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Published in:
Applied Microbiology and Biotechnology

DOI (link to publication from Publisher):
10.1007/s00253-021-11597-0

Publication date:
2021

Document Version
Accepted author manuscript, peer reviewed version

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, naphtoquinones, *Aspergillus*, *Penicillium*, *Talaromyces*, *Fusarium, Arthrinium*

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, Arthrinium* 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. nalgiolaxin, **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 (QH_2), the fully oxidized quinone state (Q) and the intermediate semi-quinone radical state ($QH^{\bullet}$) (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 that 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 anthropod 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 *Gloeophillum 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-dimethoxthydroquinone (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 Sathiavelu 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 down-stream 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 *Arthrinium 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 microbiotics.

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 laxitative agents, emodin (**98**) is also a well studied anti-cancer agent (Srinivas et al. 2007). Some quinones have shown promise as photosentitizers 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-parasiticidal 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-chlorocitreorosein (**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). Furtermore, 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 diarrhea 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 affective 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 (Kurasihi 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*, *Penicilliopsis*, *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 conidum 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; Sapmak 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 pyomelanin, which involves the BQ benzoquinoacetate (**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; Kjærbølling 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, occationally 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 asterriquonine 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 *Cremei* and *Clavati* and *Penicillium* sections *Gracilenta, 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 naphtoquinoid 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 napthgeranines 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., naphtoquinone 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 *Taleromyces* section *Trachyspermi.*

Thysanone (**80**) is a naphtopyrone 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*.

Xanthoviridicatins are 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*.

Biemodins 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 biemodins separate from what we call the *O*-biemodins, which are also composed of two emodins, but fused with an ether bond (see below). Besides the method of fusion, the biemodins are observed in *Talaromyces* sections *Islandici* and *Talaromyces*, while the *O*-biemodins are observed in *Aspergillus* section *Nidulantes*. Examples of the biemodins flavoskyrin (**94**), skyrin (**95**), dicatenarin (**96**) and rhodoislandin (**97**) are shown in Fig. 5., but many other known biemodins 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**), erythroglaucin (**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-quonine 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 variecolorquinone 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 variecolorquinone 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 xanthoviridicatins 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 where 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, xanthoviridicatins, 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 xanthoviridicatins 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**), variecolorquinone B (**64**), versicolorins and violaceoids, viocristins and juglanthraquinone A triglycoside (**116**). In *Penicillium* the unique families are DHM-AQ (**93**), anserinones, citrinoids, citriquinones, grieusins, 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 PKSs 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 semilar 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 trypacidin 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 methylidene 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 hydroxyclavatol 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 at 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 physcion (**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.

Ethical Statement

Funding: This project was funded by Novo Nordic Foundation (grant no. NNF 18OC0034952).

Conflicts of interest/Competing interests: The authors have no conflict of interest to declare.

Ethical approval: This article does not contain any studies with human participants or animals performed by any of the authors

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.

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Figure captions

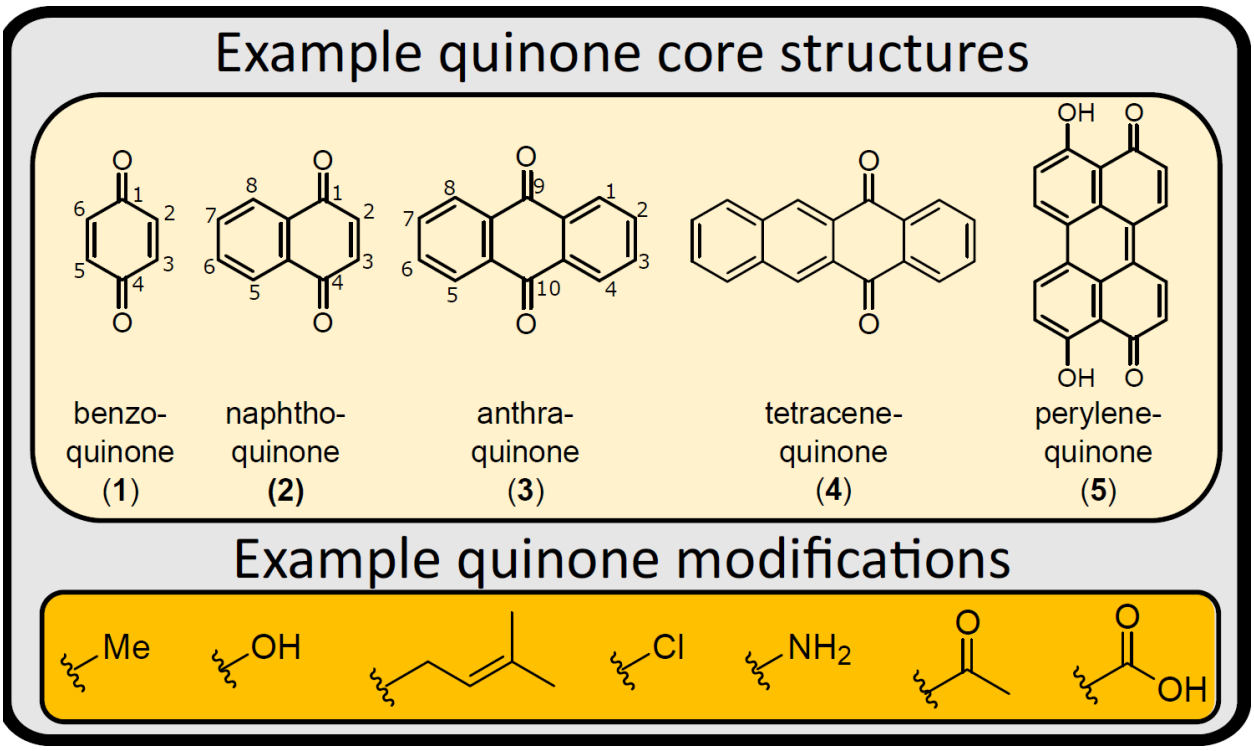


Fig. 1 Structural diversity of naturally occourring quinones. A quinone typically consist of one of several core structures, such as (**1**), (**2**), (**3**), (**4**) and (**5**) and a number of additional functional groups such as methylations, oxidations, prenylations, halogenations, aminations, acetylations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

