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# First lichenicolous records of Chaetopyrena penicillata

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ABSTRACT—*Chaetopyrena penicillata* is reported for the first time as a lichenicolous fungus. A culture and a sequence were obtained from material growing on *Xanthoria parietina*. Features of the culture on PDA and MEA, the ecology and geography, and the phylogenetic position within *Didymellaceae* based on an ITS sequence are given. A key to the lichenicolous coelomycetes with setose pycnidia is also provided.

KEY WORDS-coelomycete, Pleosporales, setose fungi, Southern Ukraine

## Introduction

The lichenized fungus *Xanthoria parietina* (L.) Th. Fr. is a fine model for the study of the diversity and ecology of lichenicolous fungi (Etayo & Berger 2009, Fleischhacker 2011, Braun & al. 2016, Khodosovtsev & Darmostuk 2016, Tsurykau & Etayo 2017). In 2016, we collected *Pyrenochaeta*-like specimens on apothecia of corticolous *Xanthoria parietina* for testing their growth in culture. Surprisingly, we found a fungus with ampulliform conidiogenous cells and large bacilliform conidia that represented neither *Pyrenochaeta xanthoriae* Diederich (Diederich 1990) nor *Pyrenochaetopsis* Gruyter & al. (de Gruyter & Boerema 2002). Instead, morphological, cultural, and molecular data allowed

us to identify the fungus as *Chaetopyrena penicillata*. Further research has revealed the presence of this species on *Peltigera rufescens* (Weiss) Humb. and *Physcia stellaris* (L.) Nyl.

*Chaetopyrena* Pass. is a poorly studied asexual genus, and its phylogenetic position in *Didymellaceae* has only recently been identified (de Gruyter & al. 2010). No modern description of the genus was provided in Hyde & al. (2013), nor are any molecular data available from the generic type, *Chaetopyrena hesperidum* Pass., described from *Citrus* (Hyde & al. 2013). Only one *Chaetopyrena* species, *C. penicillata*, has been isolated in culture for which ITS and LSU sequences have also been obtained (Arzanlou & Khodaei 2012; Wang & al. 2016). In this paper, we report for the first time a species of *Chaetopyrena* with a lichenicolous habit and provide a full description, cultural characteristics, and ITS sequence data.

#### Material & methods

#### Morphological observations and isolation

The material was examined using standard microscopic techniques. Sections for anatomical examination were cut by hand and studied microscopically in water preparations. Measurements were made in water with an accuracy of 0.2  $\mu$ m for conidia, conidiogenous cells, cell walls and hyphae; of 5  $\mu$ m for the pycnidial wall; and of 10  $\mu$ m for conidiomata. Measurements are given as (min.–) *x*–SD – *x*+SD (–max.), where *x* is the average and SD the standard deviation. Photographs were taken with a Levenhuk C510 NG camera on an Optica Italica stereomicroscope and MICROMED-2 microscope. All examined specimens are deposited in the lichenological herbarium of the Kherson State University, Ivano-Frankivsk, Ukraine (KHER) and in the personal herbarium of the first author (herb. VD).

Pure cultures were obtained from a multiconidial culture (Bomar & Knöpfel 1992). Malt extract agar (MEA) and potato dextrose agar (PDA) were used for isolation of the fungal colonies (Crous & al. 2009). Fungi isolates were deposited in culture collection of Kherson State University, but they are currently unavailable for research.

# DNA extraction, amplification and sequencing

Fungal genomic DNA was extracted from fresh mycelium and pycnidia grown on PDA at 25°C for 2 months using a modified CTAB-method (Doyle & Doyle 1990, Tarieiev & al. 2011). The internal transcribed spacer (ITS) region was PCR amplified and sequenced using universal primers ITS1–ITS4 and ITS4–ITS5 according to White & al. (1990). The PCR cycle protocols followed Ekman (2001). PCR products were visualized on a 1% agarose gel using ethidium bromide. Purification and sequencing of the PCR amplicons with ITS1 and ITS4 primers was conducted at Macrogen Inc. (http://www.Macrogen.com, The Netherlands).

TABLE 1. Strains and	sequences used	in the phy	ylogenetic anal	yses.
The new seque	ence is indicated	in <b>bold.</b> T	Type vouchers	are annotated as [T].

