Review

Secondary Metabolites and Their Bioactivities Produced by Paecilomyces

Ze-Bao Dai 1,2, Xin Wang 1,2,* and Guo-Hong Li 1,2,*

1 State Key Laboratory for Conservation and Utilization of Bio-Resources in Yunnan, Yunnan University, Kunming 650091, China; yyyg0517@163.com
2 Key Laboratory for Microbial Resources of the Ministry of Education, Yunnan University, Kunming 650091, China
* Correspondence: wang26liqun@163.com (X.W.); ligh@ynu.edu.cn (G.-H.L.);
Tel.: +86-871-65031092 (X.W.); +86-871-65032538 (G.-H.L.)

Academic Editors: Jiang Wang, Liang-Ren Zhang, Peng Zhan, Qi-Dong You, Tian-Miao Ou and Xiao-Yun Lu

Received: 29 September 2020; Accepted: 29 October 2020; Published: 1 November 2020

Abstract: Paecilomyces, a common saprobic filamentous fungus, not only plays an important role in biological control, but also has applications in medicine, food, and environmental protection. In this paper, 223 secondary metabolites and their bioactivities from 13 known species and various unidentified strains of Paecilomyces are reviewed. Their structures can be described as polyketide, terpenoid, peptide, alkaloid, quinone, pyrone, sterol, and fatty acid. They have been demonstrated varying biological activities, including antimicrobial, antitumor, insecticidal, antiplasmodial, antimalarial, nematicidal, herbicidal, and enzyme-inhibiting. This review provides a comprehensive overview of secondary metabolites and their biological activities from strains of Paecilomyces.

Keywords: paecilomyces; fungi; metabolites; bioactivities; structures

1. Introduction

Paecilomyces is a common saprobic filamentous fungus. It is found in a wide range of habitats, including soils, forests, grassland, deserts, sediments, and even sewage sludge [1]. Paecilomyces belongs to the phylum Ascomycota, and the order Eurotiales, which has septate, branching hyphae, bearing long chains of conidia from the tips of conidiophores, and flask- to oval-shaped or subglobose phialide. Colonies of Paecilomyces are at first floccose and white, then become different colors. Paecilomyces strains do not harm to health in general and are in occasion opportunistic in humans and mammals.

Many species of Paecilomyces are important entomopathogenic fungi, which refer to a class that can infect or parasitize living host organisms and are an ecologically highly specialized group of micro-organisms. Entomopathogenic fungi are well known for their ability to produce various bioactive compounds during infection and proliferation in insects, and are considered as potential sources of novel bioactive compounds. The entomopathogenic fungi belonging to the genus Paecilomyces have been extensively studied as potential biological control agents against insects. Besides, Paecilomyces species have been used as Chinese traditional medicine to treat impotence, sedation, analgesia, backache, cancer, memory loss, and also as a tonic to nourish the lungs and kidneys [2]. Moreover, strains of Paecilomyces can survive in a wide range of temperatures and pH, which allows them to grow in a variety of substrates and makes them a rich source of biologically active natural products [3].

Paecilomyces is closely related to all aspects of human life and it plays an irreplaceable role in biological control, and has an important role in medicine and health. This review presents 223 secondary metabolites and their biological activities isolated from the 13 known species and various unidentified...
strains of *Paeclomyces*. The review covers reports from 1972 until the present. The structures of all compounds are summarized in Figures 1–3, and the active metabolites are concluded in Table 1.

### 2. Secondary Metabolites from *Paeclomyces*

#### 2.1. Metabolites Derived from *Paeclomyces* with Antimicrobial Activity

Diketopiperazine terezine D (1) (Figure 1 and Table 1) was isolated from *P. cinnamomeus* BCC 9616, which was firstly found from the coprophilous fungus *Sporormiella teretispora*. It demonstrated activity against *Sordaria fimicola* (NRRL6459), causing a 50% reduction in the radial growth rate at 200 µg/disk [4,5]. A maleimide-bearing compound, farinomalein (2), was isolated from *P. farinosus* HF999, which showed potent activity against the plant pathogen *Phytophthora sojae* P6497 at 5 µg/disk [6].

A series of peptidic antibiotics: leucinostatin A (4), D (7), H (8), and K (9), were identified from *P. marquandii* [14–16]. Leucinostatin D (7) showed biological activities against Gram-positive bacteria and several fungi, for example, *Bacillus subtilis* ICI, *Micrococcus luteus* ISS, *Streptococcus pneumoniae*, *S. haemolyticus*, and *S. aureus* [15]. Leucinostatin H (8) and K (9) also exhibited activities against Gram-positive bacteria and fungi, but the antibacterial and the antymycotic activity reduce significantly upon N-oxidation [16]. A Diels-Alder product of sorbicillinoid (10) with a urea group was isolated from *P. marquandii*, an intertidal marine strain, which had antibiotic activity against *B. subtilis* ATCC 6633 and *E. coli* ATCC 25922 [17].

Cyclodepsipeptides beauvericin (11) and beauvericin A (12) were isolated from *P. tenueps* BCC 1614. The two compounds displayed antimicrobial activities [18]. Beauvericin (11) can also be obtained from several fungi, including *Beauveria bassiana*, *Polyporus sulphureus*, and *Fusarium* spp. [19–22].

Two polyketides paecilocin B (13) and C (14) were identified from P. variotii derived from the jellyfish *Nemopilema nomurai*, which showed moderate antibacterial activity against *S. aureus* SG 511 and MRSA 3089 with MIC values ranging from 5 to 40 µg/mL [23]. Two metabolites, semi-viriditoxin (15) and semi-viriditoxic acid (16), were produced by a strain of *P. variotii*, isolated from the larvae of *Dendroctonus ponderosa*, and the two metabolites (15, 16) showed weak antibacterial activity against a number of bacteria [24]. One chromosome, lawsozaheer (17) was isolated from the broth of *Paecilomyces variotii*. It demonstrated highly selective activity against *S. aureus* (NCTC 6571) with 84.26% inhibition at 150 µg/mL [25]. Two oxepine-containing diketopiperazine-type alkaloids, varioloid A (18) and B (19), were identified from the marine alga-derived *P. variotii* EN-291, exhibiting potent activity against the plant pathogenic fungus *Fusarium graminearum* with MIC values of 8 and 4 mg/mL, respectively [26].

