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EXPERIMENTAL ARTICLES

Secondary Metabolites in the Taxonomy of Fungi of the Subgenus *Penicillium*

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Abstract—The method of polyphasic taxonomy was successfully used for more precise definition of the taxonomic position of the fungi of the subgenus *Penicillium* isolated from various poorly studied and new habitats. It has been proposed to change the species name for the strains synthesizing the respective secondary marker metabolites.

Key words: microscopic fungi, *Penicillium* taxonomy, biosynthesis, secondary metabolites, species specificity.

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The fungi of the subgenus *Penicillium* are among the most widespread ones; at the same time, they are the most difficult for species identification by conventional microbiological methods.

The generally accepted identification of penicillia by micro- and macromorphological characteristics [1] often gives ambiguous results, especially for the isolates from anthropogenically disturbed and extreme habitats [2–4]. The reliability of attribution of penicillia to a certain species is of interest due to availability of the data on species-specific production of various biologically active substances, including alkaloids, antibiotics, mycotoxins, and allergens [5].

The achievements of modern biology create prerequisites for the new schemes taking into account the broader range of characteristics. The currently proposed novel polyphasic taxonomy of fungi of the subgenus *Penicillium* employs the profiles of secondary metabolites along with micro- and macromorphological characteristics [6]. Chemotaxonomy is based on empirical observations of the common physiological and biochemical characteristics in phylogenetically related organisms. The potential and actual production of secondary metabolites is a component of the physiological and biochemical identification. A constitutive metabolic mechanism has been shown for production of some of the secondary metabolites; hence, one may expect the biosynthesis of marker metabolites by certain taxa [6, 7].

The goal of this work was to use the spectrum of low-molecular secondary metabolites produced by the fungi of the subgenus *Penicillium* in polyphasic taxonomy for species identification of the strains isolated from diverse habitats of different climatic zones and from poorly studied and new fungal habitats: permafrost soils and the *Mir* space station.

MATERIALS AND METHODS

The study was carried out for 44 fungal strains of the subgenus *Penicillium* attributed by micro- and macromorphological characteristics to the species *P. aurantiogriseum* Dierckx, *P. brevicompactum* Dierckx, *P. chrysogenum* Thom, *P. expansum* Link, *P. palitans* Westling, and *P. verrucosum* Dierckx. The strains were obtained from the All-Russian Collection of Microorganisms, Skryabin Institute of Biochemistry and Physiology of Microorganisms, Russian Academy of Sciences (VKM) [8, 9], the collection of the Department of Soil Biology, Faculty of Soil Science, Moscow State University (KPB) [2], and the collection of the Institute of Medical and Biological Problems (IMBP), Russian Academy of Sciences [10]. The numbers of the strains, their species affiliation, and habitats correspond to the catalogues of the above collections and are presented in the Table. The strains were grown as submerged cultures on a mineral Abe medium containing succinic acid and mannitol as carbon sources. Isolation, purification, and identification of the metabolites are described in the works [2–4, 11–15].

RESULTS AND DISCUSSION

The secondary metabolites used in the work as standard samples belonged to 20 biosynthetic families known for the fungi of the genus *Penicillium.* The indole-containing compounds derived from tryptophan were a large group of metabolites of different structures: tryptamines and their derivatives (indolyl-acetic

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The results of polyphasic taxonomy of the strains under study