Taxon	Voucher	Ноѕт	ITS
Ascochyta pisi	CBS 108.26	_	MH854853
	Netherlands, CBS 122785 [T]	_	GU237763
	Iran, MoKhol3-2	Lathyrus sativus	MT351037
Calophoma clematidina	Netherlands, CBS 108.79	_	MH861182
	Netherlands, CBS 520.66	_	MH858873
	Netherlands, CBS 108.79 [T]	_	FJ426989
	Netherlands, CBS 201.49	_	FJ426991
	Netherlands, CBS 195.64	Clematis × jackmanii	FJ426990
	Netherlands, CBS 520.66	Selaginella sp.	FJ426992
Chaetopyrena penicillata	Ukraine, KHER 10840	Xanthoria parietina	MW478633
	Iran, Khodaei P4I1	Prunus divaricata	MK100126
	Iran, Arzanlou S5	Elaeagnus angustifolia	MK100127
	Iran, Khodaei T312I1	Salix alba	MK100128
	Iran, Khodaei T22I1	Plant litter	MK100129
	China, HGAU-091001	_	KC492443
	CCTU 260	Elaeagnus angustifolia	JQ663990
Didymella exigua	France, CBS 183.55 [T]	Rumex arifolius	EF192139
D. pisi (= Ascochyta pisi)	_	_	GU722316
Neoascochyta exitialis	Switzerland, CBS 389.86	_	MH861971
	Sweden, CBS 113693	Allium sp.	KT389513
	CBS 118.40	_	KT389514
	Netherlands, CBS 389.86	Triticum aestivum	KT389515
	Germany, CBS 811.84	Secale cereale	KT389516
	Germany, CBS 812.84	Hordeum vulgare	KT389517
Phoma clematidina (≡ Calophoma clematidina)	Netherlands, PD 95.895	Clematis sp.	FJ515599
P. herbarum	C61	_	JQ936277
	C108.1	_	JQ936274
	C28.4	_	JQ936275
Pyrenochaeta nobilis	Italy, CBS 407.76 [T]	_	EU930011
	CBS 292.74	_	MH860856
Pyrenochaetopsis leptospora	CBS 101635 [T]	_	JF740262
P. microspora	Montenegro, CBS 102876	_	MH862809
	Brazil, PB147	Cocos nucifera	MK508814

#### Sequence alignment and phylogenetic analysis

The quality of the newly produced sequence was manually checked using sequence chromatogram in Chromas software (Technelysium Pty Ltd; http://www. technelysium.com.http://au/chromas.html) and edited in BioEdit 7.2.5 (Hall 1999). We used a BLASTN search (Altschul & al. 1990) in the GenBank database for primary taxonomic interpretation of the sequence. The final analyses included the newly generated sequence and available NCBI accession number sequences with complete ITS1 region of Chaetopyrena and selected genera of Didymellaceae such as Ascochyta, Calophoma, Didymella, Neoascochyta, Phoma (TABLE 1). Pyrenochaetopsis leptospora (Sacc. & Briard) Gruyter & al. was used as outgroup. The ITS region was aligned using MAFFT 7 (Katoh & Standley 2013) with L-INS-i method (Katoh & al. 2005). The final ITS alignment contained 456 positions and 36 sequences. To determine the evolutionary models that fit best for the data set, the program iModeltest 2.1.7 (Darriba & al. 2012) was used. The best nucleotide substitution model GTR+G+I (Tavaré 1986) was selected using the Maximum Likelihood value (-lnL) criterion (Posada & Crandall 1998). Phylogenetic reconstruction of the resulting alignment was carried out using the Metropolis-coupled Markov chain Monte Carlo (MCMC) approach in MrBayes v.3.2 (Ronquist & al. 2012). Two parallel simultaneous runs, each using four independent chains and starting from a random tree, were performed over 10 000 000 generations; tree sampling was carried out every 1000th generation. The first 25% of saved data was discarded as burn-in and the 50% majority-rule consensus tree and posterior probabilities (PP) were calculated from the remainder. A maximum likelihood (ML) approach was applied to the same data using IQTree Web Server (Trifinopoulos & al. 2016) with the GTR evolutionary model selected. Non-parametric bootstrap analysis was performed with 1000 ultrafast bootstrap replicates. The maximum likelihood consensus tree is not shown, but bootstrap values (BS) are indicated at branches in the Bayesian tree. Well supported clades were considered with PP >0.95 and BS >70 The alignment and tree used in this study are publicly available in TreeBase (ID: 27741). The final tree was visualized and modified in FigTree v.1.4.4 and Inkscape v.1.0.2 software (https://inkscape.org/, Rambaut & Drummond 2018).

