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Published in:
Applied Microbiology and Biotechnology

DOI (link to publication from Publisher):
[10.1007/s00253-021-11597-0](https://doi.org/10.1007/s00253-021-11597-0)

Publication date:
2021

Document Version
Accepted author manuscript, peer reviewed version

[Link to publication from Aalborg University](#)

Citation for published version (APA):

Christiansen, J. V., Isbrandt, T., Petersen, C., Sondergaard, T. E., Nielsen, M. R., Pedersen, T. B., Sørensen, J. L., Larsen, T. O., & Frisvad, J. C. (2021). Fungal quinones: diversity, producers, and applications of quinones from *Aspergillus*, *Penicillium*, *Talaromyces*, *Fusarium*, and *Arthrinium*. *Applied Microbiology and Biotechnology*, 105(21-22), 8157-8193. <https://doi.org/10.1007/s00253-021-11597-0>

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

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Abstract

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

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

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

Key points:

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

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

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

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

6 Introduction

7 Quinones and quinols are widespread natural products in invertebrates, plants, algae, fungi, and lichens
8 (Nohl et al. 1986; Medentsev and Akimenko 1998; Donner 2015; Futuro et al. 2018; García et al. 2018,
9 Sunasse et al. 2018; Feng and Wang 2020). They are of interest to mankind because of their redox
10 characteristics and they can be used as antioxidants, antibacterials, antifungals and battery components
11 among other things (Ito et al. 1973, Kawai et al. 1978; Kawai and Nozawa 1979; Kawai and Cowger 1981; Xu
12 et al. 2019; Kristensen et al. 2020; Masi and Evidente 2020). Quinones are present as ubiquinones (coenzyme
13 Q, **6**) in mitochondria of all fungi, where they are considered primary metabolites (Kurasihi, 1985; Nohl et al.
14 1986; Sugiyama et al. 1988; Kurasihi et al. 1990), but other quinones are typical secondary metabolites, being
15 small molecules produced during chemical differentiation of organisms and of restricted taxonomical
16 distribution.

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

29 Structural diversity of quinones

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

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

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

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

23 Biological function of quinones

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

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

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

1 addition, oosporein (**48**) shows anti-bacterial effect in insect cadavers indicating that it might help the fungus
2 to avoid microbial competition after the insect host is dead (Fan et al. 2017). In fact, in an attempt to discover
3 chemicals for pest controls, a total of 41 BQs (both synthetic and non-synthetic) were tested for their toxic
4 effect on the subterranean termite *Coptotermes formosanus* (Mozaina et al. 2008). It was discovered that
5 BQs with no substitutions, or only methyl or methoxy substitutions, showed none to very low termiticidal
6 activity, while BQs which had one or two hydrophobic substitutions on one side of the ring, and one to two
7 electron donating substitutions on the other side of the ring showed the highest toxicity (Mozaina et al.
8 2008). Similar experiments against *C. formosanus* with 17 natural NQs showed that NQs with no or a non-
9 polar substitution in the quinoid ring, e.g. juglone (**75**), showed higher activity than the other NQs. The 24
10 natural AQs studied, generally had little activity against the termites (Osbrink et al. 2005). Mozaina et al.
11 (2008) lists several references in which quinones are tested for the toxicity towards other agricultural pests.

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

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

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

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

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

3 Biotechnological uses of quinones

4 Quinones can be used in many aspects of technology, including in supramolecular chemistry (Fang et al.
5 2020), in microbial fuel cells (Kracke et al. 2015; Kisieliute et al. 2019), in pest control (Segaran and Sathivelu
6 2019), as dyes and colorants (Hyde et al. 2019), as drugs (Nweze et al. 2020) and even as electrolytes in redox
7 flow batteries (Huskinson et al. 2014; Kristensen et al. 2020). On an industrial level, quinones such as AQs and
8 NQs are synthesized from raw components in coal tar (Vogel 2000; Collin et al. 2003), but the possibility of
9 producing them by fungal cultivation has great prospects as a more environmentally viable alternative. Many
10 filamentous fungi and yeasts can grow in industrially scaled bioreactors, producing valuable metabolites on
11 cheap substrates (Sen et al. 2019). Additionally, the high structural diversity of fungal quinones is desirable
12 for industries where chemical diversity is an advantage, for example in the search of new antibiotics, cancer
13 drugs, food colorants and textile dyes. Below, the prospects of using quinones as pigments and drugs on an
14 industrial level, are highlighted. When possible, examples of fungal quinones are used, but also studies where
15 quinones are plant-derived are referenced.

16 Quinones as dyes and colorants

17 Pigment production from natural sources is increasing in popularity with concerns of the adverse effects of
18 synthetic dyes (Oplatowska-Stachowiak and Elliott 2017). Traditionally, naturally occurring pigments are
19 derived from insects and plants but production is limited on an industrial scale due to factors such as
20 seasonal variability (Mapari et al. 2005; Sen et al. 2019). In contrast, microorganisms such as fungi can grow
21 in industrially scaled bioreactors with relatively cheap substrates and industrial waste products (Panesar et al.
22 2015). Additionally, many fungal pigments are secreted under submerged fermentation, improving down-
23 stream processing compared to traditional pigment sources such as plants (da Costa Souza et al. 2016;
24 Hernández et al. 2019; Suwannarach et al. 2019).

25 Fungal pigments are very diverse in structure, and besides quinones, include chemical classes such as
26 carotenoids, melanins, flavins, phenazines and azaphilones (Dufossé et al. 2014; Dufossé 2018). When
27 considering the quinoid class, AQs are the most investigated for food colorants and textile dyes (Mapari et al.
28 2005; Dufossé 2018; Räisänen 2019; Suwannarach et al. 2019) with the industrially available fungal pigment
29 Arpink Red™ as an often cited example. Arpink Red™ is pH- and heat stable and is assumedly produced by
30 *Penicillium oxalicum*, although this identification has been miscredited by Mapari et al. (2005) (Dufossé et al.
31 2005; Mapari et al. 2005). Another example is bostrycin (**148**), produced by *Nigrospora aurantiaca*
32 (Suwannarach et al. 2019) and *Arthrinium phaeospermum* (van Eijk 1975). This NQ was found to be very
33 promising as a textile dye and showed no toxicity towards human embryonic kidney cell (HEK 293T)
34 (Suwannarach et al. 2019).

