al. 2018; ³⁶Singh et al. 1991; ³⁷Del Valle et al. 2016; ³⁸Nord et al.
10 2019; ³⁹Visagie et al. 2021; ⁴⁰Gupta et al, 1997; ⁴¹Wei et al. 2009; ⁴²Hawas et al. 2013; ⁴³Gutarowska et al.
11 2014; ⁴⁴Fujimoto et al. 2001; ⁴⁵Singh et al. 2003; ⁴⁶Raistrick & Ziffer, 1951; ⁴⁷Birch & Massy-Westropp, 1957;
12 ⁴⁸Birch & Stapleford, 1967; ⁴⁹Liu et al. 2005; ⁵⁰Cheng et al. 2018; ⁵¹Yang et al. 2016; ⁵²Li et al. 2003; ⁵³Miller
13 & Huang, 1995; ⁵⁴Stack et al. 1979; ⁵⁵Lund and Frisvad 2004; ⁵⁶Hallas-Møller et al. 2018; ⁵⁷Nicolaisen et al.
14 1996, ⁵⁸Frisvad et al. 1994; ⁵⁹Houbraken et al. 2016; ⁶⁰Raper & Fennell, 1965; ⁶¹Frisvad et al. 2016; ⁶²Ali et
15 al. 2017; ⁶³Houbraken et al. 2010b; ⁶⁴Li et al. 2006; ⁶⁵Kanai et al. 2000).

Section	Subgenus	Number of species examined (number of species known in section in all)	Number of species producing quinone (percentage)	Quinones produced	Quinone families produced
<i>Alfrediorum</i>	<i>Aspergilloides</i>	1 (1)	0 (0%)	-	-
<i>Aspergilloides</i> ^{8,9}	<i>Aspergilloides</i>	11 (53)	2 (18%)	Endocrocin (112), questins (103), spinulosin (38)	Emodins (AQ), fumigatins (BQ)
<i>Charlesia</i> ^{10, 11, 12}	<i>Aspergilloides</i>	4 (9)	2 (50%)	Phoenicin (47)	Phoenicin (BQ)
<i>Cinnamopurpurea</i> ¹³	<i>Aspergilloides</i>	9 (20)	1 (11%)	Unknown BQ	-
<i>Citrina</i> ^{14,15,16,17,18, 19, 20, 21, 22, 23, 24, 25, 26, 27, 28, 28a, 28b}	<i>Aspergilloides</i>	39 (42)	15 (38%)	Aculeatusquinone B (23), anserinones (25), emodins including emodin (98), chloroemodins, carviolins (107), chlorocarviolins, chrysophanol (105), ω-hydroxyemodin (104) (=citreorosein) and citreorosein-3-O-sulfate, citrinin H1 (34), citriquinone A and B (35 , 36), DHM-AQ (93), phoenicin (47), penicillanthranins A and B (113 , 114), 2'-acetoxy-7-chlorocitreorosein (109)	Aculeatusquinones (BQ), anserinones (BQ), emodins, citrinoids (BQ), DHM-AQ (AQ), phoenicin
<i>Crypta</i>	<i>Aspergilloides</i>	0 (1)	0 (0%)	-	-
<i>Eremophila</i>	<i>Aspergilloides</i>	0 (1)	0 (0%)	-	-
<i>Exilicaulis</i> ^{27, 29, 30}	<i>Aspergilloides</i>	36 (58)	9 (25%)	Carviolins, emodin (98), fumigatin (37), spinulosin (38), phoenicin (47), unknown AQ	Emodins, fumigatins, phoenicin
<i>Gracilenta</i> ³¹	<i>Aspergilloides</i>	4 (6)	2 (50%)	Emodin (98), toluquinone (39), spinulosin (38), unknown AQs	Emodins, toluquinones (BQ), fumigatins
<i>Griseola</i>	<i>Aspergilloides</i>	1 (1)	0 (0%)	-	-
<i>Inusitata</i>	<i>Aspergilloides</i>	0 (2)	0 (0%)	-	-