Original species name and diagnostic metabolites [6]	Strain	Source of isolation	Revealed secondary metabolites	Proposed species name
P. auratiogriseum Dierckx (anacine, aurantine)	VKM FW-738	Permafrost soil, 30000 years old, Antarctica	Roquefortines C and D	*P. melanoconidium* (Frisvad) Frisvad & Samson comb. nov., 2004
	VKM FW-741	″	″	″
	VKM FW-766	Permafrost soil, 3 mln years old, Kolyma lowland, Russian Federation (RF)	″	″
	KBP no. 3	Urban environment, Moscow, Russian Federation	Tryptophanyltryptophanyldiketopiperazine	Subgenus *Furcatum*
P. brevicompactum Dierckx (brevianamide A, mycophenolic acid)	VKM FW-725	Permafrost soil, 20–30 mln years old, Kolyma lowland, RF	Mycophenolic acid	*P. bialowiezense* Zaleski
	VKM FW-791	Permafrost soil, Antarctica	″	″
P. verrucosum Dierckx (ochratoxin A, citrinine)	VKM FW-875	Water-in-suspension, 100–120 thousand years old, Kolyma lowland, RF	Ochratoxins A and B	*P. verrucosum* Dierckx
	VKM FW-877	″	″	″
	VKM FW-878	″	″	″
	VKM FW-907	Cryopeg water, Kolyma lowland, RF	″	″
	VKM FW-908	″	″	″
P. palitans Westling (fumigaclavines A and B, CPA)	VKM FW-657	Permafrost soil, 170 mln years old, Canada	Fumigaclavines A and B, festuclavine	*P. palitans* Westling
	VKM FW-667	″	″	*P. palitans* Westling
	VKM FW-690	Permafrost soil, 100 mln years old, Kolyma lowland, RF	″	*P. palitans* Westling
	VKM FW-704	Permafrost soil, 200–600 mln years old, Kolyma lowland, RF	″	*P. palitans* Westling
	VKM FW-747	″	″	*P. palitans* Westling
	VKM FW-794	″	″	*P. palitans* Westling
P. chrysogenum Thom (penicillins, roquefortine C, meleagrin, xanthocillins, PR-toxin)	KBP no. 4	Urban environment, Moscow, Russian Federation	″	*P. palitans* Westling
	VKM F-227	Soil, Leningrad oblast, RF	Roquefortines C and D, meleagrin, glandicolines A and B	*P. chrysogenum* Thom
	VKM F-316	Soil, Kyrgyzstan	Not detected	*P. dipodomyis* Frisvad, Filtenborg, Wicklow or *P. nalgiovense* Laxa
	VKM F-692	Soil, Volgograd oblast, RF	Roquefortines C and D, meleagrin, glandicolines A and B	*P. chrysogenum* Thom
	VKM F-1078	Soil, Irna, Damask, Syria	Roquefortines C and D, meleagrin, 16-N-ethyl roquefortine, isorugulosuvine	*P. chrysogenum* Thom

Table. (Contd.)

Original species name and diagnostic metabolites [6]	Strain	Source of isolation	Revealed secondary metabolites	Proposed species name
P. chrysogenum Thom (penicillins, roquefortine C, meleagrin, xanthocillins, PR-toxin)	VKM F-1987	Primitive soil, the East Pamirs, Tajikistan	Roquefortines C and D, 16-N-ethyl roquefortine, glandicolines A and B	*P. chrysogenum* Thom
	KBP no. 105	Primitive soils, the Pamirs, Kyrgyzstan	″	*P. chrysogenum* Thom
	VKM FW-621		Not detected	*P. dipodomyis* Frisvad, Filtenborg, Wicklow or *P. nalgiovense* Laxa
	VKM FW-721	″	″	″
	VKM FW-778	Permafrost soil, 5–10 thousand years old, Kolyma lowland, RF	″	″
	VKM FW-799	Permafrost soil, 1.8–3.0 mln years old, Kolyma lowland, RF	″	″
	IMBP 1-3	*Mir* orbital station	Roquefortine C, meleagrin, N-acetyltryptamine	*P. chrysogenum* Thom
	IMBP 1-4	″	″	*P. chrysogenum* Thom
	IMBP 1-5	″	Xanthocillin X, questiomycin A	*P. chrysogenum* Thom
	IMBP 1-6	″	″	*P. chrysogenum* Thom
P. expansum Link (patulin, citrinine, roquefortine C)	IMBP 2-2	″	Rugulosuvine B, isorugulosuvine, viridicatin, viridicatol	*P. polonicum* Zaleski
	IMBP 2-3	″	Rugulosuvine B, isorugulosuvine	*P. polonicum* Zaleski
	IMBP 2-4	″	Roquefortines C and D, meleagrin	*P. chrysogenum*
	IMBP 2-5	″	Roquefortine C, meleagrin	*P. chrysogenum* Thom
	IMBP 2-6	″	Isorugulosuvine, N-acetyltryptamine	*P. polonicum* Zaleski
	IMBP 2-7	″	Isorugulosuvine, xanthocillin X, questiomycin A	*P. polonicum* Zaleski