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

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

5 Quinones as pharmaceuticals

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

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

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

23 Anti-microbial: Many quinones have anti-bacterial, anti-fungal and/or anti-parasitocidal effects. When
24 regarding *Penicillium* and *Aspergillus*-derived quinones, especially AQs have been investigated for their anti-
25 microbial effects against gram-positive and gram-negative bacteria (Masi and Evidente 2020). Examples
26 include iso-rhodoptilometrin-1-methyl ether (**10**), averantin (**134**) and nidurufin (**133**) isolated from *A.*
27 *versicolor*, which all showed anti-bacterial activity against gram-positive bacteria (Lee et al. 2010; Hawas et al.
28 2012). Other examples include juglanthraquinone A triglycoside (**116**) from *A. fumigatus* and versicolorin C
29 (**130**) and isoversicolorin C from *A. nidulans*, which targets both gram-positive and gram-negative bacteria
30 (Abdel-Aziz et al. 2018; Yang et al. 2018). AQs from *Penicillium* with anti-bacterial effect include 2'-acetoxy-7-
31 chlorocitreorsein (**109**) from *P. citrinum* which showed effect against *Vibrio parahaemolyticus* (He et al.
32 2017) and penicillanthranin A (**113**) (also from *P. citrinum*) which showed activity against *Staphylococcus*
33 *aureus* (Khamthong et al. 2012). Additionally, the AQ dimers 6,6'-oxybis(1,3,8-trihydroxy-2-((S)-1-
34 methoxyhexyl)-anthracene-9,10-dione (**122**) and 6,6'-oxybis(1,3,8-trihydroxy-2-((S)-1-hydroxyhexyl)
35 anthracene-9,10-dione (**123**) isolated from *A. versicolor* and rugulosin A (**11**) isolated from *P. radicum*
36 (= *Talaromyces radicus*) showed activity against *S. aureus* (Yamazaki et al. 2010; Li et al. 2019). Mostly, AQs
37 have been tested for their antibacterial effects, but there are examples of other types of quinones:
38 stemphone C (**57**) isolated from an *Aspergillus* species, showed strong synergistic effects with other

1 antibiotics in the inhibition of methicillin-resistant *S. aureus* (Koyama et al. 2005). From *P. spathulatum*,
2 spathullin A (**53**), an 1,2-hydrobenzoquinol, showed activity against several bacteria, including *S. aureus*
3 (Nord et al. 2019). Quinones from *Fusarium* with antibiotic effects include aurofusarin (**145**) and bivakerin
4 (**146**) (Sondergaard et al. 2016). Furthermore, several BQs isolated from plants have been shown to have
5 antibacterial effects (Guntern et al. 2001; Yang et al. 2001; Drewes et al. 2005).

6 Few studies have tested the anti-fungal activity of quinones from *Penicillium* and *Aspergillus* but there are
7 some. Examples include the AQs 6,8,1'-tri-*O*-methyl averantin (**135**), aversin (**131**) and 6,8-di-*O*-methyl
8 versiconol (**12**) from a fungus identified as *Penicillium purpurogenum* which showed moderate inhibitory
9 activity towards *Botrytis cinerea* (Li et al. 2014) and juglanthraquinone A triglycoside (**116**) from *A. fumigatus*,
10 which showed activity against yeast and filamentous fungi (*Candida albicans* and *A. niger*) (Abdel-Aziz et al.
11 2018). Quinones isolated from plants also showed to have anti-fungal activity, including both BQs (Suzuku et
12 al. 1998; Guntern et al. 2001; Drewes et al. 2005) and NQs (Sasaki et al. 2002).

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

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

22 Emodin (**98**) has also been cited as a mycotoxin (Wells et al. 1975; Hasan, 1998), but most data indicated that
23 it is only marginally toxic (Izkaki, 2002; Gruber-Dorninger et al. 2017). However, other quinones such as the
24 NQs xanthomegnin (**81**) and viomellein (**83**) have been shown to be toxic (Carlton et al. 1973, Carlton et al.
25 1976, Zimmermann 1977, Hald et al. 1983, Scudamore 1986, Mills et al. 1995).

26 Taxonomic distribution of quinones and hydroquinones

27 Ubiquinones

28 Ubiquinones (**6**) are present in the mitochondria in all eukaryotic organisms, but also in bacteria, as an
29 essential part of the electron transport chain and are examples of primary metabolites (Nohl et al. 1986).
30 Despite being primary metabolites, the type of ubiquinone present in fungi has a certain taxonomical value in
31 *Aspergillus* classification (Kurasahi 1985; Sugiyama et al. 1988; Kurasahi et al. 1990; Chang et al. 1991; Kuraishi
32 et al. 2000) and *Penicillium* classification (Kurasahi et al. 1991). Ubiquinones are named by the number of
33 isoprene units and whether one or more isoprene units have had a double bond reduced, e.g. Q-10(2H)
34 denotes a ubiquinone with 10 isoprene units, where one isoprene unit is reduced (Itoh et al. 1988). In Table
35 1, where species of *Aspergillus* have been re-classified according to an updated taxonomy and phylogeny
36 (corrected according to Houbraken et al. (2020)), it can be seen that ubiquinone isoprenoid number and type

1 is section specific to a certain extent and in most cases follow the phylogeny of the large genus *Aspergillus*.
2 An interesting exception is *Aspergillus* subgenus *Circumdati* section *Nigri* that is different from the other
3 sections in subgenus *Circumdati* having ubiquinone Q-9. According to phylogenomic analysis of *Aspergillus* by
4 Steenwyk et al. (2019), section *Nigri* is a sister section to subgenus *Nidulantes* in contrast to the phylogeny
5 presented by Kocsubé et al. (2016) and Houbraken et al. (2020), but also in contrast to phenotypic characters
6 in the classification of *Aspergillus* (Frivvad and Larsen 2015; Chen et al. 2016b; Vesth et al. 2018; Barrett et al.
7 2020). A comparison of mitochondrial and nuclear genome data may help solving this taxonomic and
8 phylogenetic dilemma.

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

18 Quinones involved in conidium and sclerotium formation

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

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

1 *Candidi*, melanin is only present in the black sclerotia (Varga et al. 2007). The conidia of the *Candidi* species
2 are protected by terphenyllin (**21**) and similar secondary metabolites (Rahbæk et al. 2000; Varga et al. 2007;
3 Kjærboelling et al. 2018; Houbraken et al. 2020). In general, most filamentous fungi and some yeasts can
4 produce melanin, if not always in the conidia or the mycelium, then in sclerotia and ascomata (Butler et al.
5 2009; Chang et al. 2020). Therefore quinones may be produced by most melanin producing fungi, but it may
6 require genetic manipulation in order to have the quinones accumulated in sufficient amounts.