## Phylogenetic results

PHYLOGENY. Maximum likelihood (ML) and Bayesian trees had no topological conflicts in the clades. Newly generated and other sequences of *Chaetopyrena penicillata* formed a well-supported monophyletic clade (PP = 1, BS = 100) within *Didymellaceae* and were sister to *Calophoma* Qian Chen & L. Cai (type species *Calophoma clematidina* (Thüm.) Qian Chen & L. Cai) and *Ascochyta* Lib. (type species *Ascochyta pisi* Lib.) (FIG. 1).

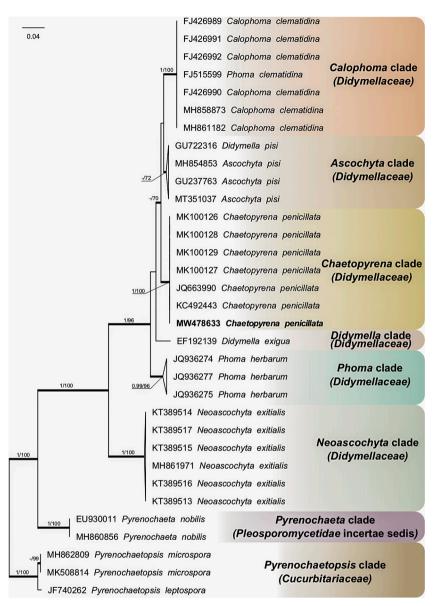


FIG. 1. Internal transcribed spacer (ITS)-based 50% majority-rule unrooted consensus tree based on a Bayesian approach for *Chaetopyrena penicillata*. Bold branches represent either bootstrap values  $\geq$ 70 and/or Bayesian posterior probabilities  $\geq$ 0.97. Newly generated sequence is indicated in bold.

#### Taxonomy

# *Chaetopyrena penicillata* (Fuckel) Höhn., Hedwigia 60: 132 (1918) FIG. 2 DESCRIPTION IN VIVO (from specimen on Xanthoria parietina)-Conidiomata pycnidia, globose to ellipsoid, fully immersed at first, emerged up to superficial when mature, dark brown to brown-black, (90-)105-140 $(-150) \times (80-)85-115(-125)$ µm [n = 20]; pycnidia covered around the ostiole with erect, brown, 4-5-septate setae, $(65-)80-130(-150) \times (4.0-)$ $5.0-6.6(-7.2) \mu m [n=20]$ ; pycnidial wall of 3-4 layers (textura angularis), (15-) $18-32(-35) \ \mu m \ [n = 20]$ thick, cells $(8.4-)9.6-13.8(-15.4) \times (6.0-)7.4-9.8$ (10.2) $\mu$ m [n = 25], with an amorphous brown pigment in cellular walls; conidiophores reduced to conidiogenous cells or with a single supporting cell, ampulliform, hvaline, smooth, with periclinal thickening, (5.2–)6.4–8.2 $(-9.0) \times (4.2-)5.4-7.6(-8.4) \ \mu m \ [n = 20];$ conidia solitary, 1-celled, hyaline, smooth, cylindrical with rounded ends, often slightly constricted in the middle (dumbbell-shaped), $(11.6-)13.0-15.6(-16.4) \times (2.2-)3.2-3.8(-4.4) \mu m$ [n = 60].

