DOI 10.12905/0380.sydowia70-2018-0011

Pluteus fenzlii (Agaricales, Pluteaceae) – taxonomy, ecology and distribution of a rare and iconic species

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Holec J., Kunca V., Ševčíková H., Dima B., Kříž M. & Kučera M. (2017): *Pluteus fenzlii* (Agaricales, Pluteaceae) – taxonomy, ecology and distribution of a rare and iconic species. – Sydowia 70: 11–26.

Pluteus fenzlii is a rare fungus known from Serbia (type locality), France, Poland, Slovakia, Hungary, Russia, Georgia, and Japan. Based on one record from Poland and numerous records from Slovakia and Hungary we analyzed data on its morphology, taxonomy, systematic position (ITS1–5.8S–ITS2 regions of the nrDNA), substrates and habitats. Vegetation of its localities in Poland and Slovakia was studied by means of vegetation samples. *Pluteus fenzlii* sequences form a strongly supported monophyletic clade sister to the clade of *P. mammillatus*, a related North American species. Both species are separated by a clear barcoding gap. Most micromorphological characters of *P. fenzlii* are variable both within one collection and among different collections. Broadleaved tree species the wood of which is inhabited by *P. fenzlii* and its habitats in Europe are summarized. The species usually occurs in hilly areas with more or less natural broadleaved habitats, mostly thermophilic ones, often protected in nature reserves. Its localities are mostly situated in the transition zone between hornbeam (alternatively beech) and oak woods. Globally, *P. fenzlii* is the Eurasian species with distribution hot-spot in Central Europe (Slovakia, Hungary). A conspecific but slightly deviating collection from Australia is discussed.

Keywords: Fungi, morphology, phylogeny, vegetation, Europe.

Pluteus fenzlii (Schulzer) Corriol & P.-A. Moreau is a rare and iconic gilled fungus distinguished by its bright yellow pileus and annulate stipe (Corriol & Moreau 2007), a character very unusual in the genus *Pluteus* (Minnis et al. 2006, Malysheva et al. 2007, Vizzini & Ercole 2011). The species was described as *Agaricus fenzlii* Schulzer (Schulzer et al. 1866) from former Slavonia, currently Serbia, close to the border with Croatia (Corriol & Moreau 2007: 243). A first detailed revision was published by Singer (1979) under the name *Chamaeota fenzlii* (Schulzer) Singer, based on records from valley of Kodori river in Abkhazia, Georgia (Singer 1929) and Slovakia (Singer 1979, Kotlaba 1981). The species has also been published from the French Pyrenees, southern Hungary (Corriol & Moreau 2007), Białowieża Forest in Poland (Gierczyk et al. 2015, Karasiński 2014, 2016), and Samara region, Russia (Malysheva et al. 2007). *Pluteus fenzlii* is also documented from Asia in Siberia, Russia (Malysheva et al. 2007, 2016) and Japan (Justo et al. 2011a,b). A record from Bunya Mountains National Park in Queensland (Australia) was sequenced and allegedly agreed with published sequences of *P. fenzlii* (Leonard 2015).

There is a very similar species in North America, *Pluteus mammillatus* (Longyear) Minnis, Sundb. & Methven (Minnis et al. 2006), originally described as *Annularia mammillata* Longyear (Longyear 1902), which differs from *P. fenzlii* only by white to greyish-red lamellar edge (yellow in *P. fenzlii*). However, Justo et al. (2011a: 469) concluded that this and also other characters of the two species are very variable, and "geographic distribution is the only reliable character to tell them apart", in addition to the maximum 2.5 % ITS sequence divergence between them. *Pluteus fenzlii* and *P. mammillatus* formed a well-supported own lineage in the phylogenies published by Justo et al. (2011a,b). Lately, in the comprehensive work of Menolli et al. (2015) the *P. fen-*

zlii-*P. mammillatus* clade was proposed to belong to the *P. ephebeus* clade within sect. *Celluloderma* together with more South and Central American species level lineages.

In the last decades, we collected rich data on occurrence and habitats of *P. fenzlii* in Slovakia and Hungary, countries hosting the highest number of its localities in Europe, and data on one record from Poland. Aims of our paper are (1) to summarize data on macro- and micromorphology of these records and their ITS nrDNA sequences, (2) to evaluate morphological variability, substrates, habitats and distribution of *P. fenzlii*, and (3) to discuss variables shaping its ecology and distribution.