A benzannulated spiroketal derivative, paeciloketal A (20), was obtained from *P. variotii* J08NF-1, a jellyfish-derived strain, which showed antibacterial activity with a MIC value of 40 µg/mL against the marine pathogen *Vibrio ichthyoeneteri* [27].
Figure 1. The structures of metabolites produced by Paecilomyces (1).
A metabolite paecilospirone (21), was reported from Paecilomyces sp., with a MIC value of 5 µg/mL against B. subtilis at 25 °C; however, at 37 °C, it did not show any antimicrobial activity [28]. Paeciloxacin A (22) was isolated from Paecilomyces sp., and it inhibited the growth of Curvularia lunata and Candida albicans ATCC 10231 with inhibition zones of 12 and 10 mm, respectively [29]. Paecilomycin M (23), monocolin VI (24) and VII (25), aigilomycin B–D (26–28), 1′,2′-epoxy aigialomycin D (29), LL-Z1640-1 (30), monocolin II (31), monocolin IV (32), and monorden D (33) were produced by Paecilomyces sp. SC0924. Compounds 23–30 exhibited weak antifungal activity against Penicillophthora litchi [30–32]. Metabolites 31–33 can be separated from Pochonia chlamydosporia and demonstrated modest activity against Xanthomonas campestris, with a MIC value of 25.6 µg/mL [33]. Aigialomycin-type compound was also reported to be derived from Aigialus parvus [34,35]. LL-Z1640-1 (30) was firstly isolated from an unidentified fungus [36] and was also obtained from the gorgonian derived fungus Cochliobolus lunatus [37].

The antimicrobial and cytotoxic polyketide paeciloside A (34) and the compound acremoauxin A (35) were identified from a strain of Paecilomyces sp. CAFT156 [38]. Compounds 34 and 35 displayed inhibitory effects on two bacteria B. subtilis and S. aureus at 40 µg/disk [38]. A metabolite, paeciloxanthone (36), was obtained from Paecilomyces sp. (tree 1–7), a strain isolated from an estuarine mangrove from the Taiwan Strait. Metabolite 36 is active against C. lunata, E. coli., and C. albicans at 40 µg/disk, producing inhibitory zones of 6, 12, and 10 mm, respectively [39].

2.2. Cytotoxic Metabolites Derived from Paecilomyces

An antitumor cyclohexadepsipeptide, paecilodepsipeptide A (37), was derived from P. cinnamomeus BCC 9616. Paecilodepsipeptide A (37) exhibits cytotoxicity against cancer cell lines, KB and BC, with IC_{50} (the half maximal inhibitory concentration) values of 5.9 and 6.6 μM, respectively [40].

Farinosone A–C (38–40), three neurotrophic alkaloidal metabolites produced by P. farinosus RCEF 0101. Farinosone A (38) and C (40) can induce neurite outgrowth in the PC-12 cell line at concentrations of 50 µM, while farinosone B is inactive [41]. A tetramic acid derivative, paecilosetin (41), along with farinosone B (39), was isolated from P. farinosus. The two metabolites showed activity against the P388 cell line with IC_{50} values of 3.1 and 1.1 μg/mL, respectively [42]. A pyridone alkaloid, (+)-N-deoxymilitarinone A (42), was obtained from a strain of P. farinosus RCEF 0097. Compound 42 induced neurite sprouting in the PC-12 cell line when tested at concentrations of 33 and 100 µM and a cytotoxic effect was observed in human neurons (IMR-32) at 100 µM [43]. The metabolite (3S,6S)-3,6-dibenzylpiperazine-2,5-dione (43) was isolated from a culture extract of marine-derived P. formosus 17D47-2; it showed selective cytotoxic activity in human pancreatic carcinoma PANC-1 cells adapted to glucose-starved conditions, with an IC_{50} value of 28 µM, whereas no effect against PANC-1 cells under general culture conditions up to 1000 µM [44].

A novel macrocyclic, tetralactams gunnilactam A (44), isolated from P. gunnii, exhibited cytotoxic activity against human prostate cancer C42B cells with an IC_{50} value of 5.4 µM [45].

A series of metabolites, including 1,2-dilinolylglycerol-2′-(N,N,N-trimethyl) homoserine (45), methyl myristate (46) [46] and cerebrosides B–D (47–49) [47], were isolated from marine-derived P. lilacinus ZBY-1. The metabolites 45 and 46 inhibited the human cancer K562, MCF-7, HL-60, and BGC-823 cells with the IC_{50} values ranging from 1.12 to 8.63 μmol/L [46]. The compounds cerebrosides B–D (47–49) inhibited K562, MCF-7, HL-60, and BGC-823 cells with IC_{50} values ranging from 9.5 to 59.6 mg/L [47]. Leucinostatin A (4) and B (5), derived from P. lilacinus A-267, as well as having antimicrobial activity, also showed antitumor activity and an uncoupling effect on rat liver mitochondrial function [11,12].

Three novel pyridone alkaloids, militarinone A (50), B (51), and D (52), were isolated from the mycelium of P. militaris [48,49]. Militarinone A (50) had a pronounced neurotrophic effect in the PC-12 cells at concentration of 10 µM [48]. Militarinone D (52) showed significant cytotoxicity against PC-12 cells with 74.0% and 30.7% at concentrations of 100 and 33 μM, respectively, and militarinone B (51)
was weakly cytotoxic at 100 µM (16.8%) [49]. In addition, militarinone B (51) and D (52) can also be obtained from a strain of *P. farinosus* RCEF 0097 [43].