7 Secondary metabolite quinones in *Aspergillus*, *Penicillium* and 8 *Talaromyces*

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

17 Benzoquinones

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

21 Anserinones have been isolated from species in *Penicillium* section *Citrina*. The family includes anserinone A
22 (**25**), anserinone B (**26**), formylanserinone B (**27**) and hydroxymethylanserinone B (**28**), all sharing a unique
23 carbon scaffold consisting of an *O*-methylated BQ ring, attached to an oxygenated three-carbon side chain.

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

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

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

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

3 Citriquinones consists of the structurally similar BQs citriquinone A (**35**) and B (**36**), isolated from *P. citrinum*
4 (Ranji et al. 2013) (Section *Citrina*), and contain a characteristic butan-2-yl formate side chain. Citriquinone A
5 (**35**) has shown antibacterial and anticancer activity (Ranji et al. 2013).

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

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

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

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

29 Spathullins appear in *Penicillium* section *Brevicompacta* and were isolated from *P. spathulatum* (Nord et al.
30 2019). Spathullin A (**53**) and spathullin B (**54**) are both quinols, while spathullin C (**55**) is an *ortho*-quinone.
31 Spathullin A (**53**) and B (**54**) has shown antibacterial activity, and the compounds in the family is are proposed
32 to be NRPS derived, originating from tyrosine and cysteine (Nord et al. 2019).

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

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

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

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

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

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

20 Naphthoquinones

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

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

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

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

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

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

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

7 Xanthomegnins are a large group of naphthopyranones and include xanthomegnin (**81**), semixanthomegnin
8 (**82**) viomellein (**83**), rubrosulphin (**84**) and viopurpurin (**85**). With the exception of semixanthomegnin (**82**),
9 these compounds are dimers, consisting of two naphthopyrones, with at least one being a quinone. They are
10 produced in *Aspergillus* section *Circumdati*, *Penicillium* sections *Fasciculata* and *Penicillium* and *Talaromyces*
11 section *Islandici*.

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

17 Anthraquinones

18 1,3-dihydroxy-6-hydroxymethyl-7-methoxyanthraquinone (DHM-AQ) (**93**) is an AQ closely related to the
19 emodins (see below). However, while the emodins have an OH or OMe group at position 8, this position is
20 non-substituted in DHM-AQ (**93**), suggesting that the polyketide backbone is reduced at this position, and
21 thus that the PKS related to this biosynthetic pathway of DHM-AQ (**93**) is different from the one for emodins,
22 by being partly reducing. DHM-AQ (**93**) is produced by *Penicillium* section *Citrina*.

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

31 Emodins are a large AQ family with a core structure similar to emodin (**98**). Besides emodin, this family
32 includes many compounds, such as catenarin (**99**), erythroglauclin (**100**), fallacinol (**101**), physcion (**102**),
33 questin (**103**), chrysophanol (**105**), rubrocristin (**106**), carviolin (**107**) and others (**108**, **109**, **110**, **111**, **112**, **139**,
34 **140**, **113**, **114**, **115**). In this family we also include penicillanthranins A (**113**) and B (**114**) which are emodins
35 attached to citrinin moieties. Emodins are produced in *Aspergillus*, *Penicillium* and *Talaromyces* across
36 multiple sections and have also been observed in *Arthrinium* sp. (Elissawy et al. 2017).

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

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

7 Nalgiovensins are Aqs with similar structures to the emodins, although with a key difference in that they
8 contain an additional two carbon atoms in the polyketide backbone. Nalgiovensins are observed in
9 *Penicillium* sections *Brevicompecta* and *Chrysogena* and in *Aspergillus* section *Flavi* and include nalgiovensin
10 (**118**), as well as the two chlorinated compounds nalgiolaxin (**119**) and 2-chloro-6-[2'(S)-hydroxypropyl]-1,3,8-
11 trihydroxyanthraquinone (CHT-AQ, **120**).

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

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

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

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

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

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

32

33 Quinone families in *Aspergillus*

34 Table 2 lists the secondary metabolite quinones observed in the genus of *Aspergillus*, which is composed of
35 446 species in total divided across 26 known sections. The quinones from one unknown *Aspergillus* spp. are

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

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

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

20

21 Quinone families in *Penicillium*

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

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

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

34

Quinone families in *Talaromyces*

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

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

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

1 Aurofusarin (**145**) was originally described as a golden pigment in 1937 (Ashley et al. 1937), but was first
2 structurally elucidated in 1966 (Baker and Roberts 1966; Shibata et al. 1966). The compound is produced by a
3 cluster (*PKS12*) of at least ten genes of which the PKS shares high sequence similarity to *wA*, found in several
4 *Aspergilli*. The two PKSs have also been shown to produce the same entry compound, YWA1 (Watanabe et al.
5 1998; Frandsen et al. 2011). Aurofusarin (**145**) is a product of dimerization of the intermediary compound
6 rubrofusarin (**142**), containing two naphthopyrones. It is structurally similar to xanthomegnin (**81**), using 4-
7 pyrones instead of 2-pyrones. Despite the pigmented properties of aurofusarin (**145**), it has not been linked
8 to UV-protection or, as other secondary metabolites, to pathogenicity, however it does affect the chemical
9 composition of quail eggs (Brown et al. 2012a;b; Brown and Proctor, 2016; Coleman 2016). Rubrofusarin
10 (**142**) can be converted into a quinone form. This quinone product is sometimes observed at higher
11 concentrations than rubrofusarin (**142**) in grain (Wang et al. 2018).