Materials and methods

Field work and vegetation sampling

Data on records of *Pluteus fenzlii* are based on our finds from Poland, Slovakia and Hungary from the period 1996–2016, herbarium specimens from these countries, and records kindly provided by local field mycologists. Vegetation and habitat characteristics of Slovak localities were sampled by T. Kučera with the help of V. Kunca, J. Holec and local mycologists (see Acknowledgements) at the area of approximately 250 (–400) m^2 surrounding the fallen trunks inhabited by *P. fenzlii*, during May 30–June 1, 2017. Vegetation samples were recorded using the Braun-Blanquet phytosociological approach, which is widely used as a standardised method for vegetation analysis (Kent 2012). Data on Polish record were obtained in the same way by M. Kříž, J. Holec and T. Kučera during their stay in Białowieża National Park in September 2016. To visualize the position of samples in vegetation system, we constructed biplot diagram using Detrended Correspondence Analysis (DCA). Diagnostic and constant species values of vegetation units were extracted from Jarolímek & Šibík (2008). Naturalness of forest stands was classified according to the scale published by Holec et al. (2015), and wood decay stages according to Heilmann-Clausen (2001). Exact coordinates of our records are not published here for purposes of nature conservation but can be obtained from authors on request. We were not able to obtain exact coordinates of Hungarian records so that their vegetation data were not sampled in the field.

Morphology

Description of macrocharacters was compiled by J. Holec from field notes and photographs based on fresh material cited below. Microscopic features were studied by H. Ševčíková on dried material mounted in water, Congo red and Melzer's reagent using an Olympus BX-50 light microscope with a magnification of 400× and 1000×. All vouchers were microscopied routinely for correct identification. In some cases, we had several vouchers from the same locality. Selected vouchers (11) were studied in detail (see below), namely those containing well-preserved material rich in spores. Microscopic description is based on 30 measurements of basidiospores, cheilocystidia and pleurocystidia (except for PVKU 1859 which is young and spores are very rare) and 20 measurements of basidia and hyphae per voucher. The expression 11/11/330 for basidiospores means 11 collections/11 basidiomata/330 spores measured in total. Morphological terminology follows Vellinga (1988). The term "plagiotrichoderm" is used in accordance with Clémençon (2004: 312). Abbreviations used: avl – mean of basidiospore length, avw – mean of basidiospore width, Q – quotient of length and width in any one basidiospore, avQ – mean of basidiospores Q values.

DNA study

Molecular examination of 15 specimens of *P. fenzlii* from France, Hungary, Slovakia and Poland was conducted by B. Dima. The official fungal barcoding region, the internal transcribed spacer (ITS) including ITS1-5.8S-ITS2 regions of the nrDNA was studied. Classical DNA extraction steps were omitted by using the Phire® Plant Direct PCR Kit (Thermo Scientific, USA). A small piece of lamella was lysed in 20 µl Dilution Buffer provided by the manufacturer. The samples were incubated at room temperature for 30 min and then 1 µl of the lysate was added as template for PCR amplification reactions. The primers ITS1F and ITS4 (White et al. 1990, Gardes & Bruns 1993) were used for amplifications, which were performed in a volume of 20 µl MasterMix containing 6.6 µl nuclease free water, 1 µl lysate (from the dilution protocol), 0.5 µM of each primer, 10 µl of 2× Phire Plant PCR Buffer and 0.4 µl of Phire Hot Start II DNA Polymerase. The PCR reactions were performed with the following protocol: 5 min at 98 °C for initial denaturation, 40 cycles of 5 s denaturation at 98 °C, 5 s annealing at 55 °C, and 20 s extension at 72 °C, followed by a final extension for 1 min at 72 °C. PCR products were visualized by gel electrophoresis in 2 % agarose gel staining with ethidium bromide. Amplicons were sequenced at LGC Genomics (Berlin, Germany) with the same primers as those applied in PCR reactions. Se-

Tab. 1. – *Pluteus* sequences used in the phylogenetic analyses.

Species	Origin	Voucher	Accession no.	Literature
P. fenzlii	Hungary	AL 89/75	MF356557	this study
P. fenzlii	Hungary	DB 6253	MF356558	this study
P. fenzlii	Hungary	AL 15/133	MF356559	this study
P. fenzlii	Slovakia	BRNM 767000	MF356560	this study
P. fenzlii	Slovakia	BRNM 788131	MF356561	this study
P. fenzlii	Poland	PRM 944961	MF356562	this study
P. fenzlii	Slovakia	PRM 888602	MF356563	this study
P. fenzlii	Slovakia	PSG 587	MF356564	this study
P. fenzlii	Hungary	FP 2014-08-02	MF356565	this study
P. fenzlii	France	GC 03091403	MF356566	this study
P. fenzlii	France	JF 0097	MF356567	this study
P. fenzlii	France	GC 0309260	MF356568	this study
P. fenzlii	Slovakia	PVKU 1859	MF356569	this study
P. fenzlii	Slovakia	PVKU 1749	MF356570	this study
P. fenzlii	Slovakia	BRNM 766999	MF356571	this study
P. fenzlii	Russia	LE 303661	KX216339	Malysheva et al. (2016)
P. fenzlii	Russia	LE 246083	FJ774082	Malysheva et al. (2009)
P. fenzlii	Japan	TNS-F12376	HM562091	Justo et al. (2011a)
P. fenzlii	Slovakia	F 1020647	HM562111	Justo et al. (2011a)
P. fenzlii	Australia	QMS MC 034*	**	Leonard (2015)
P. mammillatus	USA	ASM 7916	HM562119	Justo et al. (2011a)
P. mammillatus	USA	Singer 244A	HM562120	Justo et al. (2011a)
P. mammillatus	USA	Minnis 309202	HM562086	Justo et al. (2011a)
P. tomentosulus	USA	MO93719	KM983672	Menolli et al. (2015)
P. hispidulus var. *cephalocystis*	Spain	ARAN8200509	KM983695	Menolli et al. (2015)
P. hispidulus	Spain	A1882	KM983681	Menolli et al. (2015)
P. podospileus	USA	AJ782	KM983687	Menolli et al. (2015)
P. pallescens	Spain	AJ214	HM562056	Justo et al. (2011a)
P. eludens	USA	SF15	HM562185	Justo et al. (2011a)
P. cinereofuscus	Spain	AJ34	HM562124	Justo et al. (2011a)
P. romellii	USA	AJ857	KM983701	Menolli et al. (2015)