A peptidic antibiotic, leucinostatin D (7), was obtained from *P. marquandii*. The phytotoxicity test on tomato cuttings proved positive at 2 µg/mL, and *in vitro* cytotoxic activity assays showed that it inhibited HeLa, KB, and P388/S with ID$_{50}$ values of 850, 0.95, and 1.00 ng/mL [15].

The novel metabolite (35)-6-phenethyl-3-isopropyl-1-methyl-2,5-diketopiperazine (53) was obtained from *P. tenuipes* and showed cytotoxicity against 22RV1 and DU-145 prostate cancer cells with inhibition rates of 37.8% and 38.6% at 5 µM [50]. Cyclodepsipeptide beauvericin (11) and beauvericin A (12) derived from *P. tenuipes* BCC 1614 also showed cytotoxic activity [18].

A series of compounds, including a indolyl-6,10b-dihydro-5aH-[1]benzofuro[2,3-b]indole derivative (54), a diketopiperazine-type alkaloid varioloid B (19), and two prenylated indole alkaloids dihydrocarneamide A (55), and *iso-*notoamide B (56), were identified from the marine alga-derived *P. variotii* EN-291 [26,51,52]. Compounds 19 and 54 exhibited cytotoxicity against A549, HCT116, and HepG2 cell lines, with IC$_{50}$ values from 2.6 to 8.2 µg/mL [51]. Dihydrocarneamide A (55) and *iso-*notoamide B (56) showed cytotoxic activities against NCI-H460 with IC$_{50}$ values of 69.3 and 55.9 nmol/L, respectively [52].

Three metabolites, UCE1022 (57), saintopin (58), and paeciloxacin A (22), were identified from an unidentified species of *Paecilomyces*. UCE1022 (57) displayed *in vitro* cytotoxic activity against HeLa S3 at IC$_{50}$ 6.1 µM [53]. Saintopin (58) shows *in vitro* cytotoxic activity against HeLa S3 at IC$_{50}$ 0.35 µg/mL, and further demonstrated *in vitro* antitumor activity against murine leukemia P388 (ip) [54]. Paeciloxacin A (22) exhibited significant cytotoxicity against hepg2 with an IC$_{50}$ value of 1 µg/mL [29]. A β-resorcylic acid lactone, paecilomycin P (59), and two radicicol-type metabolites, monocillin VI and VII (60, 61) were produced by a strain of *Paecilomyces* sp. SC0924 [32]. The three compounds (59–61) exhibited cytotoxicity against MCF-7, A549, and HeLa cells [32]. The metabolites paeciloxide A (34) and acremoauxin A (35) were identified from *Paecilomyces* sp. CAFT156. The two compounds displayed moderate cytotoxicity towards *Artemia salina* [38]. The cytotoxic ergosterols, including 5α,6α-epoxy-(22E,24R)-ergosta-8,22-diene-3β,7α-diol (62), ergosta-4,6,8(14),22-tetraene-3-one (63), 3β,5α-dihydroxy-6β-methoxyer-gosta-7,22-diene (64), ergosterol (65), and ergosterol endoperoxide (66), were produced by *Paecilomyces* sp. J300 [55]. These compounds showed moderate cytotoxicity against A549, SK-OV-3, SK-MEL-2, XF498 (CNS), and HCT15 cells [55]. A sequence of metabolites, including paeciloxanthone (36) [39], paecilin A (67), secalonic acid D (68), secalonic acid A (69), tenelic acid A (70), and five anthraquinone derivates, tetracenomycin D (71), physcioin (72), emodin (73), chrysophanol (74), 1,4-dihydroxy-2-methy anthraquinone (75) were obtained from *Paecilomyces* sp. (tree 1–7) [39,56–58]. Paeciloxanthone (36) exhibited *in vitro* cytotoxicity against hepg2 with an IC$_{50}$ value of 1.08 µg/mL [39]. Paecilin A (67) showed inhibiting activity against KB and KBv cells with IC$_{50}$ values of 40 and 50 nmol/mL, respectively [56]. Secalonic acid D (68) showed cytotoxicity towards KB cells with an value of IC$_{50}$ < 1 µg/mL and inhibited human topoisomerase I with an IC$_{50}$ value of 0.16 µmol/mL [57]. Secalonic acid A (69) (Figure 2) and tenelic acid A (70) inhibited the growth of the human hepatoma cell line HepG2, with IC$_{50}$ values of 62.1 and 2.0 µg/mL, respectively [58]. Compounds 71–75 showed anticancer activity against KB and KBv, with IC$_{50}$ values of 11, 20, 8, 15, and 18 µg/mL and 17, 30, 10, 20, and 25 µg/mL, respectively [59].
Figure 2. The structures of metabolites produced by *Paecilomyces* (2).
2.3. Metabolites with Enzyme Inhibitory Activity from Paecilomyces

Paecilopeptin (76) is a novel cathepsin S inhibitor produced by *P. carneus*, which inhibits human cathepsin S in vitro with an IC₅₀ value of 2.1 nM [60]. A series of inhibitors of the protein tyrosine kinases paeciloquinone A (77), C (78), and D (79) were obtained from *P. carneus* P-177 [61,62]. Paeciloquinone A (77) and C (78) are potent and selective inhibitors of the v-abl protein tyrosine kinase with an IC₅₀ value of 0.4 µM [61]. Paeciloquinone D (79) is a protein kinase C inhibitor with an IC₅₀ value around 6 µM [63].

Two metabolites, sester-terpenoid YW3548 (80) and a cyclic peptide paecilodepsipeptide A (37), were isolated from endophytic *P. formosus* LHL10 [64]. The two compounds exhibited remarkable inhibitory rates against α-glucosidase and urease, with IC₅₀ values of 61.80 ± 5.7 and 75.68 ± 6.2, and 74.25 ± 4.3 and 190.5 ± 10.31 µg/g, respectively [64], which were also obtained from *P. cinnamomeus* [40]. Paecilomycone A–C (81–83) were identified from cultures of *P. gunnii* with IC₅₀ values of 0.11, 0.17, and 0.14 mM on Tyrosinase, respectively [65]. A pyridone alkaloid, paecilomide (84), derived from *P. lilacinus*, demonstrated an acetylcholinesterase inhibition of 57.5 ± 5.50% [66].