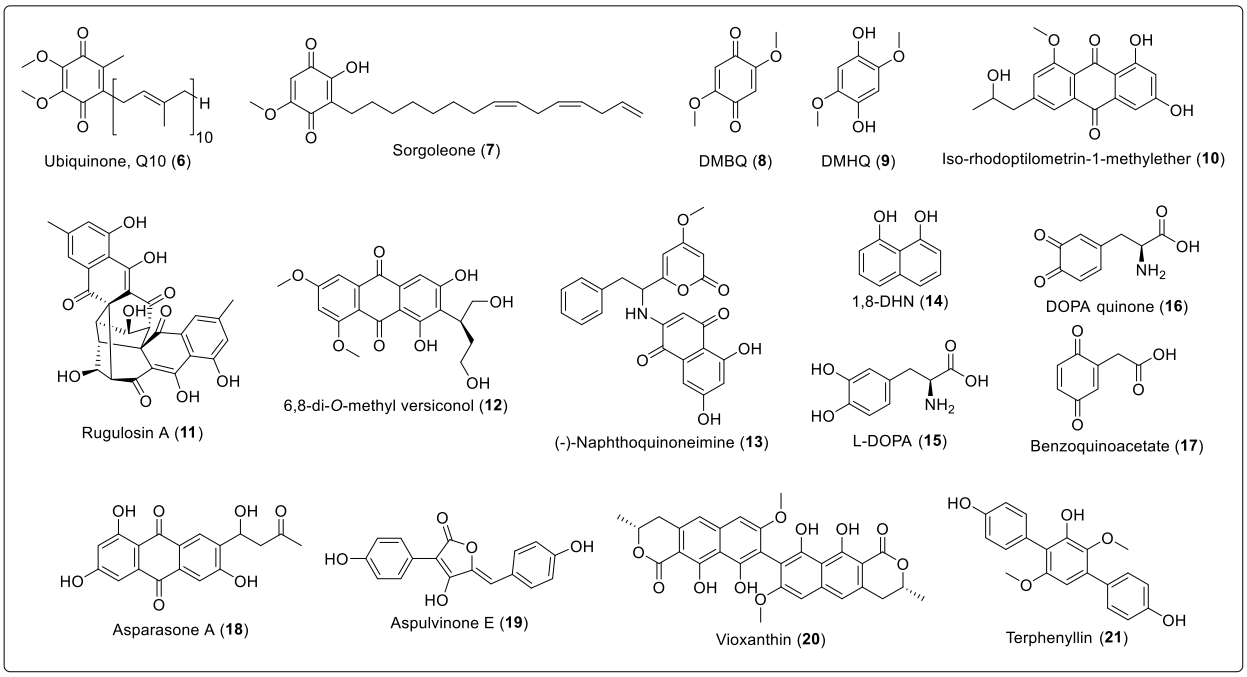


Fig. 2 Some of the quinones and related molecules mentioned in the introduction

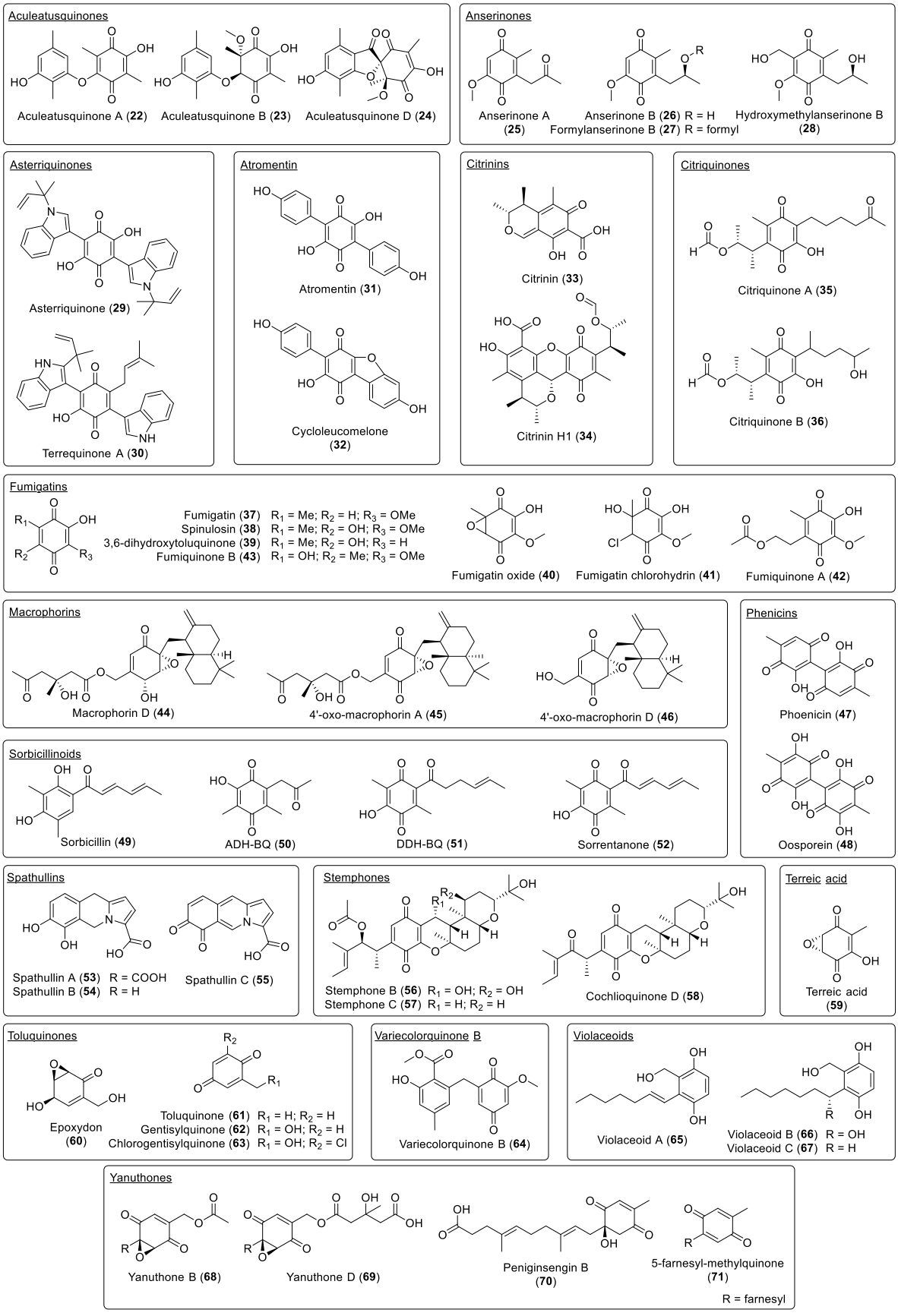


Fig. 3 Representative BQs and related molecules from the quinone families observed in *Aspergillus, Penicillium* and *Talaromyces*