* Munro Camp track, Bunya Mountains National Park, coll. Susan Nelles, 17 March 2012
** unpublished sequence (not in GenBank), obtained personally from M. Barrett (Kings Park, Perth, Western Australia)

quences were assembled and edited with the CodonCodeAligner 7.0.1. (CodonCode Corporation, USA), and submitted to GenBank (MF356557–MF356571, Tab. 1). The additional ITS and partial LSU sequence of one Australian specimen (QMS MC 034) was previously sequenced (Leonard 2015) and kindly provided to us by M. Barrett (Kings Park, Perth, Western Australia).

Initial BLAST search against GenBank and UNITE nucleotide databases was performed for searching identical or similar sequences prior to phylogenetic analysis. All ITS sequences labelled as *P. fenzlii* and *P. mammillatus* were downloaded. Additional *Pluteus* sequences were added based on previous studies (Tab. 1).

Sequences were aligned in MAFFT online version using the E-INS-i strategy (Katoh & Standley 2013) under default settings. Manual inspection of the alignment was done in SeaView (Gouy et al. 2010). The program FastGap 1.2 (Borchsenius 2009) was used for gap coding, following the simple indel coding algorithm (Simmons et al. 2001). The final alignment including nucleotide and binary information was subsequently subjected to Maximum Likelihood (ML) and Bayesian Inference (BI) analyses using RAxML (Stamatakis 2014) and

MrBayes 3.1.2 (Ronquist & Huelsenbeck 2003), respectively.

ML phylogenetic analysis was performed in raxmlGUI (Silvestro & Michalak 2012). To test branch support, rapid bootstrap analysis and 1000 replicates with GTRGAMMA substitution model to the nucleotide partitions (ITS1, 5.8S, ITS2) and the default set for the indel characters was applied. In BI analysis using Markov chain Monte Carlo (MCMC) was carried out splitting the alignment into four partitions (ITS1, 5.8S, ITS2 and indels). The GTR + ·Γ substitution model was applied to the nucleotide characters, while the two-parameter Markov model was set for the indels. Four Markov chains were run over 10 000 000 generations, sampling every 1000th generations. The first 3000 trees were discarded as burn-in (30 %). For the remaining trees, 50 % majority rule consensus phylogram with posterior probabilities as nodal supports was computed.

Phylogenetic trees from ML and BI analyses showed overall congruent topology, and the Bayesian consensus tree was further edited in MEGA 7 (Kumar et al. 2016).

Records of *Pluteus fenzlii* evaluated in this study

All records known to us are included (also those not documented by vouchers) to enlarge the dataset for evaluation of ecology and distribution. Voucher specimens (if available) are indicated in parentheses at the end of records; those studied microscopically in detail for purposes of micromorphological description are marked with asterisk (*). For each locality, only dominant tree species are given. For acronyms of institutional herbaria, see Index Herbariorum (http://sweetgum.nybg.org/science/ih/). Abbreviations: AL – private herbarium of L. Albert, alt. – altitude, DB – private herbarium of B. Dima, FP – private herbarium of P. Finy, NNR – National Nature Reserve, PSG – private herbarium of S. Glejdura, PVKU – private herbarium of V. Kunca.