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

24 The fusarubin (**143**) gene cluster is identified in all sequenced members of *Fusarium* and *Neocosmospora* and
25 is associated with black/dark purple pigmentation of perithecia (Proctor et al. 2007, Brown 2012a,b, Frandsen
26 et al. 2016), except for species within *Neocosmospora* (the *F. solani* species complex (FSSC)) where fusarubins
27 and its derivative NQs accumulate in the mycelium (Medentsev and Akimenko 1998, Short 2013). The
28 production of fusarubins in *Fusarium* spp., *Neocosmospora* (*N. solani*, *N. virguliformis* and *N. ambrosia*) and
29 *Albonectria rigidiuscula* is therefore widespread, and the class of fusarubins also encompass a range of
30 different compounds containing quinone-structures, such as anhydrofusarubin, bostrycoidin, 9-
31 desmethylherbarine, javanicin, karuquinones, lucilactaenes, norjavanicin, novarubin, solaninaphthoquinones,
32 and (+)-solaniol (Arnstein & Cook 1947; Arsenault 1968; Roos, 1977; Kimura et al. 1981; Kurobane et al. 1989;
33 Kornsakulkarn et al. 2011; Takemoto et al. 2014; Tadpetch et al. 2015; Kehelpannala et al. 2018; Choi et al.
34 2020; Maharjan et al. 2020). All exhibit the hallmark red pigmentation and are a result of the same
35 heptaketide scaffold-compound from *PKS3*, but differentiates between the many *Fusarium* species due to the
36 large genetic variation found within the *PKS3* gene-cluster (Harvey 2018; Kim 2019; Proctor 2007; Short et al.
37 2013).

38 In addition, members of the FSSC carry the *PKS35* gene cluster that is not present in other *Fusaria* (Coleman
39 2016). *PKS35* contribute to the red/orange pigmentation of perithecia in FSSC. This conclusion is based on the

1 fact that deletion of *pksN* in *N. pisi* (= *F. solani* f. *pisi*) (Graziani et al. 2004) and *PKS35* in *N. vasinfecta* (= *F.*
2 *neocosmosporiellum*) (Kim 2019) resulted in albino perithecia. Five genes within the *PKS35* gene cluster have
3 homologs in the *Penicillium herquei* gene cluster responsible for the formation of herqueinone (**141**) (Gao et
4 al. 2017). Another homologous gene cluster, *pks23* from the lichen-forming *Endocarpon pusillum*, produces
5 the herqueinone precursor prephenalenone when expressing the cluster in *Saccharomyces cerevisiae* (Harvey
6 et al. 2018). Thus, herqueinone (**141**) or a closely reassembling molecule likely causes the red pigmentation in
7 perithecia in members of the FSSC. The related NQ marticin (**144**) is an octaketide and produced by
8 *Neocosmospora cucurbitae*, *N. martii*, *N. pisi* and *N. vasinfecta* (Pfiffner 1963; Ross 1977; Kurobane et al.
9 1980; Holenstein et al. 1983).

10 Quinone production in *Arthrinium*

11 The genus *Arthrinium* has been reported in various environments worldwide including terrestrial and marine
12 ecosystems (Crous and Groenewald 2013; Heo et al. 2018). It exists as an endophyte in different plant
13 (Sharma et al. 2014; Pansanit and Pripdeevech 2018; Astuti et al. 2021) and lichen species (Yunzhe 2012) but
14 also as a plant pathogen (Martinez-Cano 1992; Mavragani et al. 2007). The literature contains several
15 examples of cutaneous infections in humans caused by *A. phaeospermum* (Hoog et al. 2021; Rai 1989; Zhao,
16 Deng, and Chen 1990) and food poisoning with fatal outcome caused by *A. saccharicola* (Birkelund et al.
17 2021). Furthermore, many natural products are produced by *Arthrinium* spp., which possess a variety of
18 industrial and pharmacological applications (Tsukada et al. 2011; Bao et al. 2018).

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

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

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

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

5 Production of fungal quinones

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

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

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

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

1

Author contributions

2

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

9

Ethical Statement

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

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

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

14

Data availability statement

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

16

Software used for making the figures

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

19

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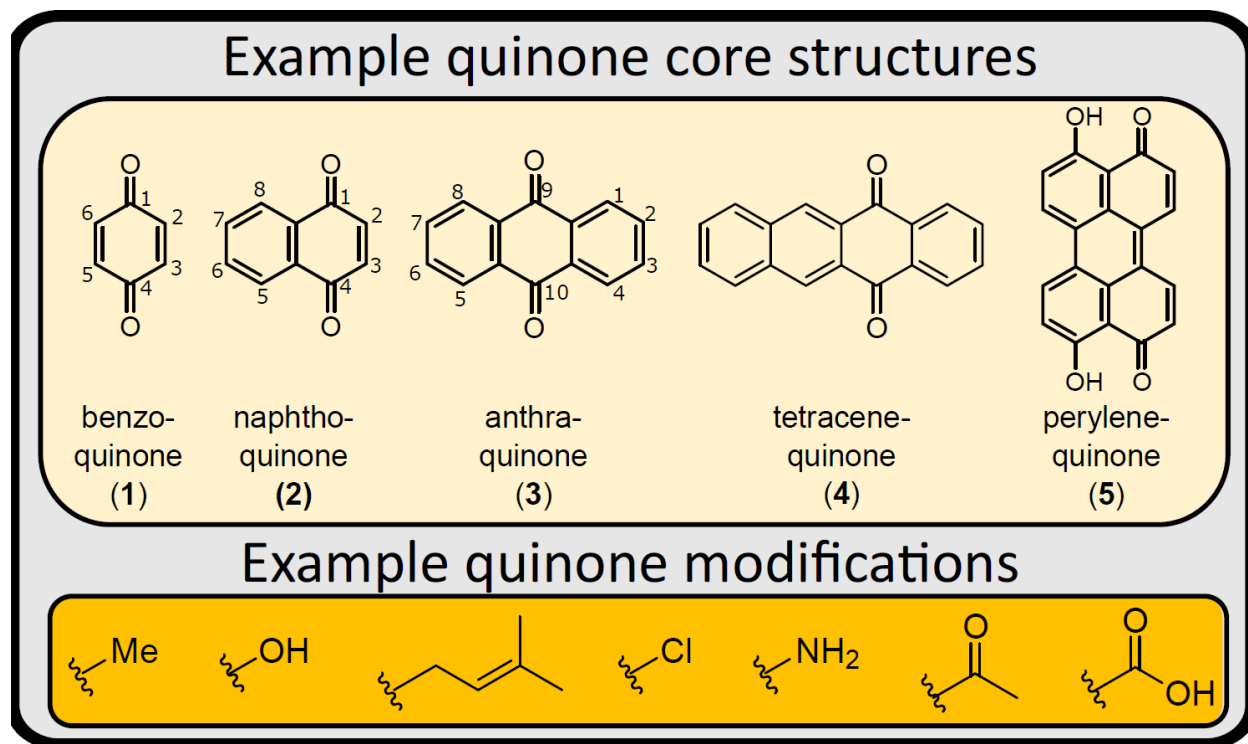
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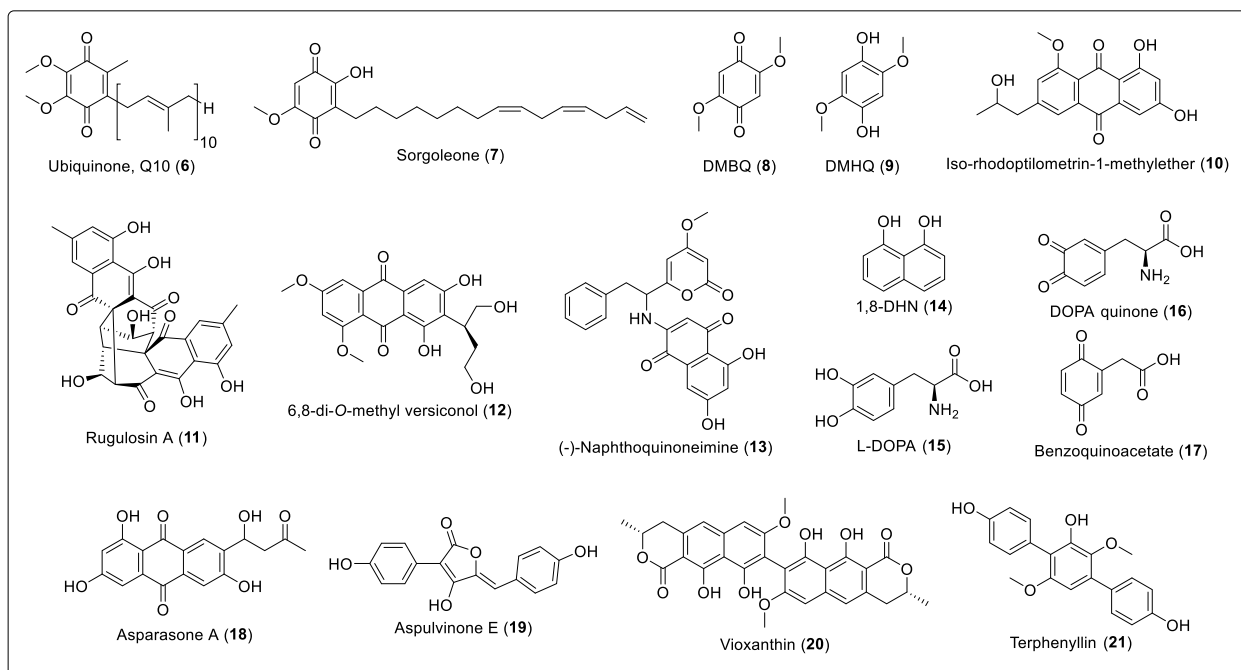
Figure captions