acid, N-acetyl tryptamine), clavine ergot alkaloids with a complete D-ring (4-dimethylallyltryptophan, chanoclavines, agroclavine-I, setoclavine, pyroclavine, festuclavine, elimoclavine, costaclavine, epicostaclavine, fumigaclavines A and B, isofumigaclavines A and B, and epoxyagroclavine-I) and with a modified D-ring (rugulovasines, clavicipitic acid, and cyclopiazonic acids), and tryptophan derivatives with diketopiperazine structure (brevianamides, roquefortines, fellutanines, puberulins, verrucosines). Another group of standard samples included benzodiazepine alkaloids (cyclopenines), quinoline alkaloids (viridicatols and quinocitrinines), and polyketide metabolites (griseofulvins, mycophenolic acid, patulines, penicillic acid, PR toxin, and citrinines). It should be noted that compounds found in the fungi may be products of the main or lateral biosynthetic branches or distant precursors of the metabolic pathways.

The spectrum of secondary metabolites produced by the three relic stains attributed to the species *P. aurantiogriseum* according to their micro- and macromorphological characteristics [3] included metabolites of the roquefortine family: roquefortine C and D (table). Benzodiazepine alkaloids (anacine and aurantine) are unambiguous chemotaxonomic markers in modern isolates of the species *P. aurantiogriseum* [6]. Production of alkaloids of the roquefortine family is typical of other species of the subgenus *Penicillium* [6]. The revealed discrepancy between species affiliation of the relic strains and their metabolites may be explained by

the difficulties of species identification of the isolates from permafrost deposits. The novel species *P. melanoconidium* (Frisvad) Frisvad & Samson comb. nov. (2004) is morphologically closest to the species *P. aurantiogriseum* among the species producing metabolites of the roquefortine family; previously it was considered to be a variant of *P. aurantiogriseum*: *P. aurantiogriseum* var. *melanoconidium* Frisvad (1989) [6]. Based on the spectrum of secondary metabolites, strains VKM FW-738, FW-741, and FW-766 can be assigned to the species *P. melanoconidium.*

The secondary metabolite of *P. aurantiogriseum* KBP no. 3 isolated from an urban environment also did not correspond to the species markers. The strains synthesized triptophanyl tryptophanyl diketopiperazine (fellutanine A) [2], previously found only in penicillia of the subgenus *Furcatum* Pitt: *P. fellutanum* Biourge [16], *P. canescens* Sopp [17], *P. simplicissium* (Oudem.) Thom (= *P. piscarium* Westling) [18]. According to the data [6], this metabolite is not a marker for any of the species of the subgenus *Penicillium* and, consequently, the strain KBP no. 3 should be assigned to the subgenus *Fucatum.*

The relic strains VKM FW-725 and FW-791 assigned to the species *P. brevicompactum* Dierckx according to their micro- and macromorphological characteristics was shown to produce only mycophenolic acid (Table). Its biosynthesis is typical of only one species: *P. bialowiezense* Zaleski [6]. Additional chemotaxonomic markers for other producers of mycophenolic acid are brevianamide A (*P. brevicompactum*), roquefortine C, patulin, isofumigaclavines A and B, penitrem A (*P. carneum* Frisvad (1996), roquefortine C, and PR-toxin (*P. roqueforti*) [6]. The species *P. brevicompactum* and *P. bialowiezense* are difficult for differentiation based on morphological characteristics. Since the synthesis of mycophenolic acid is a chemotaxonomic marker, it is possible to assign strains VKM FW-725 and FW-791 to the species *P. bialowiezense.*