POLAND, Podlasie Province, Hajnówka district, near Białowieża, **Białowieża National Park**, forest section 224D, alt. 150 m, flat terrain, hemiboreal mixed forest (*Carpinus*, *Quercus robur*, *Tilia*, *Picea*), virgin forest, deciduous tree, probably *Tilia* sp., fallen trunk, decay stage 3, 14 September 2016, leg. M. Kříž, J. Holec, T. Kučera, det. M. Kříž (PRM 944961)*; SLOVAKIA, Kremnické vrchy, Zvolen district, near Budča, **NNR Boky 1**, alt. 330 m, steep SSE slope, broadleaved forest (*Quercus cerris*, *Q. petraea*, *Carpinus*), virgin forest, *Quercus cerris*, fallen trunk, diam. 55 cm, decay stage 4, 24 September 2015, leg. & det. V. Kunca (no voucher, young basidiomata, later disappeared); Kremnické vrchy, Zvolen district, near Budča, **NNR Boky 2**, alt. 295 m, steep SE slope, broadleaved forest (*Quercus cerris*, *Carpinus*, *Acer campestre*), near-natural forest, *Quercus cerris*, fallen trunk, diam. 40 cm, decay stage 2, 24 September 2015, leg. & det. V. Kunca (PVKU 1487)*; Ibid., 28 June 2016, leg. & det. V. Kunca (PVKU 1695); Ibid., 4 August 2016, leg. & det. V. Kunca (PVKU 1749)*; Krupinská planina, Zvolen district, near Babiná, **NNR Mäsiarsky bok**, alt. 425 m, steep W slope, broadleaved forest (*Carpinus*, *Acer platanoides*, *Quercus cerris*, *Q. robur*), natural forest, *Quercus cerris*, fallen trunk, diam. 50 cm, decay stage 3, 20 September 2016, leg. & det. V. Kunca (PVKU 1859)*; Štiavnické vrchy, Krupina district, near Kráľovce-Krnišov, **Končitý vrch hill**, alt. 295 m, mild NEE slope, broadleaved forest (*Quercus cerris*, *Q. robur*, *Carpinus*), man-influenced forest, *Quercus cerris*, 2 sites: fallen trunk, diam. 10 cm; fallen branch, diam. 20 cm, decay stage 2, 3 August 2016, leg. L. Hejl, det. H. Ševčíková (BRNM 788131)*; Ostrôžky, Veľký Krtíš district, near Pravica, **Háj hill** (415 m) E of Pravica, alt. 360 m, mild W slope, broadleaved forest (*Quercus cerris*, *Q. petraea*, *Acer campestre*, *Cornus mas*, natural forest, *Quercus petraea*, fallen decaying trunk, decay stage 3, 13 August 1975, leg. F. Kotlaba, R. Singer (F1020647); Juhoslovenská kotlina, Lučenec district, near Ľuboreč, **Piesok hill 1**, alt. 245 m, mild E slope, broadleaved forest (*Quercus cerris*, *Carpinus*, *Acer campestre*), near-natural forest, wood of a broadleaved tree, fallen trunk, decay stage 4, 9 September 2014, leg. P. Smik, det. V. Kunca (BRA CR 24195); Juhoslovenská kotlina, Lučenec district, near Ľuboreč, **Piesok hill 2**, alt. 295 m, steep E slope, mixed forest (*Quercus cerris*, *Q. petraea*, *Carpinus*, *Tilia*, *Pinus sylvestris*), man-influenced forest, *Quercus sp.* (*Q. cerris* or *Q. petraea*), fallen trunk, decay stage 3, 28 August 2014, leg. P. Nociar, det. H. Ševčíková (BRNM 766999)*; Ibid., fallen trunk, diam. 15 cm, decay stage 2 to 3, 10 September 2014, leg. P. Nociar, det. H. Ševčíková (BRNM 767000, PSG 5904)*; Juhoslovenská kotlina, Poltár district, near Petrovec, **Tri chotáre hill** (276 m), alt. 240 m, mild N slope, broadleaved forest (*Quercus cerris*, *Q. petraea*, *Carpinus*, *Populus tremula*), man-influenced forest, *Populus tremula*, fallen trunk, diam. 20–30 cm, decay stage 2, 21 September 2015, leg. & det. M. Macalák (no voucher); Juhoslovenská kotlina, Rimavská Sobota district, near Teplý Vrch, **Malá obora protected area**, alt. 230 m, mild NE slope, broadleaved forest (*Quercus robur*, *Tilia*, *Carpinus*), man-influenced forest (former park), *Quercus* sp., fallen trunk, decay stage 3, 10 July 1996, leg. & det. J. Holec (PRM 888602)*; Cerová vrchovina, Rimavská Sobota district, near Petrovce, **hill (315 m) between Petrovce and Jestice villages**, alt. 290 m, mild S slope, broadleaved forest (*Quercus cerris*, *Q. robur*, *Carpinus*, *Acer campestre*), man-influenced forest, *Quercus cerris*, fallen trunk, decay stage 2, 10 October 2015, leg. & det. S. Glejdura (PSG 5873); HUNGARY, Börzsöny Mts., Pest county, near Kemence, **Királyháza**, broadleaved forest (*Luzulo-Fagetum*) on andesite, near-natural forest, *Fagus sylvatica*, fallen trunk, decay stage 4, 2 August 2014, leg. & det. P. Finy (FP2014-08-02)*; Börzsöny Mts., Pest County, **near Hont**, broadleaved forest on andesite, near-natural forest, *Cerasus avium* ?, branch, decay stage 2, 25 Aug 2007, leg. S. Farkas, det. B. Dima (voucher nonexistent); Bakony Mts., Veszprém County, **near Uzsa**, broadleaved forest (*Quercus*, *Carpinus*) on sandstone, near-natural forest, *Carpinus betulus*, decaying trunk, decay stage 3, 12 August 1989, leg. & det. L. Albert (AL 89/75)*; Zselic Hills, Somogy County, **near Bőszénfa**, broadleaved forest (*Fagus*, *Quercus*, *Carpinus*) on alluvial deposits (slightly acidic loess and clay), near-natural forest, *Fagus sylvatica*, decaying trunk, decay stage 3, 4 October 2015, leg. I. Bugyik, det. L. Albert (AL 15/133)*; Mecsek Mts., Baranya County, **near Magyaregregy**, broadleaved forest on deposits in area of generally *Quercus-Carpinus-Fagus* forests with submediterranean elements such as *Ruscus aculeatus*, near-natural forest, *Tilia platyphyllos*, decaying trunk, decay stage 3, 25 July 2016, leg. & det. L. Boros (DB6253)*.