2

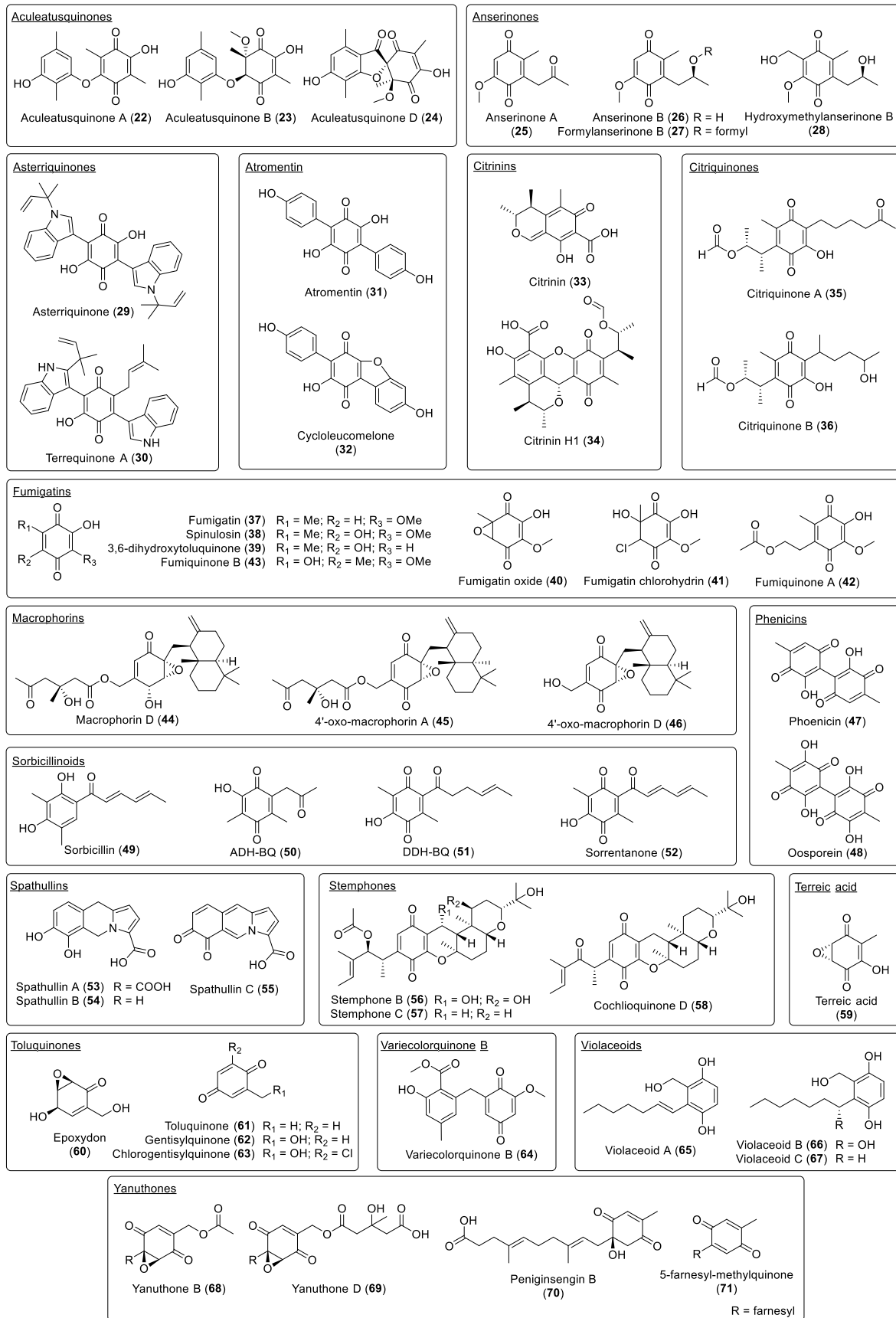
3 **Fig. 1** Structural diversity of naturally occurring quinones. A quinone typically consist of one of several core
4 structures, such as (1), (2), (3), (4) and (5) and a number of additional functional groups such as methylations,
5 oxidations, prenylations, halogenations, aminations, acetylations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