Sphingofungins E (85) and F (86) are novel structures in the sphingofungin family which can inhibit serinepalmitoyl transferase at nanomolar levels; the estimated IC₅₀ values were 7.2 and 57 nM, respectively, which were obtained from a strain of *P. variotii* ATCC 74097 [67]. A oxybis cresol, verticilatin (87), was identified from cultures of *P. verticillatus*. Verticilatin (87) exhibited significant inhibitory activity against CDC25B, cathepsin B, MEG2, and SHP2 enzyme, with IC₅₀ values of 11.5, 3.5, 7.8, and 15 µg/mL, respectively [68]. A metabolite of the compactin family, 3α-hydroxy-3,5-di hydro ML-236C (88), was isolated from *P. viridis* L-68, and the in vitro activity of HMG-CoA reductase was inhibited by approximately 50% by this compound 88 [69].

The cadinane-type sesquiterpenoid analogs, 12-hydroxyalbrassitriol (89) and 2-hydroxyalbrassitriol (90), were obtained from the endophytic fungus *Paecilomyces* sp. TE-540. The two compounds showed moderate activities against acetylcholinesterase (AChE), with IC₅₀ values of 43.02 ± 6.01 and 35.97 ± 2.12 µM, respectively [70]. Phenopicolinic acid (91), a potent inhibitor of dopamine β-hydroxylase, was found in culture filtrates of *Paecilomyces* sp. AF2562. The LD₅₀ (median lethal dose or concentration) of phenopicolinic acid (91) for mice was about 350 mg/kg through intraperitoneal injection [71].

Two novel protein farnesyltransferase (PFTase) inhibitors, kurasoin A (92) and B (93), were derived from the cultured broth of *Paecilomyces* sp. FO-3684 [72]. The two metabolites inhibited PFTase in a dose-dependent, with IC₅₀ values of 59.0 and 58.7 µM, respectively [72]. The metabolites paeciloxanthone (36) and secalonic acid D (68) were isolated from *Paecilomyces* sp. (tree 1–7). Paeciloxanthone (36) exhibited in vitro AChE inhibition with an IC₅₀ value of 2.25 µg/mL [39], and secalonic acid D (68) inhibited human topoisomerase I with an IC₅₀ value of 0.16 µmol/mL [57].

2.4. Insecticidal, Nematicidal, Antiplasmodial, and Antimalarial Metabolites Derived from Paecilomyces

Catenioblin C (94) and phomalactone (95) were identified from *P. catenioblinus* YMF1.01799 [73]. The polyketide-derived phomalactone (95) had a significant inhibitory effect on the growth of the cotton bollworm *Helicoverpa armigera*, while the terpenoid derived metabolite catenioblin C (94) promoted the growth of the larvae [73]. Beauvericin (11) and beauvericin A (12) with diversiform bioactivities obtained from *P. tenuipes* BCC 1614, also demonstrated promising insecticidal activity [18]. The metabolite cerebrosides A (96) was isolated from marine-derived *P. lilacinus* ZBY-1, and its nematicidal activity against *Bursaphelenchus xylophilus* was investigated. The result showed that the average mortality of *B. xylophilus* treated with cerebrosides A (96) at the mass concentrations of 1000, 100, and 10 µg/mL were 100%, 100%, and 11.1%, respectively [74].

A nematicidal metabolite 4-(4′-carboxy-2′-ethyl-hydroxypentyl)-5,6-dihydro-6-methyl-cyclobut[b]pyridine-3,6-dicarboxylic acid (97), was produced by *Paecilomyces* sp.YMF1.01761. Within 24 h, the LD₅₀ value was 50.86 mg/L against *Panagrellus redivivus*, 47.1 mg/L against *Meloidogyn incognita*, and 167.7 mg/L against *B. xylophilus* [75]. Paecloxazine (98) was isolated from *Paecilomyces*
sp. BAUA3058, demonstrating moderate nematicidal activity against *Rhabditis pseudoelongata* and weak activity against some insects [76].

The metabolite paecilodepsipeptide A (37) was obtained from *P. cinnamomeus* BCC 9616. It possesses three D-amino acid residues and can act against the malarial parasite *Plasmodium falciparum* K1, with an IC$_{50}$ value of 4.9 µM [4,40]. The compound harzialactone A (99) was isolated from the marine-derived fungus *Paecilomyces* sp. 7A22. It exhibited significant activity against *Leishmania amazonensis* with an IC$_{50}$ value of 5.25 µg/mL and a moderate activity against intracellular amastigotes with an IC$_{50}$ value of 18.18 mg/mL [77].

Two novel β-resorcylic acid lactones, paecilomycin E, F (100, 101), along with aigilomycin B (102) and aigialomycin F (103) were isolated from a strain of *Paecilomyces* sp. SC0924 [78]. Paecilomycin E (100) and aigialomycin F (103) exhibited antiplasmodial activity against the *Plasmodium falciparum* line 3D7 with IC$_{50}$ values of 20.0 and 10.9 nM, respectively, and paecilomycin E, F (100, 101) and aigilomycin B (102) showed moderate activity against the *P. falciparum* line Dd2 [78]. Four metabolites containing pyrenocine I (104), pyrenocine A, B (105, 106) and citreoviridin (107) were produced by *Paecilomyces* sp. FKI-3573 [79]. These compounds exhibit *in vitro* antitrypanosomal activity, and pyrenocine A (105) showed the most potent activity with an IC$_{50}$ value of 0.12 mg/mL [79].