Character of studied sites in Poland and Slovakia

Białowieża National Park

52°46.324 N, 23°51.383 E, forest section 224D, altitude ca 150 m a.s.l., flat undulating plains of ground moraine with boulder clay of different thickness.

Vegetation is formed by broad-leaved trees, such as hornbeam (*Carpinus betulus*), northern maple (*Acer platanoides*), small-leaved lime (*Tilia cordata*), pedunculate oak (*Quercus robur*), and conifers – Norway spruce (*Picea abies*) and Scots pine (*Pinus sylvestris*). Both potential and actual vegetation consists of complex unit belonging to association Tilio cordatae-Carpinetum betuli. This unit should be assigned to Natura 2000 habitat 9170 Galio-Carpinetum oak-hornbeam forests (subtype 2: subcontinental oak hornbeam forests Tilio-Carpinetum). Different sites are represented by more individual subassociations differing by herb layer composition (Kwiatkowski 1994, Matuszkiewicz et al. 2012). This "subcontinental" vegetation occurs in eastern part of Poland (where *Fagus sylvatica* does not occur) but from the European viewpoint it is assigned to hemiboreal forests (Bohn et al. 2004).

Southern Slovakia

Altitudinal range 230–425 m a.s.l.

Vegetation (Faliński 1986) is formed by deciduous trees without admixture of conifers. Instead of hornbeam the dominant and subdominant tree is Turkey oak (*Quercus cerris*). Additional oaks are pedunculate oak (*Q. robur* agg. including *Q. robur* s.str. and *Q. pedunculiflora*) and sessile oak (*Q. petraea* agg. including *Q. petraea* s.str., *Q. dalechampii*, and *Q. polycarpa*). Due to the minor morphological differences between these taxa (Požgaj & Horváthová 1986) and their morphological plasticity (Gömöry et al. 2001) they were distinguished only at aggregate level in the field.

Potential and actual vegetation belongs to thermophilous oak woodlands (association Quercetum petraeae-cerris) transitional to other units on the altitudinal, soil and nutrient gradients: hornbeam woods of suballiance Carici pilosae-Carpinenion betuli, beech rich sub-mountain forests of suballiance Eu-Fagenion, xerothermic submediterranean oak woods of the alliance Quercion pubescenti-petraeae and subcontinental oak forests of the association Potentillo albae-Quercetum (Michalko 1986, Roleček 2005). In Natura 2000, these woods belong to priority habitats 91G0* Pannonic woods with *Quercus petraea* and *Carpinus betulus* and 91M0 Pannonian-Balkanic Turkey Oak-Sessile Oak forests (Stanová & Valachovič 2002).

Results

Morphology

Pluteus fenzlii (Schulzer) Corriol & P.-A. Moreau, Persoonia 19(2): 248 (2007) – Figs. 1–10

≡ *Agaricus fenzlii* Schulzer, in Schulzer, Kanitz & Knapp, Verh. zool.-bot. Ges. Wien 16(Abh.): 49 (1866).

≡ *Annularia fenzlii* (Schulzer) Schulzer, in Kalchbrenner, Icon. Sel. Hymenomyc. Hung. (Budapest): tab. 10, fig. 1 (1873).

≡ *Chamaeota fenzlii* (Schulzer) Singer, Sydowia 31(1–6): 198 (1979).