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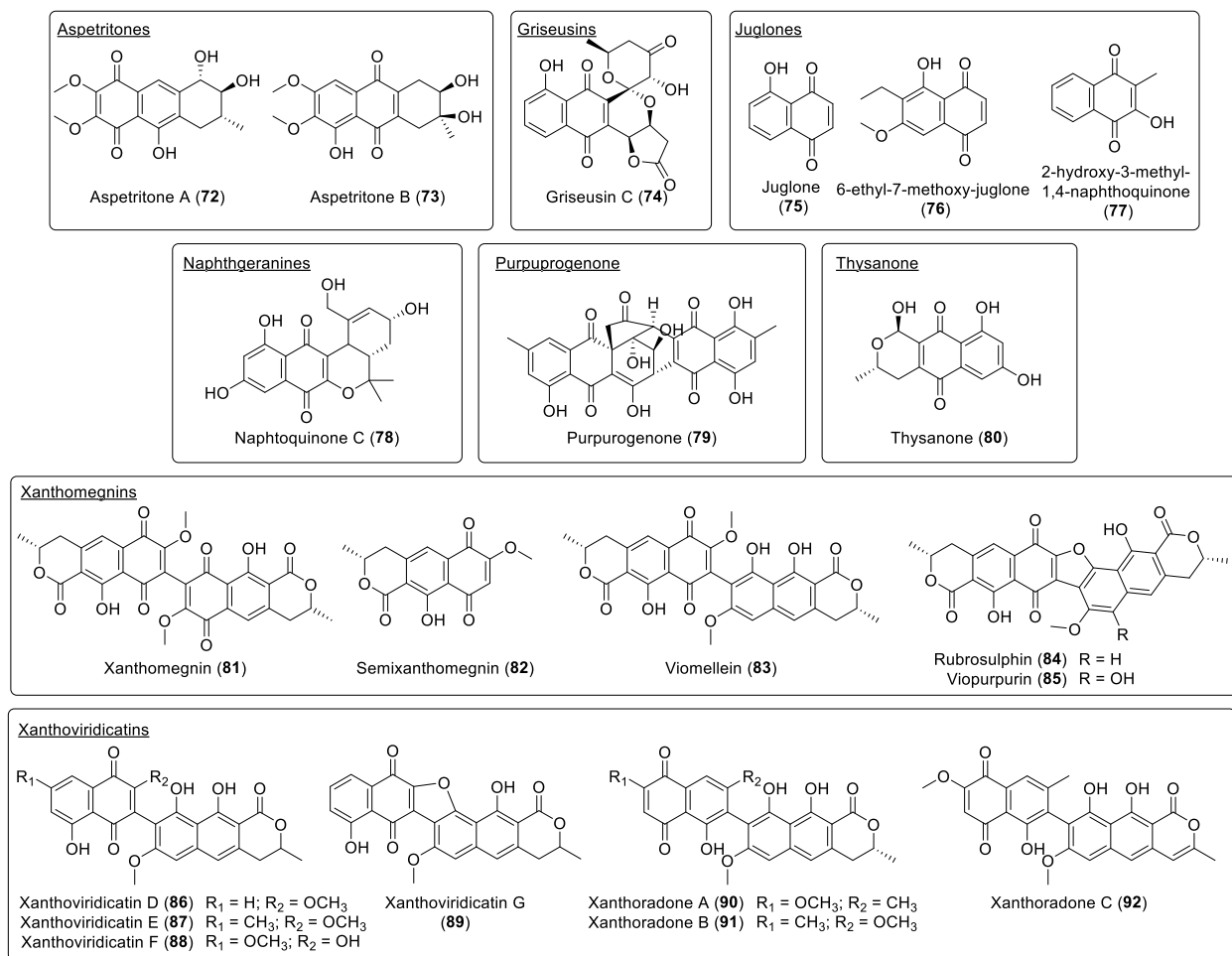


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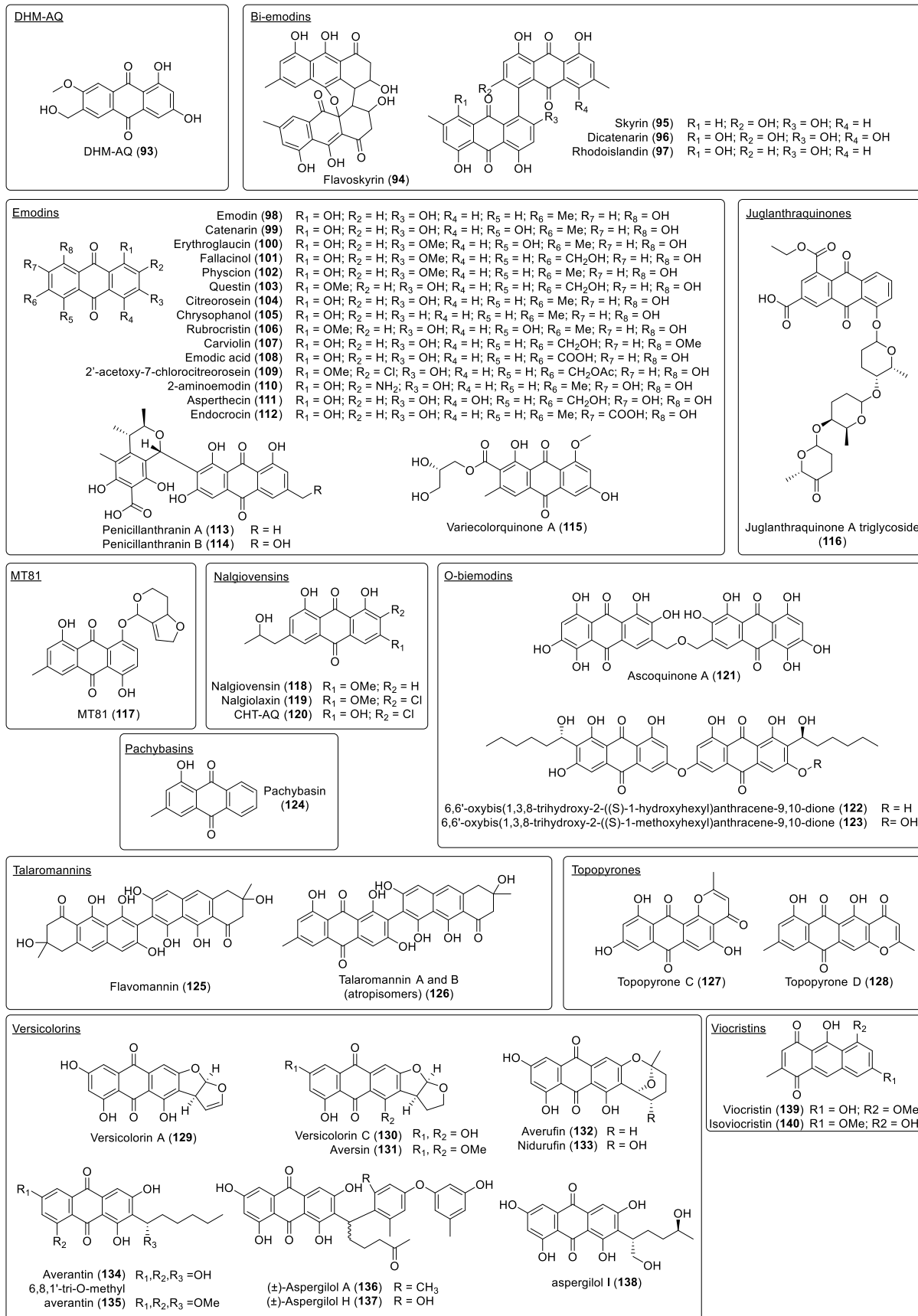
2 **Fig. 2** Some of the quinones and related molecules mentioned in the introduction