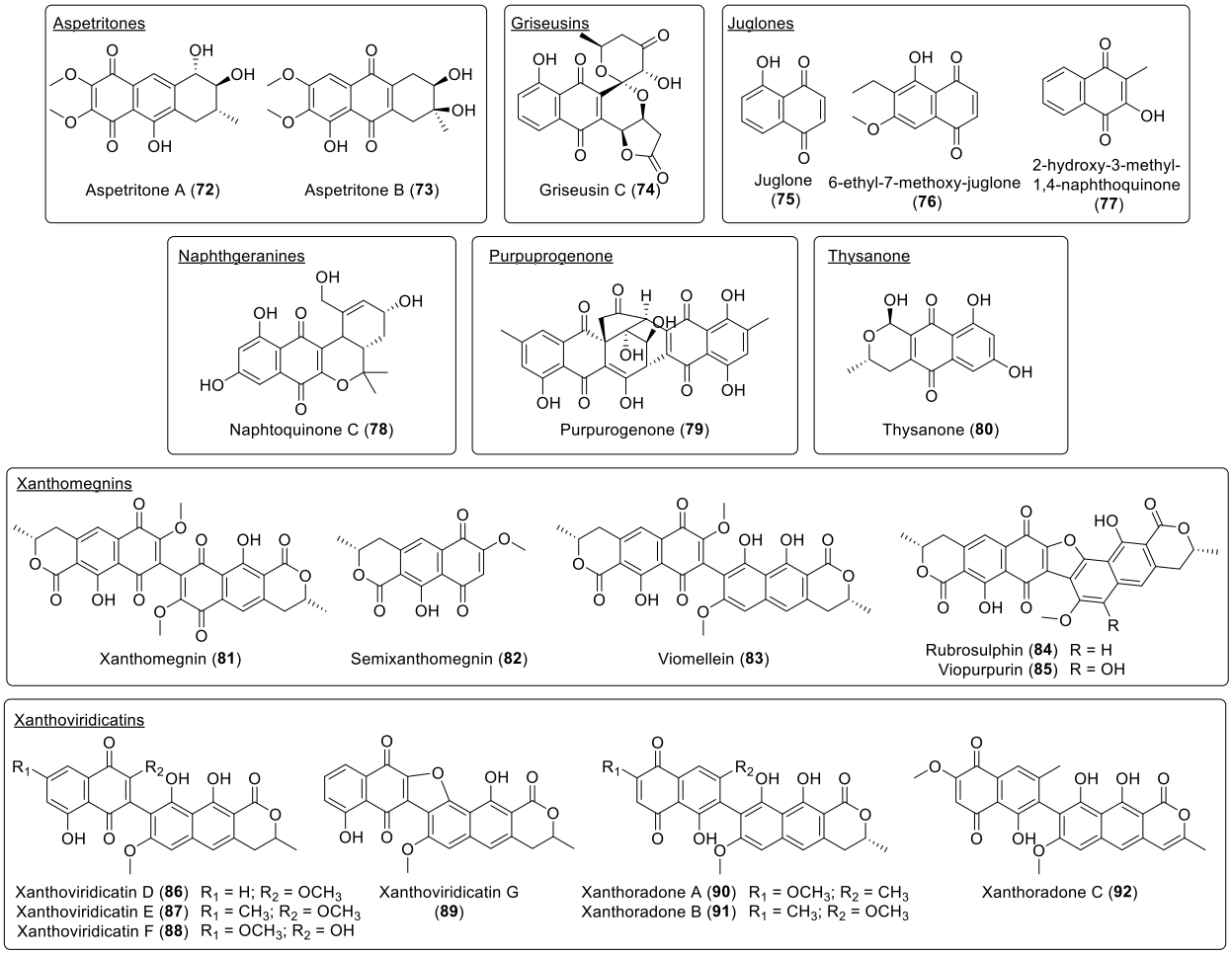
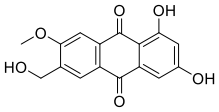


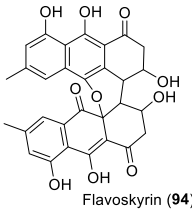
Fig. 4 Representative NQs and related molecules from the quinone families observed in *Aspergillus, Penicillium* and *Talaromyces*