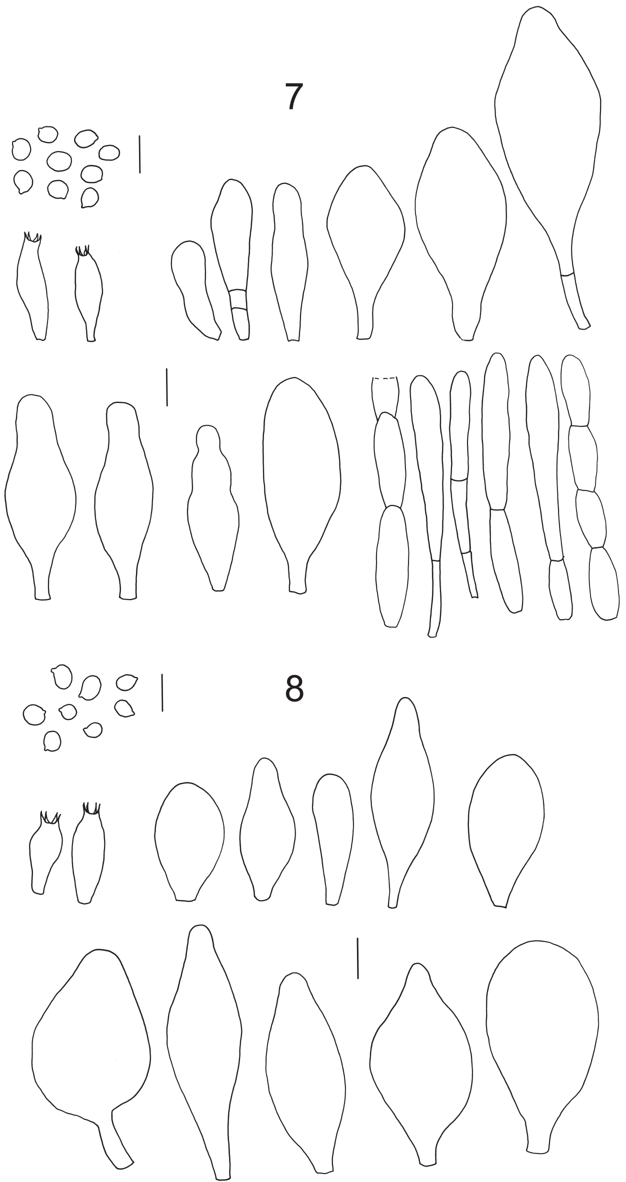
≡ *Pluteus fenzlii* (Schulzer) E.F. Malysheva, O.V. Morozova & Zvyagina, Acta Mycologica, Warszawa 42(2): 155 (2007), superfluous combination (see Borovička 2008) published 23 days after Corriol & P.-A. Moreau (2007).

Basidiomata appearing from late June to the beginning of October; solitary or in small groups, at first tough and compact, then expanding and fragile. – Pileus 30–70 mm when mature, hemispherical with inflexed margin or paraboloid when young, then convex to broadly campanulate, sometimes with slightly undulate or lobed margin, surface finely and densely fibrillose-scaly, scales at first vividly lemon yellow, chrome yellow to bright yellow, at centre sometimes orange, brownish to rusty brown, later becoming sparse, fibrillose, adpressed, finally pale yellowish-brownish, background colour bright yellow when young and mature, discolouring to pale lemon yellow to whitish when dry or old, margin sometimes striate to radially splitted in such state. – Lamellae crowded, ventricose, free, 3–7 mm high, with 1–3 lamellulae between two lamellae, white, pale cream to pinkish-whitish when young, then pink, edge bright yellow when young, at least close to pileus margin, later fading. – Stipe 30–60 × 4–8 mm, cylindrical or gradually thickened downwards, mostly with subbulbous base, solid, white to yellowish-whitish in upper part, surface more or less yellow fibrillose, in lower or basal part with annular zone or distinct, 1–2 mm wide annulus, arachnoid to fibrillose-membranal, running from below, then protruding perpendicularly with inflexed margin, bright yellow, sometimes with rusty yellow edge, later disappearing and sometimes almost invisible, stipe below the annular zone bright yellow or paler, sometimes finely scaly above the basal bulb, the bulb itself yellow-white with tomentose to fibrillose basal mycelium. – Context white in most tissues, lemon yellow below the pileus cuticle. – Odour indifferent. – Taste mild, sweetish.