DESCRIPTION IN VITRO (PDA) – Vegetative hyphae (3.2–)4.2–6.6(–7.2) µm wide [n = 25] with oil drops, conidiomata pycnidia, subglobose to pyriform, initially hyaline (3-5 days), then dark brown to brown-black (14 days), erumpent with one or few (2-3) necks, (150-)230-300(-360) µm wide and  $(300-)340-440(-520) \ \mu m \ high \ [n = 30]; \ neck \ (90-)120-240(-300) \ [n = 20]$  $\mu$ m long, with a central ostiole,  $\leq$ 30  $\mu$ m diam., setose; setae 2–3-septate, medium brown, numerous, erect, smooth, tapering towards hyaline to pale brown obtuse ends,  $(75-)100-170(-225) \times (3.0-)5.2-8.4(-9.6) \mu m [n = 40];$ pycnidial wall of 3–5 layers (textura angularis),  $(30-)40-50(-60) \mu m [n = 30]$ thick, internal layer thin, hyaline to pale brown, outer layer wider, medium brown to dark brown; cells  $(5.2-)8.2-14.4(-18.4) \times (4.0-)6.2-10.8(-14.2) \mu m$ [n = 40], with an amorphous brown pigment in cellular walls; conidiophores reduced to conidiogenous cells or with a single supporting cell, ampulliform, hyaline, smooth, with periclinal thickening,  $(6.2-)7.2-9.8(-10.4) \times (5.2-)$ 7.6–9.8(–10.0)  $\mu$ m [n = 20]. Conidia solitary, 1-celled, hyaline, smooth, cylindrical with obtuse ends, rarely pyriform to slightly constricted in the middle,  $(12.0-)13.0-14.6(-15.4) \times (2.6-)3.2-4.6(-5.6) \mu m [n = 60]$ .

CULTURE CHARACTERISTICS – On MEA, colonies flat,  $\leq$ 2.5 cm diam. after 7 days, spreading with sparse hyaline aerial mycelium, hyaline to pale brown internal mycelium, even, smooth margins, surface dirty white to pale brown,

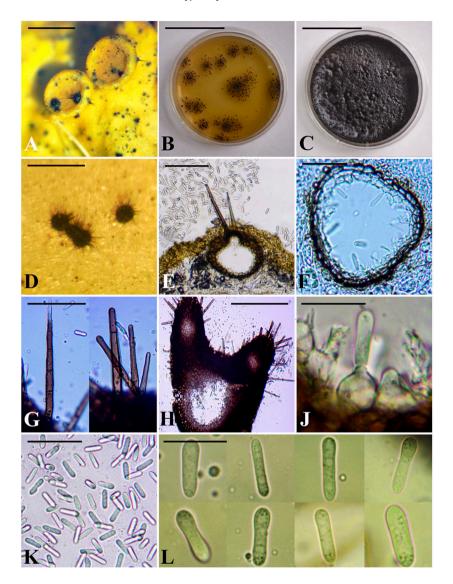


FIG. 2. *Chaetopyrena penicillata* (KHER 10840): A. pycnidia on apothecia of *Xanthoria parietina*; B. one month old culture (MEA); C. one month old culture (PDA); D. pycnidia (MEA); E. section through pycnidium (in water); F. pycnidial wall, conidiogenous cells, and conidia (in water); G. setae (in water); H. apical taper of pycnidium (in water); J. ampulliform conidiogenous cells and conidium (in water); K, L. conidia (in water). Scale bars: A, D = 1 mm; B, C = 5 cm; E, H = 100  $\mu$ m; F, G, K = 50  $\mu$ m; J = 25  $\mu$ m; L = 15  $\mu$ m.

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similar in reverse. On PDA, colonies flat, ≤6 cm diam. after 7 days, spreading with hyaline to pale brown sparse aerial mycelium, medium brown to dark brown internal mycelium, even, smooth margins, surface olivaceous-grey to lead-black, olivaceous-black in reverse.

SPECIMENS EXAMINED – UKRAINE. KHERSON REGION. Skadovskyi district, village Kardashynka, private summer house, 46.5548°N 32.6463°E, alt. 1 m, on *Xanthoria parietina*, on *Salix alba*, 28.XII.2015, A. Khodosovtsev (KHER 10840; culture KHER\_56 NCBI accession number MW478633); **MYKOLAIV REGION**, **Pervomaiskyi district**, near Kuripchyne village, National Nature Park Buzkyi Gard, 47.9953°N 31.0017°E, alt. 48 m, on *Peltigera rufescens*, on soil, 21.IX.2019, V. Darmostuk (herb. VD 281); **Voznesenskyi district**, near Vysoka Hora village, Dubova balka, 47.8908°N 31.6131°E, alt. 37 m, on *Physcia stellaris* and *X. parietina*, on *Fraxinus* twig, 21.X.2020, V. Darmostuk (herb. VD 906).