### 2.5. Other Active Metabolites Derived from Paecilomyces

The metabolites spirotenuipesine A, B (108, 109) and paecilomycine A (110) were obtained from *P. tenuipes*. The three compounds showed potent activity in neurotrophic factor biosynthesis in glial cells [80,81]. A pyrrolooxazine, formoxazine (111), a dipyrroloquinone derivative, terreusinone (112), and a 2-oxazolidinone analogue, 3-[(2Z)-1-oxo-2-buten-1-yl]oxazolidin-2-one (113) were isolated from the marine-derived *P. formosus* [82]. The compounds 111 and 113 displayed potent radical-scavenging activity against DPPH, with IC$_{50}$ values of 0.1 and 10 µM [82]. Terreusinone (112) exhibited a UV-A absorbing activity with an ED$_{50}$ value of 70 µg/mL [83]. Phytotoxin 14-hydroxycornexistin (114), a member of the nonadride family, was obtained from *P. variotii*, exhibiting a potent activity against broadleaf weeds and a selectivity to corn [84]. A herbicidal antibiotic, cornexistin (115), was isolated from *P. variotii* SANK 21086, which shows non-selective, broad spectrum herbicidal activity against annual plants including mono- and dicotyledonous weeds and may be useful for postemergence weed control with selective protection of corn [85,86]. In addition, cornexistin (115) was also isolated from *P. tenuipes* [25].

### 2.6. Metabolites with Unknown Activity Derived from Paecilomyces

The metabolites paeciloquinone B (116) and paeciloquinone E, F (117, 118) were obtained from *P. carneus* P-177 [61,62]. Two compounds, catenioblina A, B (119, 120) were identified from *P. catenioblina* YMF1.01799 for the first time [73]. The metabolites paecilodepsipeptide B and C (121, 122), a xanthone glycoside, norlichexanthone-6-O-(4-O-methylglucopyranoside) (123), and hopane triterpene zeorin (124) were produced by *P. cinnamomeus* BCC 9616 [4,40]. Two novel macrocyclic tritactalamts, gunniiactam B, C (125, 126) were produced by *P. gunnii* [45].

A series of compounds, including two α-pyrones, paecilopyrone A, B (127, 128); two cyclohexenones, phomalogil B, C (129, 130); and the analogues, phomapyrone B (131) and C (6); kojic acid (132), phomaligol A (3), methylphomaligol A (133), phomaligol A$_1$ (134), acetylpomatigol A (135), phomaligol A hydroperoxide (136), and phomaligol A$_1$ hydroperoxide (137), were identified from a strain of *P. lilacinus* derived from the marine sponge *Petrosia* sp. The compounds kojic acid (132), phomaligol A (3), and methylphomaligol A (133) were evaluated for their cytotoxicity against a small panel of human solid tumor cell lines and were found to be inactive up to a concentration of 30 µg/mL [7]. In addition, phomaligol A$_1$ (134) can also be obtained from the blackleg fungus *L. maculans* [9]. Eleven metabolites, including paecilaminol (138), paecilaminol hydrochlorate (139), methyl linoleate (140), linoleate (141), oleic acid (142), indole-3-carboxaldehyde (143), indolyl-3-carboxylic acid (144), 4-hydroxybenzoic acid (145), 9(11)-dehydroergosterol peroxide
(146), (22E,24R)-5α,6α-epoxy-3β-hydroxyergosta-22-ene-7-one (147), and ergosterol peroxiden (148) were isolated from marine derived P. lilacinus ZBY-1 [46,47].

A novel pyridone alkaloid, militarinone C (149), was obtained from the mycelium of P. militaris [49]. Six secondary metabolites were obtained from P. tenuipes, which include (4S,10R)-4-hydroxy-8-oxygen-10-methyl solactone (150), tenuipesine A (151), paecilomycines B, C (152, 153), cepharosporolide C (154) (Figure 3) and E (155) [50,80,87]. Paecilocin A (156) and D (157), 4-(2-hydroxyethyl) phenol (158), stigmasta 4,6,8(14),22-tetraen-3-one, β-sitosterol (159) and stigmaster (160) were reported from P. varioti [23,25]. Two bicyclic fatty acids, paecilocic acid A (161) and B (162), together with two benzannulated spiroketal derivatives, paeciloketal B (163) and 1-epi-paeciloketal B (164) were obtained from jellyfish-derived strain of P. variotii J08NF-1 [27,88]. The metabolites 5-methylresorcinol (165) and 2,4-dihydroxy-3,6-dimethylbenzaldehyde (166) were isolated from cultures of P. verticillatus [68].