<i>Lanata-Divariata</i> ^{32, 33, 34}	<i>Aspergilloides</i>	43 (76)	13 (30%)	Aloe-emodin, chrysophanol (105), ω-hydroxyemodin (104), emodin (98), toluquinone (39), unknown AQs, xanthomegnin (81)	Emodins, toluquinones, xanthomegnins (NQ)
<i>Lasseniorum</i>	<i>Aspergilloides</i>	1 (1)	0 (0%)	-	-
<i>Ochrosalmonea</i> ³¹	<i>Aspergilloides</i>	2 (2)	1 (50%)	1 unknown BQ and 1 unknown AQ	-
<i>Ramigena</i>	<i>Aspergilloides</i>	6 (6)	0 (0%)	-	-
<i>Sclerotium</i> ³⁵	<i>Aspergilloides</i>	24 (35)	2 (8%)	Physcion (102)	Emodins
<i>Stolkia</i>	<i>Aspergilloides</i>	7 (7)	0 (0%)	-	-
<i>Thysanophora</i> ³⁶	<i>Aspergilloides</i>	2 (8)	1 (50%)	Thysanone (80)	Thysanone (NQ)
<i>Torulomyces</i>	<i>Aspergilloides</i>	0 (15)	0 (0%)	-	-
<i>Brevicompacta</i> ^{37, 38}	<i>Penicillium</i>	11 (11)	1 (10%)	CHT-AQ (120), spathullin C (55)	Nalgiovensins (AQ), spathullins (BQ),
<i>Canescentia</i> ^{39, 40}	<i>Penicillium</i>	19 (21)	7 (37%)	Spinulosin (38) or fumigatin (37), MT81 (117), patulin*, unknown AQ	Fumigatins, MT81 (AQ), toluquinones
<i>Chrysogena</i> ^{41, 42, 43, 44, 45, 46, 47, 48, 49, 50, 51, 52, 53}	<i>Penicillium</i>	18 (19)	8 (44%)	ADH-BQ (50), cycloleucomelone (32), DDH-BQ (51), emodin (98), 5-farnesyl-methylquinone (71), 2-ω-hydroxyemodin, 2-hydroxy-3-methyl-1,4-naphthoquinone (77), nalgiovensin (118), nalgolaxin (119), 4'-oxo-macrophorin A (45) and D (46), peniginsengin B (70), sorrentanone (52), xanthoviridicatin E (87) and F (88)	Sorbicillinoids (BQ), atromentins (BQ), emodins, yanuthones (BQ), juglones (NQ), nalgiovensins, macrophorins (BQ), xanthoviridicatin (NQ)
<i>Eladia</i>	<i>Penicillium</i>	2 (2)	0 (0%)	-	-
<i>Fasciculata</i> ^{1,2, 54, 55, 56, 57, 58}	<i>Penicillium</i>	30 (32)	8 (21%)	Emodin (98), physcion (102), patulin*, unknown AQs, rubrosulphin (84), viomellein (83), viopurpurin (85), xanthomegnin (81), xanthoviridicatin D (86) and G (89)	Emodins, xanthomegnins, toluquinones, xanthoviridicatin
<i>Formosana</i> ²	<i>Penicillium</i>	1(1)	1 (100%)	Patulin*	Toluquinones
<i>Osmophila</i> ⁵⁹	<i>Penicillium</i>	2 (2)	1 (50%)	Patulin*	Toluquinones
<i>Paradoxa</i> ⁶⁰	<i>Penicillium</i>	4 (9)	1 (25%)	Pachybasin (124)	Pachybasin (AQ)
<i>Penicillium</i> ^{1,2}	<i>Penicillium</i>	7 (8)	4 (57%)	Patulin*, viomellein (83), xanthomegnin (81)	Toluquinones, xanthomegnins
<i>Ramosum</i> ^{59, 61}	<i>Penicillium</i>	12 (17)	1 (8%)	Unknown AQ	-
<i>Robsamsonia</i> ^{1,2, 59, 62}	<i>Penicillium</i>	11 (14)	8 (73%)	Gentisyl quinone (62), hydroxychlorogentisyl quinone ⁶² , patulin*	Toluquinones
<i>Roquefortorum</i> ^{1,2,63}	<i>Penicillium</i>	4 (5)		Patulin*	Toluquinones
<i>Turbata</i>	<i>Penicillium</i>	3(4)	0 (0%)	-	-
Unknown section ⁶⁴	-	-	-	Griseusin C (74), naphthoquinone C (78)	Griseusins (NQ), naphthgeranines (NQ)
Unknown section ⁶⁵	-	-	-	Topopyrone C (127) and D (128)	Topopyrones (AQ)

*Patulin is not itself a quinone but quinones such as toluquinone (**61**), chlorogentisyl quinone (**63**) and hydroxychlorogentisyl quinone have been reported from patulin producers, as precursors or shunt products in the biosynthetic pathway (Ali et al. 2017).