Species identification by micro- and macromorphological characteristics of eleven slow-growing cultures of the subgenus *Penicillium* isolated from ancient permafrost deposits gave uncertain results. The species names obtained as a result of repeated identifications of these strains were different: *P. verricosum* Dierckx, *P. puberullum, P. commune, P. granulatum*, and *P. aurantiogriseum* [12]. The study of the composition of secondary metabolites produced by these cultures showed that strains VKM FW-657, FW-667, FW-690, FW-704, FW-747, and VKM FW-794 synthesized ergot alkaloids of the clavine series: fumigaclavines A and B and festuclavine (Table). Such metabolic composition was typical also of the strain KBP no. 4 isolated from an anthropogenically disturbed ecosystem and assigned by the morphological characteristics to the species *P. chrysogenum* [2]. Fumigaclavines A and B are chemotaxonomic markers of the species *P. palitans* Westling [6]. Affiliation of producers of these compounds with other species is questioned by the authors of polyphasic taxonomy of *Penicillium* fungi. Thus, based on production of fumigaclavines A and B, the strains VKM FW-657, FW-667, FW-690, FW-704, FW-747, VKM FW-794, and KBP no. 4 can be assigned to the species *P. palitans* Westling, in spite of ambiguity of their morphological identification.

Other slow-growing relic strains, VKM FW-875, FW-877, FW-878, FW-907, and FW-908, were shown to produce ochratoxins A and B (Table). These metabolites are synthesized by the species *P. verrucosum* Dierckx and *P. nordicum* Dragoni, Cantoni ex Ramirez, which are close by micro- and most of the macromorphological characteristics. Some of the *P. verrucosum* isolates can synthesize citrinine and verrucolone in addition to ochratoxin A; the chemotaxonomic marker in *P. nordicum*, besides ochratoxin B and verrucolone, is an indole-containing compound, anacin [6]. The red–brown reverse on agarized YES medium and the absence of biosynthesis of any indole-containing metabolites by the strains VKM FW-875, FW-877, FW-878, FW-907, and FW-908 are undoubted evidence of their affiliation with the species *P. verrucosum.*

The 21 analyzed strains of the species *P. chrysogenum* Thom were isolated from various habitats of different climatic zones and from poorly studied sites: permafrost soils and the habitable module of the *Mir* space station (Table). Chemotaxonomic markers of the species *P. chrysogenus* are penicillins, roquefortine C, and chrysogin. The production of another metabolite of the roquefortine family, meleagrin, as well as PR-toxin and xanthocillin, is possible as well [6]. It should be noted that identification of penicillins, biosynthesis of which unambiguously indicates affiliation of the isolates with the species *P. chrysogenum* (section *Chrysogena*), was not performed. The strains *P. chrysogenum* VKM F-227, VKM F-692, VKM F-1078, and VKM F-1987, isolated from the soils of different climatic zones, synthesized metabolites of the roquefortine family only: roquefortines C and D, meleagrin, and glandicolines A and B [11]. Production of other chemotaxonomic markers of the species was not detected.

Strains of the species *P. chrysogenus* isolated from the habitable modules of the *Mir* space station [2, 13, 14] synthesized the marker metabolites of the species (Table). Strains IMBP 1-3 and IMBP 1-4 were shown to produce metabolites of the roquefortine family (roquefortine C and meleagrin) and N-acetyltryptamine, and the concurrent biosynthesis of xanthocillin X and questiomycin A was observed in IMBP 1-5 and IMBP 1-6.