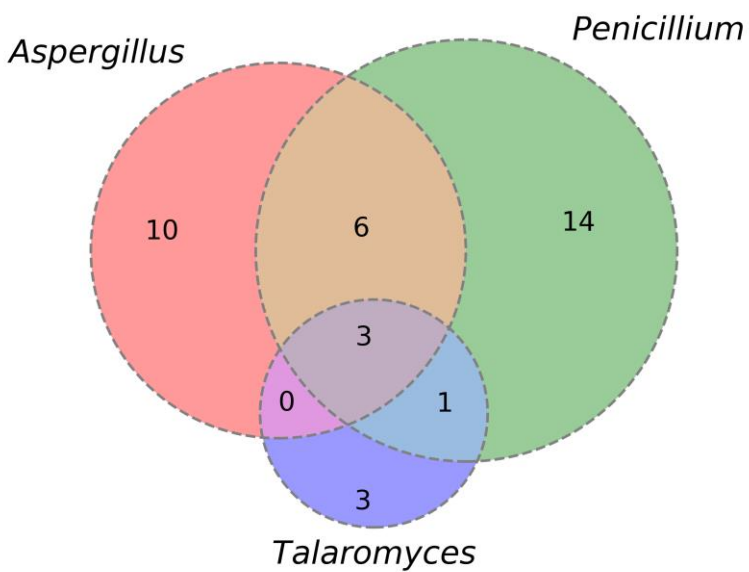
1 **Fig. 3** Representative BQs and related molecules from the quinone families observed in *Aspergillus*,
 2 *Penicillium* and *Talaromyces*



3
 4 **Fig. 4** Representative NQs and related molecules from the quinone families observed in *Aspergillus*,
 5 *Penicillium* and *Talaromyces*

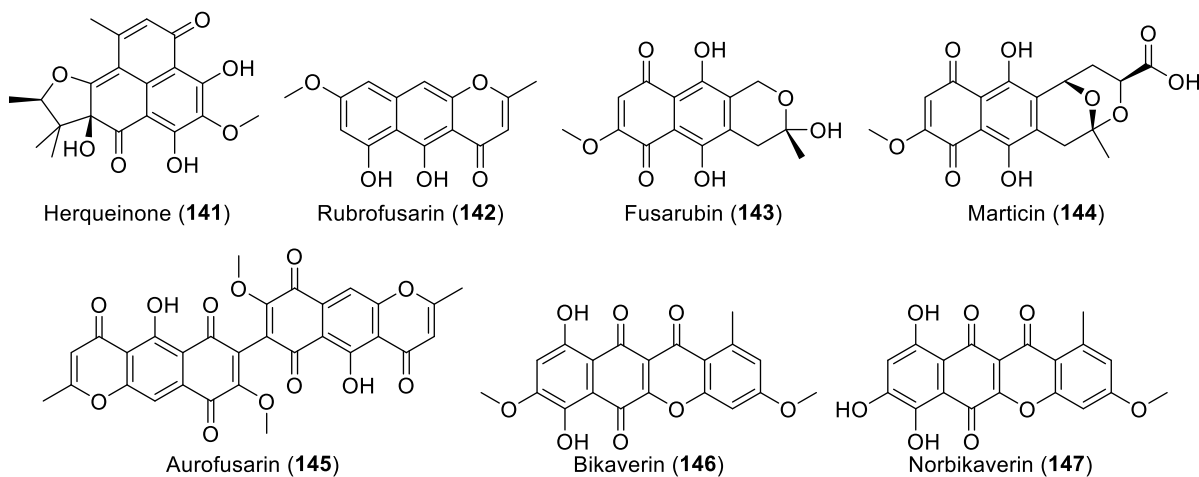


- 1 **Fig. 5** Representative AQs and related molecules from the quinone families observed in *Aspergillus*,
- 2 *Penicillium* and *Talaromyces*

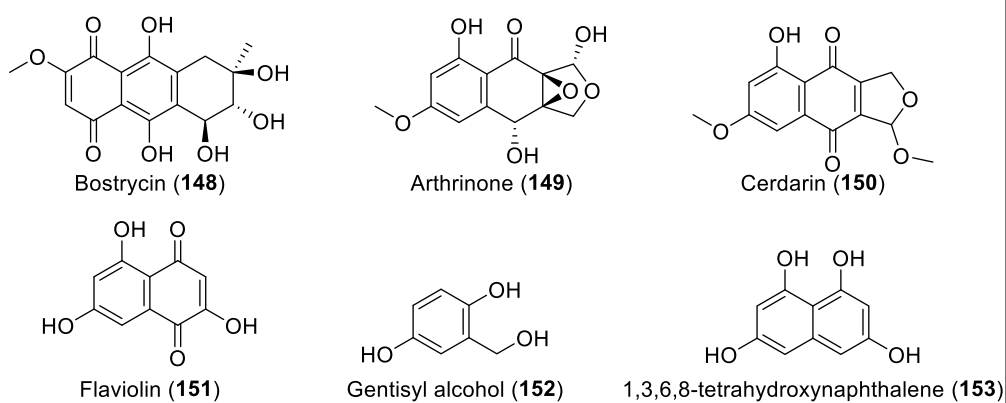


- 3
- 4 **Fig. 6** Venn-diagram showing the number of quinone families appearing in genera *Aspergillus*, *Penicillium* and
- 5 *Talaromyces*