| Metabolites         | Paecilomyces Strain | Biological Activities          | References |
|---------------------|---------------------|--------------------------------|------------|
| terezine D (1)      | P. cinnamomeus BCC 9616 | antifungal                    | [4]        |
| farinomalein (2)    | P. farinosus HF599  | antifungal                    | [6]        |
| phomaligol A (3)    | P. blacinas         | antibacterial                 | [7,8]      |
| leucinostatin A (4) | P. lilacinus A-267  | uncoupling effect on rat liver mitochondrial function antimicrobial, antitumor, uncoupling effect on rat liver mitochondrial function antimicrobial, antitumor, | [10–12] |
| leucinostatin B (5) | P. lilacinus A-267  | uncoupling effect on rat liver mitochondrial function antimicrobial, antitumor, | [10–12] |
| phomapyrone C (6)   | P. blacinas         | antibacterial                 | [7,13]     |
| leucinostatin D (7) | P. marquandi       | antimicrobial, cytotoxic, phytotoxicity | [15] |
| leucinostatin H (8) | P. marquandi       | antimicrobial                  | [16]       |
| leucinostatin K (9) | P. marquandi       | antimicrobial                  | [16]       |
| sorbicillinoid (10) | P. marquandi       | antibacterial                  | [17]       |
| beauvericin (11)    | P. tenuipes BCC 1614 | antimicrobial, cytotoxic, insecticidal | [18] |
| beauvericin A (12)  | P. tenuipes BCC 1614 | antimicrobial, cytotoxic, insecticidal | [18] |
| paecilolin B (13)   | P. varioti          | antibacterial                  | [23]       |
| paecilolin C (14)   | P. varioti          | antibacterial                  | [23]       |
| semi-viriditoxin (15)| P. varioti        | antibacterial                  | [24]       |
| semi-viriditoxic acid (16)| P. varioti    | antibacterial                  | [24]       |
| lawsozaheer (17)    | P. varioti          | antibacterial                  | [25]       |
| varioloid A (18)    | P. varioti EN-291  | antifungal                     | [26]       |
| varioloid B (19)    | P. varioti EN-291  | antifungal                     | [26]       |
| paeciloketal A (20) | P. varioti J08NF-1 | antibacterial                  | [27]       |
| paecilosporine (21) | Paeilomyces sp.    | antibacterial                  | [28]       |
| paeciloxin A (22)   | Paeilomyces sp.    | antifungal, cytotoxic          | [29]       |
| paecilomycin M (23) | Paeilomyces sp. SC0924 | antifungal                    | [31]       |
| monocillin VI (24)  | Paeilomyces sp. SC0924 | antifungal                    | [32]       |
| monocillin VII (25) | Paeilomyces sp. SC0924 | antifungal                    | [32]       |
| aigilomycin B (26)  | Paeilomyces sp. SC0924 | antifungal                    | [30]       |
| aigilomycin C (27)  | Paeilomyces sp. SC0924 | antifungal                    | [30]       |
| aigilomycin D (28)  | Paeilomyces sp. SC0924 | antifungal                    | [30]       |
| 1′,2′-epoxy aigialomycin (29) | Paeilomyces sp. SC0924 | antifungal                    | [30]       |
| monocillin Il (31)  | Paeilomyces sp. SC0924 | antifungal                    | [33]       |
| monocillin IV (32)  | Paeilomyces sp. SC0924 | antifungal                    | [33]       |
| monorden D (33)     | Paeilomyces sp. SC0924 | antifungal                    | [33]       |
| paeciloside A (34)  | Paeilomyces sp. CAFT156 | antibacterial, cytotoxic      | [38]       |
| acremosaux A (35)   | Paeilomyces sp. CAFT156 | antibacterial, cytotoxic      | [38]       |

Table 1. The active metabolites derived from Paecilomyces.
Table 1. Cont.

| Metabolites                                      | Paecilomyces Strain            | Biological Activities                                                                 | References |
|--------------------------------------------------|--------------------------------|---------------------------------------------------------------------------------------|------------|
| paeciloxanthone (36)                             | Paecilomyces sp. (tree 1–7)    | antimicrobial, cytotoxic, enzyme inhibition, cytotoxic, enzyme inhibition              | [39]       |
| paecilodepsipeptide A (37)                       | P. cinnamomeum BCC 9616       | cytotoxic, enzyme inhibition, antimalarial induce neurite                              | [40]       |
| farinosone A (38)                                | P. farinosus RCEF 0101         | outgrowth in the PC-12 cell line                                                      | [41]       |
| farinosone B (39)                                | P. farinosus RCEF 0101         | cytotoxic                                                                              | [41,42]    |
| farinosone C (40)                                | P. farinosus RCEF 0101         | outgrowth in the PC-12 cell line                                                      | [41]       |
| paeiclosetin (41)                                | P. farinosus RCEF 0097         | cytotoxic                                                                              | [42]       |
| (+)-N-deoxymilitarinone A (42)                   | P. farinosus RCEF 0097         | cytotoxic, induce neurite sprouting in PC-12 cell line                                 | [43]       |
| (3S,6S)-3,6-dibenzylpiperazine-2,5-dione (43)     | P. formous 17D47-2             | cytotoxic                                                                              | [44]       |
| 1,2-dinilinolylglycerol-0,4’-(N,N,N-trimethyl) homoserine (45) | P. gunnii            | cytotoxic                                                                              | [45]       |
| methyl myristate (46)                            | P. lilacinus ZBY-1             | cytotoxic                                                                              | [46]       |
| cerebroside B (47)                               | P. lilacinus ZBY-1             | cytotoxic                                                                              | [46]       |
| cerebroside C (48)                               | P. lilacinus ZBY-1             | cytotoxic                                                                              | [47]       |
| cerebroside D (49)                               | P. lilacinus ZBY-1             | cytotoxic                                                                              | [47]       |
| militarinone A (50)                              | P. militaris                  | neurotrophic effect in PC-12 cells                                                     | [49]       |