ECOLOGY—*Chaetopyrena penicillata* was originally described from stems of *Medicago sativa* (Fuckel 1867) and subsequently reported as a saprotroph on dry leaves of *Medicago* spp. and on fruits of *Elaeagnus angustifolia* showing dry rot symptoms (Arzanlou & Khodaei 2012), endophytic in stems of *Ephedra intermedia* (Wang & al. 2016), and from leaves of *Fraxinus chinensis* (Vettraino & al. 2017). Moreover, it is known as a saprophyte on soil, dead twigs, fruit, and stubble (Wang & al. 2016). Here it is reported for the first time growing on the lichens *Peltigera rufescens*, *Physcia stellaris*, and *Xanthoria parietina*, forming pycnidia on weakened thalli and apothecia in wet seasons. The infection of lichens by *Chaetopyrena penicillata* does not induce gall formation, but sometimes (depending on the host species) causes a discoloration of the host thallus; on *Xanthoria parietina* it does not induce discoloration, but we observed totally discolored thalli on *Physcia stellaris*, and a few necrotic parts on *Peltigera rufescens*.

DISTRIBUTION—Specimens on *Physcia stellaris* and *Peltigera rufescens* have the same morphological features. Our data fit the measurements given by other authors (Fuckel 1867, Arzanlou & Khodaei 2012, Wang & al. 2016). The fungus is known from Europe (Czech Republic, Germany, Romania, Russia), Asia (China, Iran, Turkey), and Africa (South Africa) (Fuckel 1867, Arzanlou & Khodaei 2012, Wang & al. 2016). It is here reported from Ukraine for the first time.

COMMENTS—Visually, *Chaetopyrena penicillata* is similar to *Pyrenochaeta xanthoriae*, which can be distinguished by acro-pleurogenous conidiogenous cells and shorter conidia (Diederich 1990). Another lichenicolous coelomycete with setose pycnidia "*Pyrenochaeta*" collematis Vouaux has cylindrical

conidiogenous cells and smaller conidia and grows on thalli of Enchylium tenax (Hawksworth 1981, Clauzade & al. 1989). This species is dubious due to the lost type and lack of modern records and description. The facultatively lichenicolous Pyrenochaetopsis microspora (Gruyter & Boerema) Gruyter & al. (*Cucurbitariaceae*) differs by much smaller conidia  $(3.5-4.5 \times 1.5-2 \mu m)$ vs.  $12-15.5 \times 2.6-5.7 \mu m$  in *C. penicillata*; de Gruyter & Boerema 2002). The asexual stage of Coniothyrium sidae Quaedvl. & al. (Coniothyriaceae) differs in slightly smaller  $(9-13 \times 2.5-3 \ \mu\text{m})$  conidia and smaller  $(4-7 \times 4-6 \ \mu\text{m})$ conidiogenous cells and grows on the angiosperm Sida (Quaedvlieg & al. 2013). The setose coelomycetous Paraphoma Morgan-Jones & J.F. White and Setophoma Gruyter & al. belong to different clades within Phaeosphaeriaceae (de Gruyter & al. 2010) and have slight morphological differences. Dinemasporium strigosum (Pers.) Sacc., a common coelomycete, growing mostly on dead grasses but also reported from Peltigera thalli, differs in producing conidia with a single filiform appendage at each end (Sutton 1980, Nag Raj 1993, Sérusiaux & al. 2003). Lichenicolous coelomycetes with setose pycnidia are also known in Karsteniomyces D. Hawksw. and Keratosphaera H.B.P. Upadhyay (Upadhyay 1964, Boqueras & Diederich 1993, Matzer 1996).

# Key to the lichenicolous coelomycetes with setose pycnidia

1. Setae light brown to brown 2
<ol> <li>Setae hyaline, conidiophores cylindrical, 30-40 μm long, conidiogenous cells monoblastic, indistinguishable from conidiophores, conidia hyaline, elongate, 1-septate, on <i>Parmelina quercina</i></li></ol>
2. Conidia with filiform apical appendages32. Conidia without filiform apical appendages7
<ul> <li>3. Conidia ≤20 µm long</li></ul>
4. Conidia 0-1-septate       5         4. Conidia 2-4-septate, on Mazosia phyllosema       Keratosphaera batistae
<ul> <li>5. Setae unforked at the distal end</li></ul>
<ul> <li>6. Apical part of setae distinctly pointed and paler, 35 × 8 μm, on <i>Porina epiphylla</i> and <i>Pyrenula nitida</i></li></ul>
on Dimercum spp