DHM-AQ

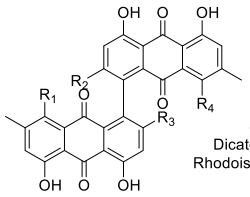


DHM-AQ (**93**)

Bi-emodins

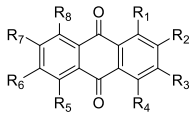


Flavoskyrin (**94**)

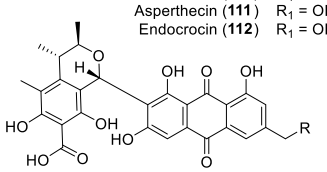


Skyrin (**95**) R_1 = H; R_2 = OH; R_3 = OH; R_4 = H
Dicatenarin (**96**) R_1 = OH; R_2 = OH; R_3 = OH; R_4 = OH
Rhodoislandin (**97**) R_1 = OH; R_2 = H; R_3 = OH; R_4 = H

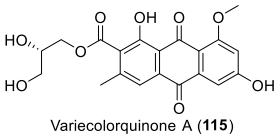
Emodins



Emodin (**98**) R_1 = OH; R_2 = H; R_3 = OH; R_4 = H; R_5 = H; R_6 = Me; R_7 = H; R_8 = OH
Catenarin (**99**) R_1 = OH; R_2 = H; R_3 = OH; R_4 = H; R_5 = OH; R_6 = Me; R_7 = H; R_8 = OH
Erythroglaucin (**100**) R_1 = OH; R_2 = H; R_3 = OMe; R_4 = H; R_5 = OH; R_6 = Me; R_7 = H; R_8 = OH
Fallacinol (**101**) R_1 = OH; R_2 = H; R_3 = OMe; R_4 = H; R_5 = H; R_6 = CH_2OH; R_7 = H; R_8 = OH
Physcion (**102**) R_1 = OH; R_2 = H; R_3 = OMe; R_4 = H; R_5 = H; R_6 = Me; R_7 = H; R_8 = OH
Questin (**103**) R_1 = OMe; R_2 = H; R_3 = OH; R_4 = H; R_5 = H; R_6 = CH_2OH; R_7 = H; R_8 = OH
Citreorosein (**104**) R_1 = OH; R_2 = H; R_3 = OH; R_4 = H; R_5 = H; R_6 = Me; R_7 = H; R_8 = OH
Chrysophanol (**105**) R_1 = OH; R_2 = H; R_3 = H; R_4 = H; R_5 = H; R_6 = Me; R_7 = H; R_8 = OH
Rubrocristin (**106**) R_1 = OMe; R_2 = H; R_3 = OH; R_4 = H; R_5 = OH; R_6 = Me; R_7 = H; R_8 = OH
Carviolin (**107**) R_1 = OH; R_2 = H; R_3 = OH; R_4 = H; R_5 = H; R_6 = CH_2OH; R_7 = H; R_8 = OMe
Emodic acid (**108**) R_1 = OH; R_2 = H; R_3 = OH; R_4 = H; R_5 = H; R_6 = COOH; R_7 = H; R_8 = OH
2'-acetoxy-7-chlorocitreorosein (**109**) R_1 = OMe; R_2 = Cl; R_3 = OH; R_4 = H; R_5 = H; R_6 = CH_2OAc; R_7 = H; R_8 = OH
2-aminoemodin (**110**) R_1 = OH; R_2 = NH_2; R_3 = OH; R_4 = H; R_5 = H; R_6 = Me; R_7 = OH; R_8 = OH
Asperthecin (**111**) R_1 = OH; R_2 = H; R_3 = OH; R_4 = OH; R_5 = H; R_6 = CH_2OH; R_7 = OH; R_8 = OH
Endocrocin (**112**) R_1 = OH; R_2 = H; R_3 = OH; R_4 = H; R_5 = H; R_6 = Me; R_7 = COOH; R_8 = OH

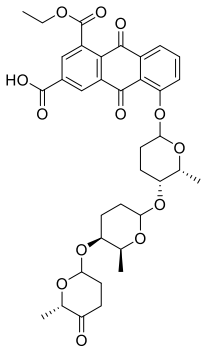


Penicillanthranin A (**113**) R = H
Penicillanthranin B (**114**) R = OH



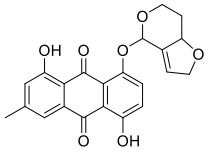
Variecolorquinone A (**115**)

Juglanthraquinones



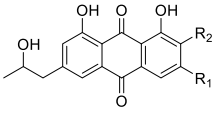
Juglanthraquinone A triglycoside (**116**)

MT81



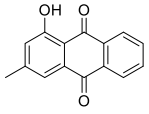
MT81 (**117**)

Nalgiovensins



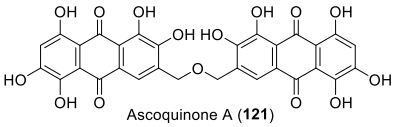
Nalgiovensin (**118**) R_1 = OMe; R_2 = H
Nalgiolaxin (**119**) R_1 = OMe; R_2 = Cl
CHT-AQ (**120**) R_1 = OH; R_2 = Cl

Pachybasins

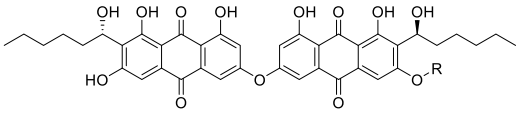


Pachybasin (**124**)

O-biemodins

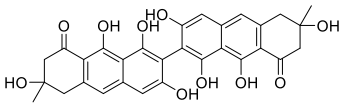


Ascoquinone A (**121**)

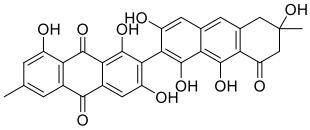


6,6'-oxybis(1,3,8-trihydroxy-2-((S)-1-hydroxyhexyl)anthracene-9,10-dione (**122**) R = H
6,6'-oxybis(1,3,8-trihydroxy-2-((S)-1-methoxyhexyl)anthracene-9,10-dione (**123**) R= OH