| militarinone B (51)                              | P. farinosus RCEF 0097         | cytotoxic                                                                              | [43,48]    |
| militarinone D (52)                              | P. tenuipes                   | cytotoxic                                                                              | [50]       |
| (3S)-6-phenethyl-3-isopropyl-1-methyl-2,5-diketopiperazine (53) | P. varioti EN-291            | cytotoxic                                                                              | [51]       |
| indoly-6,10b-dihydro-Sah[1]benzofuro[2,3-b]indole derivative (54) | P. varioti EN-291            | cytotoxic                                                                              | [52]       |
| dihydrocarneamide A (55)                        | P. varioti EN-291             | cytotoxic                                                                              | [52]       |
| iso-notoamide B (56)                            | P. varioti EN-291             | cytotoxic                                                                              | [52]       |
| UCE1022 (57)                                    | Paecilomyces sp.              | cytotoxic                                                                              | [53]       |
| saultin (58)                                     | Paecilomyces sp.              | cytotoxic                                                                              | [53]       |
| paecilomycin P (59)                             | Paecilomyces sp. SC0924       | cytotoxic                                                                              | [32]       |
| monocillin VI (60)                              | Paecilomyces sp. SC0924       | cytotoxic                                                                              | [32]       |
| monocillin VII (61)                             | Paecilomyces sp. SC0924       | cytotoxic                                                                              | [32]       |
| 5α,6α-epoxy-(22E,24R)-ergosta-8,22-diene-3β,7α-diol (62) | Paecilomyces sp. J300         | cytotoxic                                                                              | [55]       |
| ergosta-4,6,8(14),22-tetraene-3-one (63)         | Paecilomyces sp. SC0924       | cytotoxic                                                                              | [55]       |
| 3β,5α-dihydroxy-6β-methoxygosta-7,22-diene (64)  | Paecilomyces sp. J300         | cytotoxic                                                                              | [55]       |
| ergosterol (65)                                  | Paecilomyces sp. J300         | cytotoxic                                                                              | [55]       |
| ergosterol endoperoxide (66)                     | Paecilomyces sp. J300         | cytotoxic                                                                              | [55]       |
| paeclin A (67)                                   | Paecilomyces sp. (tree 1–7)    | cytotoxic                                                                              | [56]       |
| scelonic acid D (68)                             | Paecilomyces sp. (tree 1–7)    | cytotoxic, enzyme inhibition                                                          | [57]       |
| scelonic acid A (69)                             | Paecilomyces sp. (tree 1–7)    | cytotoxic                                                                              | [58]       |
| tenelic acid A (70)                              | Paecilomyces sp. (tree 1–7)    | cytotoxic                                                                              | [58]       |
| tetracenomycin D (71)                            | Paecilomyces sp. (tree 1–7)    | cytotoxic                                                                              | [58]       |
| phycocyanin (72)                                 | Paecilomyces sp. (tree 1–7)    | cytotoxic                                                                              | [59]       |
| ermodin (73)                                     | Paecilomyces sp. (tree 1–7)    | cytotoxic                                                                              | [59]       |
| chrysophansol (74)                               | Paecilomyces sp. (tree 1–7)    | cytotoxic                                                                              | [59]       |
| 1,4-dihydroxy-2-methy لناthaquinone (75)          | Paecilomyces sp. (tree 1–7)    | cytotoxic                                                                              | [59]       |
| paeclopeptin (76)                                | P. carneus                   | inhibiting human cathepsin S                                                          | [60]       |
| paeclouquine A (77)                              | P. carneus P-177              | enzyme inhibition                                                                      | [61]       |
| paeclouquine C (78)                              | P. carneus P-177              | enzyme inhibition                                                                      | [61]       |
| paeclouquine D (79)                              | P. carneus P-177              | enzyme inhibition                                                                      | [63]       |
| YW3548 (80)                                      | P. formous LHL 10             | enzyme inhibition                                                                      | [64]       |
| paeclomycone A (81)                              | P. gunnii                    | enzyme inhibition                                                                      | [65]       |
| paeclomycone B (82)                              | P. gunnii                    | enzyme inhibition                                                                      | [65]       |
| paeclomycone C (83)                              | P. gunnii                    | enzyme inhibition                                                                      | [65]       |
| paeclomide (84)                                  | P. lilacinus                 | enzyme inhibition                                                                      | [66]       |
Two novel unique spirochroman-2,1′(3′H)-isobenzofuran] derivative (167), (3R*,5E, 7E,9R*,11E,13Z)-1-((3′aS*,6′aR*)-2-amino-5-oxo-3′a,5′,6′,6′α-tetrahydrofuro-[3′,2-b]furan-3-yl)-3,7,9,11-tetramethylheptadeca-5,7,11,13-tetraene-1,2-dione (168), together with cholesteryl linoleate (169), and 2,5-furandimethanol (170) were isolated from marine-derived strains of Paecilomyces [3,89].