Table 4. Distribution of quinones in the genus *Talaromyces* (¹Frisvad et al. 1990; ²Samson et al. 2011c; ³Yilmaz et al. 2014; ⁴Frisvad, 2015; ⁵Houbraken et al. 2020; ⁶Sun et al. 2020a; ⁷Zhai et al. 2016; ⁸Lan and Wu, 2020; ⁹Chen et al. 2016c; ¹⁰Takeda et al. 1973; ¹¹Howard & Raistrick, 1954; ¹²Yamazaki et al. 2010; ¹³Yamazaki et al. 2009; ¹⁴Breen et al. 1955; ¹⁵Yilmaz et al. 2016; ¹⁶Sedmera et al. 1978; ¹⁷Mondal et al. 2020; ¹⁸Hussain et al. 2015; ^{18a}Bara et al. 2013; ¹⁹Samson et al. 1989; ²⁰Seifert et al. 2004; ²¹Frisvad et al. 1990; ²²van-Reenen Hoekstra et al. 1990; ²³van Eijk, 1973; ²⁴Fuska et al. 1991; ²⁵Proksa et al. 1994; ²⁶Fujimoto et al. 1986; ²⁷Roberts and Thompson, 1971; ²⁸Wang et al. 2011; ²⁹Kalansuryia et al. 2019).

Section	Number of species (number of species known in section in all)	Number of species producing quinone (percentage)	Quinones produced	Quinone families produced
<i>Bacillispori</i>	2 (7)	0 (0%)	-	-
<i>Helici</i> ⁹	4 (13)	1 (25%)	Emodin (98) (secalonic acid BF)	Emodins (AQ)
<i>Islandici</i> ^{9,10,11,12,13,14,15,16,17,18,18a}	17 (34)	11 (65%)	Emodins and biemodins ^{10,11} (emodins: catenarin (99), chrysophanol (105), chrysophanic acid, emodin (98), endocrocin (112), ω-hydroxyemodin (104), islandicin, biemodins: (+)-aurantioskyrin, (+)-auroskylin, (+)-deanhydrorugulosin, (-)-deoxyluteoskyrin, (-)-deoxyrubroskyrin, dicatenarin (96), (-)-flavoskyrin (94), (+)-iridoskyrin, (-)-luteoskyrin, (-)-4a-oxyluteoskyrin, (+)-4a-oxyluteoskyrin, (+)-oxyskyrin, (+)-punicoskyrin, (+)-rhodoislandin A & B, (+)-roseoskyrin, (-)-rubroskyrin, rugulin, (-)-rugulosin, rugulosin B, rugulosin C, (+)-skyrin (95), skyrinol) (luteoskyrin BF), xanthoradone A-C (90 , 91 , 92), xanthomegnin (81) & viomellein (83), talaromannin A and B (126)	Emodins, biemodins (AQ), xanthoviridicatin (NQ), xanthomegnins (NQ), talaromannins (AQ)
<i>Purpurei</i> ¹⁹	5 (13)	2 (40%)	Emodin (98) (secalonic acid BF)	Emodins
<i>Subinflati</i> ^{19,20}	2 (6)	0 (0%)	-	-
<i>Talaromyces</i> ^{21,22,23,24,25,26}	42 (78)	8 (19%)	Catenarin (99), emodin (98) (secalonic acid BF), erythroglaucon (100), juglone (75), rugulosine, skyrin (95)	Emodins, juglones (NQ), biemodins (AQ)
<i>Tenuis</i>	0 (1)	0 (0%)	-	-
<i>Trachyspermi</i> ^{7,8,27,28}	12 (28)	2 (17%)	Emodin (98), ω-hydroxyemodin (104) (secalonic acid BF), purpurogenone (79)	Emodins (AQ), purpurogenone (NQ)
Unknown section and species ²⁹			Talaroquinone ^{28*}	

*Potentially an artificial oxidation product.