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#### Literature cited

- Altschul SF, Gish W, Miller W, Myers EW, Lipman DJ. 1990. Basic local alignment search tool. Journal of Molecular Biology 215: 403–410. https://doi.org/10.1016/S0022-2836(05)80360-2
- Arzanlou M, Khodaei S. 2012. Phenotypic and molecular characterization of *Chaetopyrena* penicillata from Iran with descristion of a hyphomycete synanamorph. Mycosphere 3(1): 73–77. https://doi.org/10.5943/mycosphere/3/1/9
- Bomar MT, Knöpfel SA. 1992. A method for the estimation of the culturing quality of dehydrated mycological media. International Journal of Food Science and Technology 27(5): 589–592. https://doi.org/10.1111/j.1365-2621.1992.tb01226.x
- Boqueras M, Diederich P. 1993. New or interesting lichenicolous fungi. III: Karsteniomyces llimonae sp. nov. and Sclerococcum serusiauxii sp. nov. (Deuteromycotina). Mycotaxon 47: 425–431.
- Braun U, Khodosovtsev AYe, Darmostuk VV, Diederich P. 2016. Trichoconis hafellneri sp. nov. on Athallia pyracea and Xanthoria parietina, a generic discussion of Trichoconis and keys to the species of this genus. Herzogia 29(2): 307–314. https://doi.org/10.13158/heia.29.2.2016.307
- Clauzade GP, Diederich P, Roux C. 1989. Nelikeniĝintaj fungoj likenloĝaj. Ilustrita determinlibro Bulletin de la Société Linnéenne de Provence, Numéro spécial 1. 142 p.
- Crous PW, Verkley GJM, Groenewald JZ, Samson RA. 2009. Fungal Biodiversity. [CBS Laboratory Manual Series no.1.] Utrecht: CBS-KNAW Fungal Biodiversity Centre.
- Darriba D, Taboada GL, Doallo R, Posada D. 2012. jModelTest 2: more models, new heuristics and parallel computing. Nature Methods 9(8): 772. https://doi.org/10.1038/nmeth.2109
- de Gruyter J, Boerema GH. 2002. Contributions toward a monograph of *Phoma* (coelomycetes) VII. Section *Paraphoma*: taxa with setose pycnidia. Persoonia 17: 541–561.

- de Gruyter J, Woudenberg JH, Aveskamp MM, Verkley GJ, Groenewald JZ, Crous PW. 2010. Systematic reappraisal of species in *Phoma* section *Paraphoma*, *Pyrenochaeta* and *Pleurophoma*. Mycologia 102(5): 1066–1081. https://doi.org/10.3852/09-240
- Diederich P. 1990. New or interesting lichenicolous fungi. 1. Species from Luxembourg. Mycotaxon 37: 297–330.
- Doyle JJ, Doyle JL. 1990. Isolation of plant DNA from fresh tissue. Focus 12: 13–15.
- Ekman S. 2001. Molecular phylogeny of the Bacidiaceae (Lecanorales, lichenized Ascomycota). Mycological Research 105(7): 783–797. https://doi.org/10.1017/S0953756201004269
- Etayo J, Berger F. 2009. About a fast developing community of lichenicolous deuteromycetes decaying *Xanthoria parietina*. Österreichische Zeitschrift für Pilzkunde 18: 111–115.
- Fleischhacker A. 2011. The lichenicolous fungi invading *Xanthoria parietina*. Magisterarbeit, Karl-Franzens-Universität, Graz.

[http://unipub.uni-graz.at/obvugrhs/download/pdf/217334].