A diterpenoid, paecilomycin B (171), with a five-membered lactone ring, and three labdane diterpenoids, botryosphaerin E (172), agathic acid (173), and rel-(1R,5S,4aS,5R,8aS)-5-[3′(3E)-4-carboxy-3-methylbut-3-en-1-yl]dehydro-3-hydryx-1,4a-dimethyl-6-methylidenenaphthalene-1-carboxylic acid (174) were identified from the solid culture of Paecilomyces sp. ACCC 37762 [90]. A number of β-resorcylic acid lactones paecilomycin A–D (175–178), paecilomycin G–L (179–184), paecilomycin N, O (185,186), 4′-hydroxymonocillin IV (187), 4′-methoxymonocillin IV (188), zeanol (189), aigialospiril (190), zeearalenone (191), 7′-dehydrozearalenone (192), trans-7′,8′-dehydrozearalenol (193), monocillin I (194), monocillin III (195), radicicol (196), lasicicol (197), and hypothermycin (198) were produced by a strain of Paecilomyces sp. SC0924 [30–32,78]. Furthermore, the compound 7′-dehydrozearalenone (192) was firstly isolated from Gibberella zeae [91].

| Metabolites                      | Paecilomyces Strain | Biological Activities | References  |
|----------------------------------|---------------------|-----------------------|-------------|
| Sphingofungin E (85)             | P. variotii ATCC 74097 | enzyme inhibition     | [67]        |
| Sphingofungin F (86)             | P. variotii ATCC 74097 | enzyme inhibition     | [67]        |
| verticillatin (87)               | P. verticillatus     | enzyme inhibition     | [68]        |
| 3α-hydroxy-3,5-dihydro ML-236C (88) | P. viridis L-68     | enzyme inhibition     | [69]        |
| 12-hydroxyalbrassitiol (89)      | Paecilomyces sp. TE-540 | enzyme inhibition     | [70]        |
| 2-hydroxyalbrassitiol (90)       | Paecilomyces sp. TE-540 | enzyme inhibition     | [70]        |
| phenopolic acid (91)             | Paecilomyces sp. AF2562 | enzyme inhibition     | [71]        |
| karsosin A (92)                  | Paecilomyces sp. FO-3684 | enzyme inhibition     | [72]        |
| karsosin B (93)                  | Paecilomyces sp. FO-3684 | enzyme inhibition     | [72]        |
| cateniobin C (94)                | P. cateniobiolius YMFI.01799 | the larvae of cotton  | [73]        |
| phomalactone (95)                | P. cateniobiolius YMFI.01799 | inhibition cotton     | [73]        |
| cerebroside A (96)               | P. lilacinus ZBY-1   | nematicidal           | [74]        |
| 4-(4′-carboxy-2′-ethyl-hydroxypentyl)-5,6-dihydro-6-methyl-cyclobutyl[3,6-dicarboxylic acid (97) | Paecilomyces sp. YMFI.01761 | nematicidal     | [75]        |
| paeciloaxazine (98)              | Paecilomyces sp. BAUA3058 | Nematicidal, insecticidal | [76]        |
| harzialactone A (99)             | Paecilomyces sp. FA2725 | insecticidal         | [77]        |
| paecilomycin E (100)             | Paecilomyces sp. SC0924 | antiplasmodial       | [78]        |
| paecilomycin F (101)             | Paecilomyces sp. SC0924 | antiplasmodial       | [78]        |
| agilomycin B (102)               | Paecilomyces sp. SC0924 | antiplasmodial       | [78]        |
| agilomycin F (103)               | Paecilomyces sp. SC0924 | antiplasmodial       | [78]        |
| pyrrocolinc I (104)              | Paecilomyces sp. FKI-3573 | antitrypanosomal     | [79]        |
| pyrrocolinc A (105)              | Paecilomyces sp. FKI-3573 | antitrypanosomal     | [79]        |
| pyrrocolinc B (106)              | Paecilomyces sp. FKI-3573 | antitrypanosomal     | [79]        |
| citroavidin (107)                | Paecilomyces sp. FKI-3573 | antitrypanosomal     | [79]        |
| spirotenupiesine A (108)         | P. tenuipes          | factor biosynthesis in glial cells | [81]        |
| spirotenupiesine B (109)         | P. tenuipes          | factor biosynthesis in glial cells | [81]        |
| paecilomycine A (110)            | P. tenuipes          | factor biosynthesis in glial cells | [80]        |
| formoxazine (111)                | P. formosus          | radial-scavenging activity | [82]        |
| terreusinine (112)               | P. formosus          | UV-A absorbing activity | [83]        |
| 3′-(2Z)-1-oxo-2-buten-1-yl]oxazolidin-2-one (113) | P. formosus | radial-scavenging activity | [82]        |
| 15-hydroxycornexistin (114)      | P. variotii          | herbicidal           | [84]        |
| cornexistin (115)                | P. variotii SANK 21086 | herbicidal         | [85,86]     |
Figure 3. The structures of metabolites produced by Paecilomyces (3).
The metabolites 1,5-dideoxy-3-C-methyl-arabitol (199) and adenosine (200) were identified from a strain of Paecilomyces sp. CAFT156 [38]. Several compounds, including a indolinepeptide, 3β,5-dihydroxy-1-N-methyl-indole-2β-carbonyl amino-o-alanyl-erythro-β-hydroxyisoleucinyl-glycine (201), (4E, 8E, 2S, 2′R, 3R)-N-2’-hydroxy-hexadecanoyl-l-O-β-D-glucopyranosyl-9-methyl-4, 8-sphingadienin (202), alloxazine (203), along with the ergosterol derivatives, 3β,5α-dihydroxy-ergosta-7,22-diene (204), 5α,6α-epoxy-(22E,24R)-ergosta-8(14),22-diene-3β,7α-diol (205), were isolated from Paecilomyces sp. J300 [2,55]. Two cadinane-type sesquiterpenoids, paecilacadinol A and B (206, 207), two drimane-type sesquiterpenoids, ustusol D (208) and ustusol E (209), and the four analogs, deoxyuvidin B (210), 3β,9α,11-trihydroxy-6-oxodrim-7-ene (211), 2α,11-dihydroxy-6-oxodrim-7-ene (212), and ustusol B (213) were obtained from the endophytic fungus Paecilomyces sp. TE-540 [70]. The metabolite, paecilin B (214) [57], and nine cyclic peptides, viscumamide (215), cyclo(Pro-Is0) (216), cyclo(Phe-Gly) (217), cyclo(Phe-Ana) (218), cyclo(Gly-Pro) (219), cyclo(Gly-Leu) (220), cyclo(Trp-Ana) (221), necoeshinulin A (222), and cyclo(Pro-Thr) (223) were identified from Paecilomyces sp. (tree 1–7) [92].

3. Conclusions

Since Paecilomyces were first described, many have been proven to be insect pathogens. As a result of the hardiness, wide adaptability, and ease of culture of most species of Paecilomyces, they play an important role in pest control, medicine, functional foods, environmental pollution control, and genetic engineering. Furthermore, Paecilomyces species are a source of bioactive natural products. At present, more than two hundred metabolites have been isolated and identified from Paecilomyces. In this paper, 223 metabolites produced from 13 species and various unidentified species of Paecilomyces were reviewed.

The structures of metabolites from Paecilomyces vary and have been reported ranging from polyketide, terpenoid, peptide, alkaloid, quinone, pyrone, sterol, fatty acid, xanthone, macrocyclic, pyrenocine analog, to radicicol-type forms. The representative secondary metabolites are the highly toxic linear peptides known as leucinostatins, the tyrosine kinase inhibitors paeciloquinones, the biological activities, such as antimicrobial, antiviral, antitumor, herbicidal, insecticidal, antiplasmodial, antitrypanosomal, nematicidal, cytotoxic, enzyme inhibitors, phytotoxicity, and radical scavenging. The control effect of Paecilomyces is mainly the result of insecticidal activity of its metabolites. Many Paecilomyces metabolites not only directly cause disease in insects, but also have indirect insecticidal effect. For example, the fermentation filtrate of P. lilacinus showed obvious avoidance of soybean cyst nematode larvae and noticeably inhibited the infection of nematodes in roots [93].

In summary, Paecilomyces is a type of fungi with huge potential for development in various applications. With further study, Paecilomyces will play an increasingly important role in biological control, medicine and environmental protection.

Author Contributions: Investigation and collection references, D.Z.B., W.X., and L.G.H.; Writing, D.Z.B., W.X., and L.G.H.; Funding acquisition, W.X. and L.G.H. All authors have read and agreed to the published version of the manuscript.

Funding: This research was funded by National Natural Science Foundation of China (31860015, 31760024) and by the Applied Basic Research Foundation of Yunnan Province (202001BB050061, 2018FA006, 2018FB024).

Conflicts of Interest: The authors declare no conflict of interest.

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