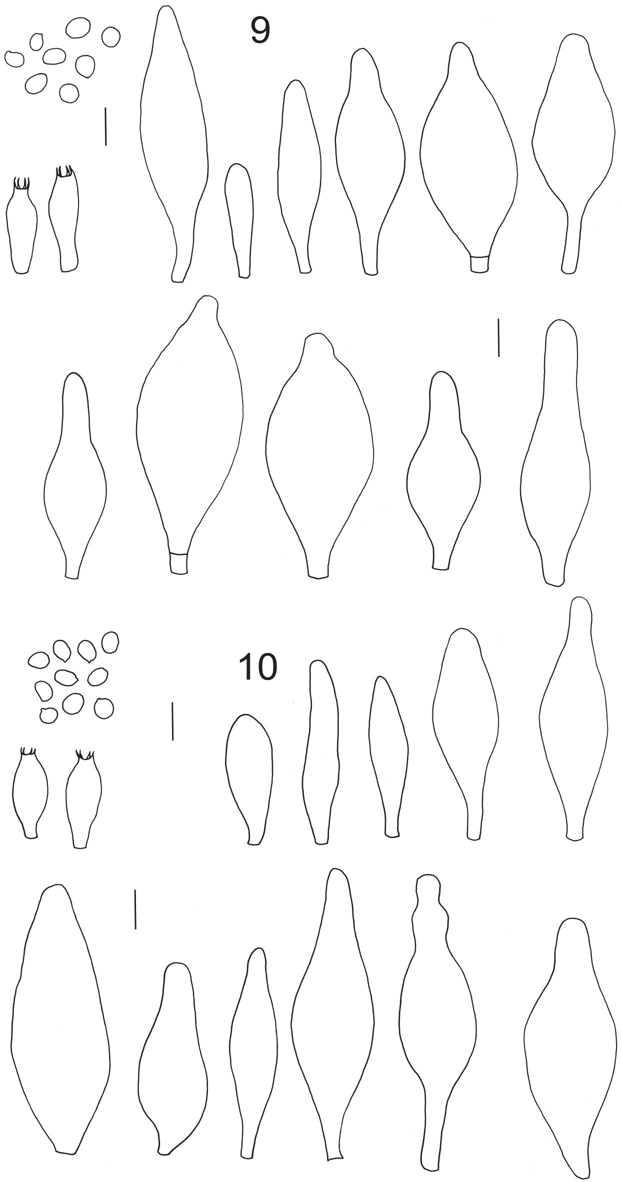
Basidiospores [11/11/330] (4.0)5.0–8.0(9.0) × 4.0–6.0 µm, avl × avw = 6.02 × 5.05 µm, Q = 1.00–1.40, avQ = 1.22, broadly ellipsoid or subglobose, rarely globose to slightly ovoid, smooth, slightly thick-walled, colourless or pale brownish pink in water and in Melzer's reagent, inamyloid. – Basidia tetrasterigmate, rarely bisterigmate, 19–25(30) × 7–10(11) µm with 2–3 µm long sterigmata, most frequently clavate to fusiform, rarely utriform, thin-walled, with or without yellow-ochre granular content in Melzer's reagent, colourless in water. – Lamellar edge sterile, cheilocystidia forming a well-developed strip. – Cheilocystidia (15)20–78(88) × 7–32 µm, abundant, variable in size and shape, mostly narrowly to broadly fusiform with short to long pedicel (up to 38 µm) or clavate to ventricose, less frequently lageniform or subcylindrical, thin-walled, some of them with slightly thick-

Figs. 1–6. *Pluteus fenzlii*, basidiomata arranged from young to old ones. **1.** Slovakia, Piesok hill, photo P. Nociar, no voucher (but there are other vouchers from the same site). **2.** Poland, Białowieża National Park, PRM 944961, photo M. Kříž. **3.** Hungary, near Magyaregregy, DB6253, photo L. Boros. **4.** Slovakia, Piesok hill, photo P. Nociar, no voucher (but there are other vouchers from the same site). **5.** Slovakia, Malá obora protected area, PRM 888602, photo J. Holec. **6.** Slovakia, NNR Boky, PVKU 1487, photo V. Kunca. For details on localities and vouchers see Materials and methods. Bars 10 mm.

ened wall in the middle part (up to 0.5–0.7 µm), colourless or with yellow intracellular pigment in water. – Pleurocystidia 38–83(90) × 10–31 µm, moderately abundant, most frequently fusiform or lageniform with short or long (up to 18 × 9 µm) pedicel, less frequently ventricose to fusiform-clavate with short or longer pedicel, rarely fusiform with constricted apex or ovoid with long pedicel,



Figs. 7–8. *Pluteus fenzlii*, microcharacters. **7.** Poland, Białowieża National Park, PRM 944961, basidiospores, basidia, cheilocystidia, pleurocystidia, pileipellis cells. **8.** Slovakia, NNR Boky, PVKU 1487, basidiospores, basidia, cheilocystidia, pleurocystidia. Bars 10 µm. Del. H. Ševčíková.



Figs. 9–10. *Pluteus fenzlii*, microcharacters. **9.** Slovakia, NNR Boky, PVKU 1749, basidiospores, basidia, cheilocystidia, pleurocystidia. **10.** Slovakia, Malá obora protected area, PRM 888602, basidiospores, basidia, cheilocystidia, pleurocystidia. Bars 10 µm. Del. H. Ševčíková.

colourless in Melzer's reagent and in water, thin-walled, some of them with slightly thickened wall in the middle part. – Content of lamellar trama yellow-ochre to pale yellow in Melzer's reagent, colourless in water. – Lamellar trama inverse. – Pileipellis a plagiotrichoderm consisting of thin-walled, cylindrical hyphae (3)5–15(20) µm wide with partially erect hyphal ends inflated up to the width of 20 µm, sometimes forming clusters, colourless or with pale yellow intracellular pigment in water, sometimes with brownish black intracellular pigment at central part of pileus in water and in Melzer's reagent. – Stipitipellis a cutis consisting of cylindrical hyphae (3)5–10(15) µm wide, thin-walled, colourless or with pale yellow intracellular pigment in water. – Caulocystidia absent. – Annulus consisting of cylindrical hyphae (3)5–8(10) µm wide, thin-walled, with very pale yellow intracellular pigment in water, with or without yellow-ochre granular contents in Melzer's reagent. –