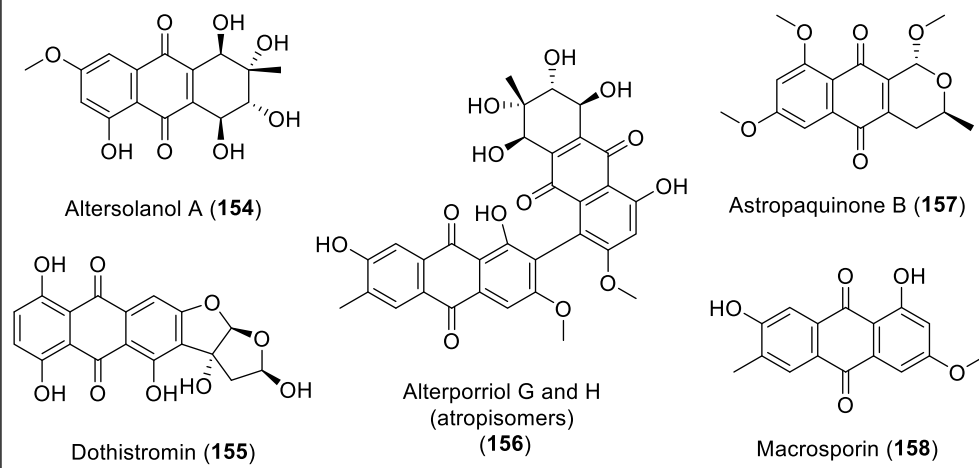
Fusarium quinones



Arthrinium quinones



Alternaria quinones



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

Tables

1

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

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

5

6

7 Table 2. Quinones in the genus *Aspergillus*¹⁻⁴ (Frisvad 2015¹; Frisvad and Larsen 2016²; Samson et al. 2014³;
8 Houbraken et al. 2020⁴; Chen et al. 2017⁵; Du et al. 2014^{5a}; Wang et al. 2007^{5b}; Du et al. 2007^{5c}; Laatsch et al.
9 1982^{5d}; Sklenář et al. 2017⁶; Rahbæk et al. 2000⁷; Varga et al. 2007⁸; Hubka et al. 2018a⁹; Frisvad et al.
10 2004¹⁰; Visagie et al. 2014¹¹; Varga et al. 2011a¹²; Frisvad et al. 2019¹³; Kjærboelling et al. 2020¹⁴; Heathcote
11 and Dutton 1969^{14a}; Chen et al. 2014^{14b}; Caceres et al. 2020^{14c}; Mandelare et al. 2018; Samson et al. 2011¹⁵;
12 Hubka et al. 2015¹⁶; Arzanlou et al. 2016¹⁷; Hubka et al. 2016a¹⁸; Varga et al. 2011b¹⁹; Samson et al.
13 2004²⁰; Samson et al. 2007a²¹; Perrone et al. 2011²²; Vesth et al. 2018²³; Theobald et al. 2018²⁴; Chen et al.
14 2013²⁵; Myobataka et al. 2014^{25a}; Holm et al. 2014^{25b}; Bugni, et al. 2000^{25c}; Jurjevics et al. 2015²⁶; Barros
15 Correia et al. 2020²⁷; Samson et al. 2011a²⁸; Balajee et al. 2009²⁹; Kiriya et al. 1977^{29a}; Hubka et al.
16 2016a³⁰; Chen et al. 2016a³¹; Varga et al. 2007³²; Visagie and Houbraken 2020³³; Anslow and Raistrick
17 1938³⁴; Samson et al. 2007b³⁵; Larsen et al. 2007³⁶; Frisvad et al. 2009³⁷; Frisvad and Larsen 2016³⁸; Hubka et
18 al. 2013³⁹; Hubka et al. 2017⁴⁰; Talbot et al. 2017⁴¹; Hubka et al. 2018b⁴²; Yang et al. 2013^{42a}; Lim et al.
19 2012^{42b}; Yamamoto et al. 1974^{42c}; Hayashi et al. 2007^{42d}; Turner 1971^{42e}; Yamamoto et al. 1968^{42f}; Abdel-Aziz

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

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

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

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

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

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

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

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

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

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

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

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

Section	Number of species (number of species known in section in all)	Number of species producing quinone (percentage)	Quinones produced	Quinone families produced
<i>Bacillispori</i>	2 (7)	0 (0%)	-	-
<i>Helici</i> ⁹	4 (13)	1 (25%)	Emodin (98) (secalonic acid BF)	Emodins (AQ)
<i>Islandici</i> ^{9,10,11,12,13,14,15,16,17,18,18a}	17 (34)	11 (65%)	Emodins and biemodins ^{10,11} (emodins: catenarin (99), chrysophanol (105), chrysophanic acid, emodin (98), endocrocin (112), ω-hydroxyemodin (104), islandicin, biemodins: (+)-aurantioskyrin, (+)-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), xanthoviridicatin (NQ), xanthomegnins (NQ), talaromannins (AQ)
<i>Purpurei</i> ¹⁹	5 (13)	2 (40%)	Emodin (98) (secalonic acid BF)	Emodins
<i>Subinflati</i> ^{19,20}	2 (6)	0 (0%)	-	-
<i>Talaromyces</i> ^{21,22,23,24,25,26}	42 (78)	8 (19%)	Catenarin (99), emodin (98) (secalonic acid BF), erythroglaucon (100), juglone (75), rugulosine, skyrin (95)	Emodins, juglones (NQ), biemodins (AQ)
<i>Tenues</i>	0 (1)	0 (0%)	-	-
<i>Trachysperm</i> ^{7,8,27,28}	12 (28)	2 (17%)	Emodin (98), ω-hydroxyemodin (104) (secalonic acid BF), purpurogenone (79)	Emodins (AQ), purpurogenone (NQ)
Unknown section and species ²⁹			Talaroquinone ^{28*}	

8 *Potentially an artificial oxidation product.