Talaromannins

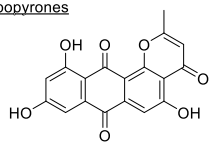


Flavomannin (**125**)

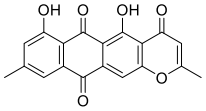


Talaromannin A and B (atropisomers) (**126**)

Topopyrones

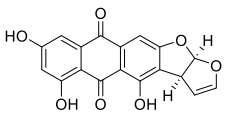


Topopyrone C (**127**)

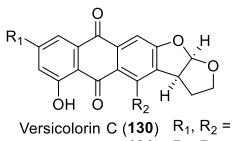


Topopyrone D (**128**)

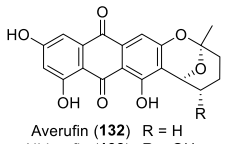
Versicolorins



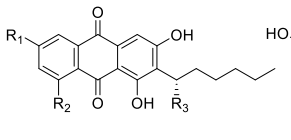
Versicolorin A (**129**)



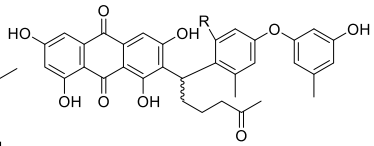
Versicolorin C (**130**) R_1, R_2 = OH
Aversin (**131**) R_1, R_2 = OMe



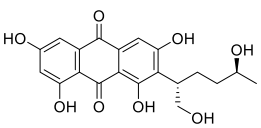
Averufin (**132**) R = H
Nidurufin (**133**) R = OH



Averantin (**134**) R_1,R_2,R_3 =OH
6,8,1'-tri-O-methyl averantin (**135**) R_1,R_2,R_3 =OMe

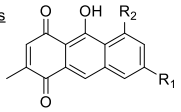


(±)-Aspergilol A (**136**) R = CH_3
(±)-Aspergilol H (**137**) R = OH



aspergilol I (**138**)

Viocristins



Viocristin (**139**) R1 = OH; R2 = OMe
Isoviocristin (**140**) R1 = OMe; R2 = OH

1

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

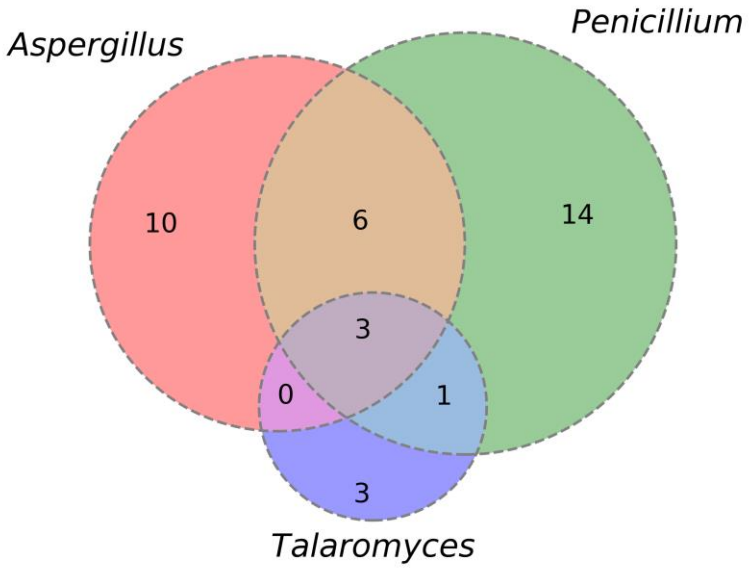


Fig. 6 Venn-diagram showing the number of quinone families appearing in genera Aspergillus, Penicillium and Talaromyces