- Fuckel L. 1867. Fungi Rhenani Exsiccati, Supplementi Fasc. 5: no. 1941.
- Hall TA. 1999. BioEdit: a user-friendly biological sequence alignment editor and analysis program for Windows 95/98/NT. Nucleic Acids Symposium Series 41: 95–98.
- Hawksworth DL. 1981. The lichenicolous coelomycetes. Bulletin of the British Museum (Natural History), Botany Series 9: 1–98.
- Hyde KD, Jones EG, Liu JK, Ariyawansa H, Boehm E, Boonmee S, Diederich P & al. 2013. Families of *Dothideomycetes*. Fungal Diversity 63. 313 p. http://dx.doi.org/ 10.1007/s13225-013-0263-4
- Katoh K, Standley DM. 2013. MAFFT multiple sequence alignment software version 7: improvements in performance and usability. <u>Molecular Biology and Evolution 30: 772–780</u>. https://doi.org/10.1093/molbev/mst010
- Katoh K, Kuma K, Toh H, Miyata T. 2005 MAFFT version 5: improvement in accuracy of multiple sequence alignment. Nucleic Acids Research 33: 511–518. https://doi.org/10.1093/nar/gki198
- Khodosovtsev AYe, Darmostuk VV. 2016. Pleospora xanthoriae sp. nov. (Pleosporaceae, Pleosporales), a new lichenicolous fungus on Xanthoria parietina from Ukraine, with a key to the known lichenicolous species of Dacampia and Pleospora. Opuscula Philolichenum 15: 6–11.
- Matzer M. 1996. Lichenicolous ascomycetes with fissitunicate asci on foliicolous lichens. Mycological Papers 171. 202 p.
- Nag Raj T R. 1993. Coelomycetous anamorphs with appendage-bearing conidia. Mycologue Publications, Waterloo Ontario.
- Posada D, Crandall KA. 1998. ModelTest: testing the model of DNA substitution. Bioinformatics 14: 817–818. https://doi.org/10.1093/bioinformatics/14.9.817
- Quaedvlieg W, Verkley GJM, Shin HD, Barreto RW, Alfenas AC, Swart WJ, Groenewald JZ, Crous PW. 2013. Sizing up Septoria. Studies in Mycology 75: 307–390. https://doi.org/10.3114/sim0017
- Rambaut A, Drummond AJ. 2018. FigTree v1.4.4. Institute of Evolutionary Biology. University of Edinburgh, Edinburgh.
- Ronquist F, Teslenko M, van der Mark P, Ayres D, Darling A, Hohna S, Larget B, Liu L, Suchard MA, Huelsenbeck JP. 2012. MrBayes 3.2: Efficient Bayesian phylogenetic inference and model choice across a large model space. <u>Systematic Biology 52: 696–704</u>. https://doi.org/10.1093/sysbio/sys029
- Sérusiaux E, Diederich P, Ertz D, van den Boom P. 2003. New or interesting lichens and lichenicolous fungi from Belgium, Luxembourg and northern France. IX. Lejeunia, n.s., 173: 1–48.

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Sutton BC. 1980. The coelomycetes. Kew: Commonwealth Mycological Institute.

- Tarieiev AS, Girin AI, Karpenko NI, Tyshchenko OV, Kostikov IYu. 2011. Modified method of DNA extraction from herbarium specimens. Chornomorski Botanical Journal 7(4): 309–317.
- Tavaré S. 1986. Some probabilistic and statistical problems in the analysis of DNA sequences. 57–86, in: RM Miura (ed.). Lectures on Mathematics in the Life Sciences, vol. 17. American Mathematical Society, Providence.
- Trifinopoulos J, Nguyen LT, von Haeseler A, Minh BQ. 2016. W-IQ-TREE: a fast online phylogenetic tool for maximum likelihood analysis. Nucleic Acids Research 44(1): 232-235. https://doi.org/10.1093/nar/gkw256
- Tsurykau A, Etayo J. 2017. *Capronia suijae* (*Herpotrichiellaceae*, *Eurotiomycetes*), a new fungus on *Xanthoria parietina* from Belarus, with a key to the lichenicolous species growing on *Xanthoria* s. str. Lichenologist 49: 1–12. https://doi.org/10.1017/s0024282916000530
- Upadhyay HBP. 1964. Three new hyperparasites for *Mazosia phyllosema* (Nyl.) A. Zahlbr. from Amazonas valley. Instituto de Micologia; Manaus: INPA.
- Vettraino AM., Li HM, Eschen R, Morales-Rodriguez C, Vannini A. 2017. The sentinel tree nursery as an early warning system for pathway risk assessment: fungal pathogens associated with Chinese woody plants commonly shipped to Europe. PLOS ONE 12(11): e0188800. https://doi.org/10.1371/journal.pone.0188800
- Wang Y, Jin L, Lin L, Zhu TT, Chen XR, Chao LP. 2016. New hosts for *Bartalinia* and *Chaetopyrena* in China. Mycotaxon 131(1): 1–6. https://doi.org/10.5248/131.1
- White TJ, Bruns T, Lee S, Taylor J. 1990. Amplification and direct sequencing of fungal ribosomal RNA genes for phylogenetics. 315–322, in: MA Innis & al. (eds). PCR protocols: a guide to methods and applications. Academic Press, San Diego, CA. https://doi.org/10.1016/B978-0-12-372180-8.50042-1