Production of the studied metabolites (markers of the species *P. chrysogenum*) was not detected in the strains *P. chrysogenum* VKM FW-653, FW-659, FW-679, FW-684, FW-694, FW-720, FW-721, FW-778, and FW-799 isolated from ancient permafrost deposits [9] (Table). The absence of their biosynthesis may be evidence of affiliation of these isolates with other spe-

cies of the section *Chrysogena*: *P. dipodomyis* Frisvad, Filtenborg, Wicklow, or *P. nalgiovense* Laxa [6].

Confirmation of the species diagnostics in six strains of *P. expansum* Link isolated at the *Mir* space station is difficult due to the lack of correspondence between the spectrum of secondary metabolites and the species markers. The set of marker metabolites of the species *P. expansum* includes roqiefortine C, patulin, and citrinine [6]. *P. expansum* strains isolated at the *Mir* space station were not shown to produce patulin and citrinine [13, 14]. The ability for roquefortine C biosynthesis was revealed only in the strains IMBP 2-4 and IMBP 2-5. Other metabolites of the roquefortine family, roquefortine D and meleagrin, were identified in these strains as well. Such a set of metabolites is typical of the species *P. chrysogenum*, which makes it possible to assign the strain under study to this species [6]. Xanthocillin X and questiomycin A found in IMBP 2-7 are chemotaxonomic markers of the species *P. chrysogenum, P. flavigenum*, or *P. italicum*, but not *P. expansum* [6]. It should be noted that this strain after several reinoculations on agarized media began to produce isorugulosuvine only. The ability of a culture adapted to artificial maintenance conditions to synthesize xanthocillin X and questiomycin A appeared again after the introduction of zinc ions into the Abe medium [14]. The strains IMBP 2-2, IMBP 2-3, and IMBP 2-6 synthesized isorugulosuvine and rugulosuvine B, and IMBP 2-2, in addition to these three metabolites, they synthesized viridicatin and viridicatol (Table). Simultaneous biosynthesis of rugulosuvines and viridicatins is typical of the species *P. polonicum* Zaleski and is possible in *P. tricolor* [6].

Thus, most of the strains isolated from permafrost soils, the *Mir* space station, and the sites exposed to anthropogenic load showed a discrepancy between species diagnoses based on the micro- and macromorphological characteristics and on the marker's secondary metabolites known for the type cultures (Table). This discrepancy can be explained, first of all, by the difficulties in morphological identification of the isolates from the habitats with conditions other than those of the type ones. Morphological deviations of the isolates from the type cultures are adaptive and, apparently, phenotypic. These deviations are caused by development of the fungi under some or other specific environmental conditions, which result in development of a modified morphological phenotype. Morphological variability in different isolates of a species is a significant problem for taxonomy of these fungi [1]. All species of the subgenus have numerous synonyms and variants [1, 6].

The phenotypic concept of a species is as follows: each species is genetically homogenous and a distinct phenotypic cluster takes place at a great distance from other clusters. The species following this way demonstrate correspondence to other species concepts based on ecology and phylogeny. The criteria applied by Samson and Frisvad in the taxonomy of fungi of the subgenus *Penicillium*, i.e., combination of micro- and macromorphological characteristics, some physiological characteristics, and the spectrum of secondary metabolites, made it possible to create the currently most adequate taxonomy of these fungi.

As a result of analysis of the profiles of secondary metabolites of the fungi isolated from permafrost soils, *Mir* orbital station, and the sites exposed to anthropogenic load, together with their comparison with the marker metabolites, it is proposed to introduce the following modifications into the species names of respective strains: VKM FW-738, FW-741, FW-766—*P. melanoconidium*; VKM FW-725, FW-791—*P. bialowiezense*; KBP no. 4—*P. palitans*; VKM FW-316, FW-621, FW-721, FW-778, FW-799—*P. dipodomyis* or *P. nalgiovense*; IMBP 2-4 and 2-5—*P. chrysogenum;* IMBP 2-2, 2-3, 2-6, and 2-7—*P. polonicum.* It is also proposed to attribute strain KBP no. 3 to the subgenus *Furcatum.*

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