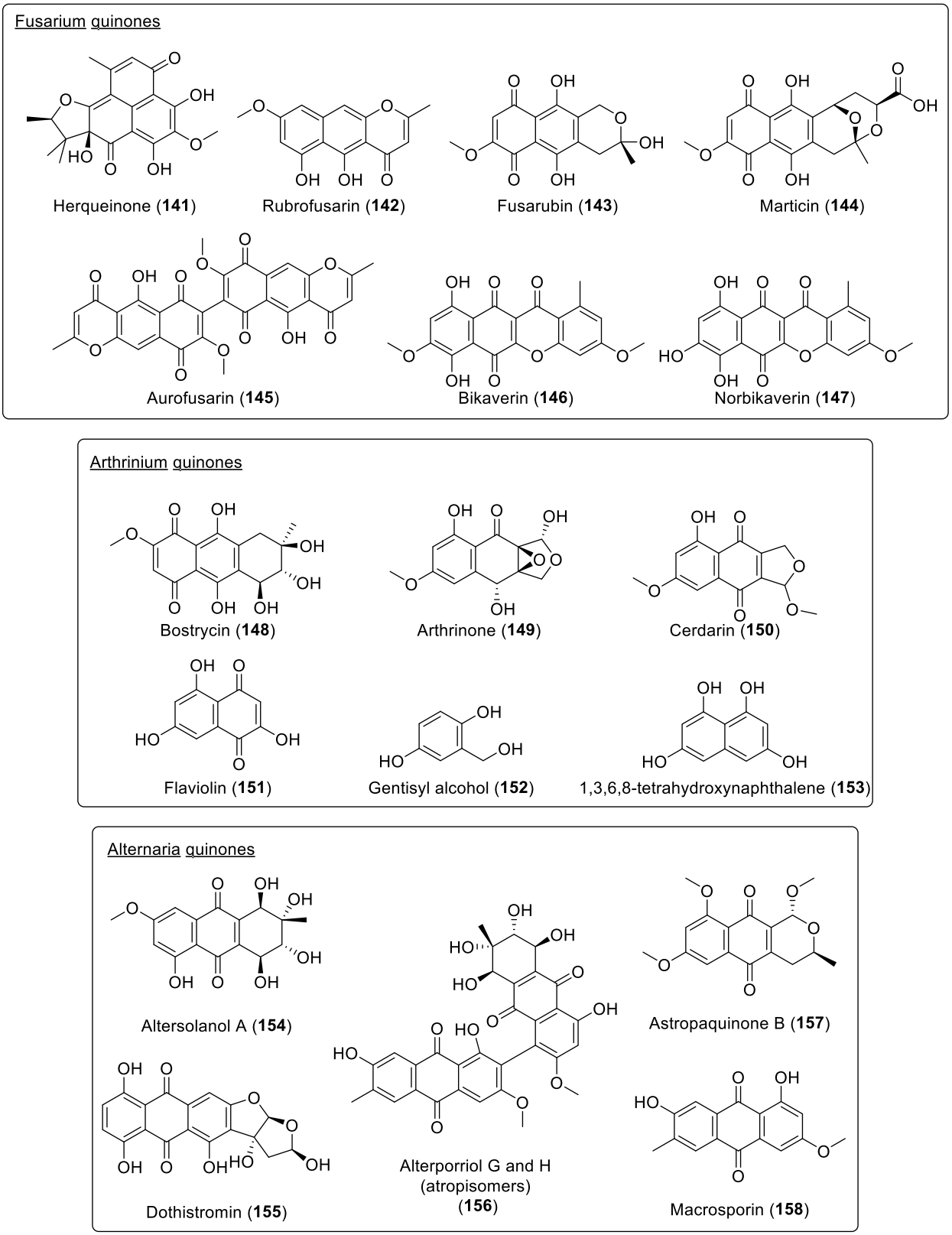


Fig. 7 Quinones and related molecules associated with *Fusarium* and related fusaroid genera, *Arthrinium* and *Alternaria*

Tables

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

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

Table 2. Quinones in the genus *Aspergillus*[1-4] (Frisvad 2015[1]; Frisvad and Larsen 2016[2]; Samson et al. 2014[3]; Houbraken et al. 2020[4]; Chen et al. 2017[5]; Du et al. 2014[5a]; Wang et al. 2007[5b]; Du et al. 2007[5c]; Laatsch et al. 1982[5d]; Sklenář et al. 2017[6]; Rahbæk et al. 2000[7]; Varga et al. 2007[8]; Hubka et al. 2018a[9]; Frisvad et al. 2004[10]; Visagie et al. 2014[11]; Varga et al. 2011a[12]; Frisvad et al. 2019[13]; Kjærbølling et al. 2020[14]; Heathcote and Dutton 1969[14a]; Chen et al. 2014[14b]; Caceres et al. 2020[14c]; Mandelare et al. 2018; Samson et al. 2011[15]; Hubka et al. 2015[16]; Arzanlou et al. 2016[17]; Hubka et al. 2016a[18]; Varga et al. 2011b[19]; Samson et al. 2004[20]; Samson et al. 2007a[21]; Perrone et al. 2011[22]; Vesth et al. 2018[23]; Theobald et al. 2018[24]; Chen et al. 2013[25]; Myobataka et al. 2014[25a]; Holm et al. 2014[25b]; Bugni, et al. 2000[25c]; Jurjevics et al. 2015[26]; Barros Correira et al. 2020[27]; Samson et al. 2011a[28]; Balajee et al. 2009[29]; Kiriyama et al. 1977[29a]; Hubka et al. 2016a[30]; Chen et al. 2016a[31]; Varga et al. 2007[32]; Visagie and Houbraken 2020[33]; Anslow and Raistrick 1938[34]; Samson et al. 2007b[35]; Larsen et al. 2007[36]; Frisvad et al. 2009[37]; Frisvad and Larsen 2016[38]; Hubka et al. 2013[39]; Hubka et al. 2017[40]; Talbot et al. 2017[41]; Hubka et al. 2018b[42]; 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

et al. 2018; Steenwyk et al. 2020[43]; Varga et al. 2010a[44]; Sun et al. 2020b[45]; Chen et al. 2016b[46]; Hubka et al. 2016b[47]; Wu et al. 2016[47a]; Huang et al. 2017[47b]; Chiang et al. 2010[47c]; Brown and Salvo 1994[47d]; Li et al. 2019[47e]; Houbraken et al. 2007[48]; Samson et al. 2011b[49]; Steyn and Vleggaar, 1974[49a]; Tanney et al. 2017[50]; 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
Aspergillus[5, 5a, 5b, 5c,5d]	*Aspergillus*	30 (31)	27 (90%)	Emodins including erythroglaucin (**100**), fallacinol (**101**), questin (**103**), questinol, rubrocristin (**106**), variecolorquinone A (**115**), viocristin (**139**), isoviocristin (**140**) and others*, variecolorquinone B (**64**)	Emodins (AQ), variecolorquinone B (BQ), viocristins (AQ)
Restricti[6]	*Aspergillus*	20 (21)	1 (5%)	Emodin (**98**)	Emodins
Candidi[7,8,9]	*Circumdati*	7	2 (29%)	Aspetritone A (**72**) and B (**73**), emodin	Aspetritones (NQ), emodins
Circumdati[10,11]	*Circumdati*	27 (28)	21 (78%)	Emodin, xanthomegnins (**81**)	Emodins (AQ), xanthomegnins (NQ)
Flavi[12,13,14,14a,14b,14c,14d]	*Circumdati*	35 (37)	22 (63%)	Versicolorins**, nalgiovensin (**118**), nalgiolaxin (**119**)	Versicolorins (AQ), nalgiovensins (AQ)
Flavipedes[15,16,17,18]	*Circumdati*	15	4 (27%)	Emodin (**98**)	Emodins
Janorum[16]	*Circumdati*	4	0 (0%)	-	-
Nigri[19,20,21, 22, 23, 23,24,25,25a,25b,25c]	*Circumdati*	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)
Petersoniorum[26]	*Circumdati*	4	0 (0%)	-	-
Robusti[11]	*Circumdati*	1	0 (0%)	-	-
Tannerorum[11]	*Circumdati*	1	0 (0%)	-	-
Terrei[27,28,29, 29a]	*Circumdati*	17	5 (29%)	Asterriquinones***, 3,6-dihydroxytoluquinone (**39**), emodin (**98**), questin (**103**), terreic acid (**59**)	Asterriquinones (BQ), fumigatins (BQ), emodins, terreic acid (BQ)
Cremei[30]	*Circumdati*	17	8 (47%)	Emodin (**98**) (bisanthrons are end-products), patulin****	Emodins, toluquinones (BQ)
Cervini[31]	*Fumigati*	10	6 (60%)	Terreic acid (**59**), 6-ethyl-7-methoxy-juglone (**76**)	Terreic acid, juglones (NQ)
Clavati[32,33]	*Fumigati*	6 (8)	3 (50%)	Patulin****	Toluquinones
Fumigati[34,35,36,37,38,39,40,41,42,42a, 42b,42c,42d,42e,42f, 42g]	*Fumigati*	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
Vargarum[43]	*Fumigati*	1	0 (0%)	-	-
Aenei[44]	*Nidulantes*	11	8 (73%)	Emodin (**98**), versicolorins**	Emodins, versicolorins
Cavernicolarum[45]	*Nidulantes*	5	0 (0%)	-	-

Nidulantes[46,47,47a,47b, 47c,47d,47e]	*Nidulantes*	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-biemodins (AQ), asterriquinones, versicolorins
Ochraceorosei[46]	*Nidulantes*	3	2 (66%)	Versicolorins**	Versicolorins
Raperorum[46]	*Nidulantes*	2	1 (50%)	Unknown AQ	-
Silvatici[46]	*Nidulantes*	1	0 (0%)	-	-
Sparsi[47]	*Nidulantes*	9	0 (0%)	-	-
Usti [45,46,48,49,49a]	*Nidulantes*	25	5 (20%)	Versicolorins**	Versicolorins
Polypaecilum[50]	*Polypaecilum*	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, secalonic acids, trypacidin, 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**), averythrin, 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-methylnidurufin, 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 terreiquinone 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).

Table 3. Distribution of quinones in the genus *Penicillium* ([1]Frisvad and Samson, 2004; [2]Frisvad et al. 2004a;b; [3]Visagie et al. 2014; Houbraken et al. [4]Houbraken et al. 2010a: [5]Houbraken et al. 2011; [6]Houbraken et al. 2014; [7]Houbraken et al. 2020; [8]Mahmoodian and Stickings, 1964; [9]Anslow and Raistrick, 1938; [10]Friedheim, 1938; [11]Curtin et al. 1940, [12]Posternak et al. 1943; [13]Peterson et al. 2015; [14]Shang et al. 2016;[15]Ranji et al. 2013;[16]Abdelwahab et al. 2018; [17]Gautschi et al. 2004; [18]Smetanina et al. 2016; [19]Sun et al. 2013; [20]Ngan et al. 2017; [21]Luo et al. 2019; [22]Zhan et al. 2004; [23]Aly et al. 2011; [24]Morehouse et al. 2020; [25]Hind, 1940; [26]Elbanna et al. 2021; [27]Christensen et al. 1998; [28]Ngan et al. 2017; [28a]Khamthong et al. 2012; [28b]He et al. 2017; [29]Janso et al. 2005; [30]Visagie et al. 2016; [31]Unpublished observations; [32]Frisvad and Filtenborg, 1990; [33]Bao et al. 2014, [34]Wang et al. 2014; [35]Li et al. 2018; [36]Singh et al. 1991; [37]Del Valle et al. 2016; [38]Nord et al. 2019; [39]Visagie et al. 2021; [40]Gupta et al, 1997; [41]Wei et al. 2009; [42]Hawas et al. 2013; [43]Gutarowska et al. 2014; [44]Fujimoto et al. 2001; [45]Singh et al. 2003; [46]Raistrick & Ziffer, 1951; [47]Birch & Massy-Westropp, 1957; [48]Birch & Stapleford, 1967; [49]Liu et al. 2005; [50]Cheng et al. 2018; [51]Yang et al. 2016; [52]Li et al. 2003; [53]Miller & Huang, 1995; [54]Stack et al. 1979; [55]Lund and Frisvad 2004; [56]Hallas-Møller et al. 2018; [57]Nicolaisen et al. 1996, [58]Frisvad et al. 1994; [59]Houbraken et al. 2016; [60]Raper & Fennell, 1965; [61]Frisvad et al. 2016; [62]Ali et al. 2017; [63]Houbraken et al. 2010b; [64]Li et al. 2006; [65]Kanai 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
Alfrediorum	*Aspergilloides*	1 (1)	0 (0%)	-	-
Aspergilloides[8,9]	*Aspergilloides*	11 (53)	2 (18%)	Endocrocin (**112**), questins (**103**), spinulosin (**38**)	Emodins (AQ), fumigatins (BQ)
Charlesia[10, 11, 12]	*Aspergilloides*	4 (9)	2 (50%)	Phoenicin (**47**)	Phoenicin (BQ)
Cinnamopurpurea[13]	*Aspergilloides*	9 (20)	1 (11%)	Unknown BQ	-
Citrina[14,15,16,17,18, 19, 20, 21, 22, 23, 24, 25, 26, 27, 28, 28a, 28b]	*Aspergilloides*	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
Crypta	*Aspergilloides*	0 (1)	0 (0%)	-	-
Eremophila	*Aspergilloides*	0 (1)	0 (0%)	-	-
Exilicaulis[27, 29, 30]	*Aspergilloides*	36 (58)	9 (25%)	Carviolins, emodin (**98**), fumigatin (**37**), spinulosin (**38**), phoenicin (**47**), unknown AQ	Emodins, fumigatins, phoenicin
Gracilenta[31]	*Aspergilloides*	4 (6)	2 (50%)	Emodin (**98**), toluquinone (**39**), spinulosin (**38**), unknown AQs	Emodins, toluquinones (BQ), fumigatins
Griseola	*Aspergilloides*	1 (1)	0 (0%)	-	
Inusitata	*Aspergilloides*	0 (2)	0 (0%)	-	

Lanata-Divaricata[32, 33, 34]	*Aspergilloides*	43 (76)	13 (30%)	Aloe-emodin, chrysophanol (**105**), ω-hydroxyemodin (**104**), emodin (**98**), toluquinone (**39**), unknown AQs, xanthomegnin (**81**)	Emodins, toluquinones, xanthomegnins (NQ)
Lasseniorum	*Aspergilloides*	1 (1)	0 (0%)	-	-
Ochrosalmonea[31]	*Aspergilloides*	2 (2)	1 (50%)	1 unknown BQ and 1 unknown AQ	-
Ramigena	*Aspergilloides*	6 (6)	0 (0%)	-	-
Sclerotiorum[35]	*Aspergilloides*	24 (35)	2 (8%)	Physcion (**102**)	Emodins
Stolkia	*Aspergilloides*	7 (7)	0 (0%)	-	-
Thysanophora[36]	*Aspergilloides*	2 (8)	1 (50%)	Thysanone (**80**)	Thysanone (NQ)
Torulomyces	*Aspergilloides*	0 (15)	0 (0%)	-	-
Brevicompacta[37, 38]	*Penicillium*	11 (11)	1 (10%)	CHT-AQ (**120**), spathullin C (**55**)	Nalgiovensins (AQ), spathullins (BQ),
Canescentia[39, 40]	*Penicillium*	19 (21)	7 (37%)	Spinulosin (**38**) or fumigatin (**37**), MT81 (**117**), patulin*, unknown AQ	Fumigatins, MT81 (AQ), toluquinones
Chrysogena[41, 42, 43, 44, 45, 46, 47, 48, 49, 50, 51, 52, 53]	*Penicillium*	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**), nalgiolaxin (**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), xanthoviridicatins (NQ)
Eladia	*Penicillium*	2 (2)	0 (0%)	-	-
Fasciculata[1,2, 54, 55, 56, 57, 58]	*Penicillium*	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, xanthoviridicatins
Formosana[2]	*Penicillium*	1(1)	1 (100%)	Patulin*	Toluquinones
Osmophila[59]	*Penicillium*	2 (2)	1 (50%)	Patulin*	Toluquinones
Paradoxa[60]	*Penicillium*	4 (9)	1 (25%)	Pachybasin (**124**)	Pachybasin (AQ)
Penicillium[1,2]	*Penicillium*	7 (8)	4 (57%)	Patulin*, viomellein (**83**), xanthomegnin (**81**)	Toluquinones, xanthomegnins
Ramosum[59, 61]	*Penicillium*	12 (17)	1 (8%)	Unknown AQ	-
Robsamsonia[1,2, 59, 62]	*Penicillium*	11 (14)	8 (73%)	Gentisyl quinone (**62**), hydroxychlorogentisyl quinone[62], patulin*	Toluquinones
Roquefortorum[1,2,63]	*Penicillium*	4 (5)		Patulin*	Toluquinones
Turbata	*Penicillium*	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* ([1]Frisvad et al. 1990; [2]Samson et al. 2011c; [3]Yilmaz et al. 2014; [4]Frisvad, 2015; [5]Houbraken et al. 2020: [6]Sun et al. 2020a; [7]Zhai et al. 2016; [8]Lan and Wu, 2020; [9]Chen et al. 2016c; [10]Takeda et al. 1973; [11]Howard & Raistrick, 1954; [12]Yamazaki et al. 2010; [13]Yamazaki et al. 2009; [14]Breen et al. 1955; [15]Yilmaz et al. 2016; [16]Sedmera et al. 1978; [17]Mondal et al. 2020; [18]Hussain et al. 2015; [18a]Bara et al. 2013; [19]Samson et al. 1989; [20]Seifert et al. 2004; [21]Frisvad et al. 1990; [22] van-Reenen Hoekstra et al. 1990; [23]van Eijk, 1973; [24]Fuska et al. 1991; [25]Proksa et al. 1994; [26]Fujimoto et al. 1986; [27]Roberts and Thompson, 1971; [28]Wang et al. 2011; [29]Kalansuryia 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
Bacillispori	2 (7)	0 (0%)	-	-
Helici[9]	4 (13)	1 (25%)	Emodin (**98**) (secalonic acid BF)	Emodins (AQ)
Islandici[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, (+)-auroskyrin, (+)-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), xanthoviridicatins (NQ), xanthomegnins (NQ), talaromannins (AQ)
Purpurei[19,]	5 (13)	2 (40%)	Emodin (**98**) (secalonic acid BF)	Emodins
Subinflati[19,20]	2 (6)	0 (0%)	-	
Talaromyces[21,22,23,24,25, 26]	42 (78)	8 (19%)	Catenarin (**99**), emodin (**98**) (secalonic acid BF), erythroglaucin (**100**), juglone (**75**), rugulosine, skyrin (**95**)	Emodins, juglones (NQ), biemodins (AQ)
Tenues	0 (1)	0 (0%)	-	
Trachyspermi[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.