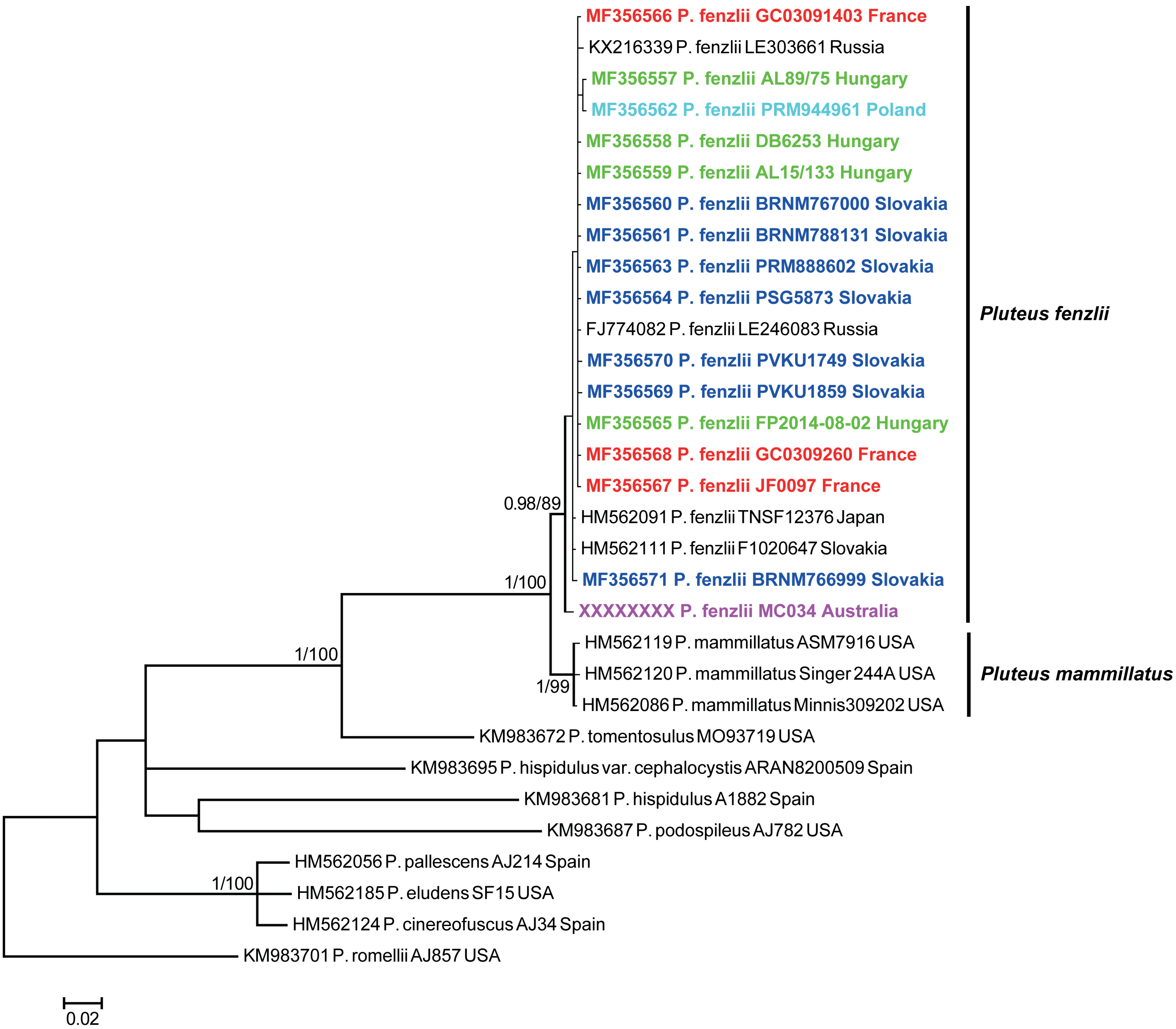


Fig. 11. 50 % majority rule Bayesian phylogram inferred from nrITS sequences of selected *Pluteus* species focused on *Pluteus fenzlii*. GenBank as well as voucher numbers, and country origins are given. XXXXXXXX: unpublished sequence (not in GenBank), obtained personally from M. Barrett (Kings Park, Perth, Western Australia). Bayesian PP and Maximum Likelihood BS values are shown at branches only when PP > 0.95 and BS > 70 %. Newly generated sequences are marked in boldface and in various colours, according to their origins. Bar indicates 0.02 expected change per site per branch.

Clamp connections absent in all studied tissues.

DNA study

The final ITS dataset consisted of 31 sequences of 721 characters including gaps which were coded as presence/absence data and used as separate partition (70 additional binary characters) in the phylogenetic analyses. Both ML and BI analyses recovered *Pluteus fenzlii* as strongly supported monophyletic clade (Fig. 11) including our 15 newly generated sequences and the four previously published ones from Slovakia, Russia, and Japan (Tab. 1). The Australian sequence (QMS MC 034) deviated from the Eurasian ones by 4–5 substitution and indel positions in contrast to the intraspecific variation within the North Hemisphere sequences which represented maximally 2 changes. The range of the intraspecific ITS variation of the *P. fenzlii* sequences was 0.00–0.47 % (maximum five nucleotide or indel differences), while the range of interspecific ITS variation towards the sister species *P. mammillatus*

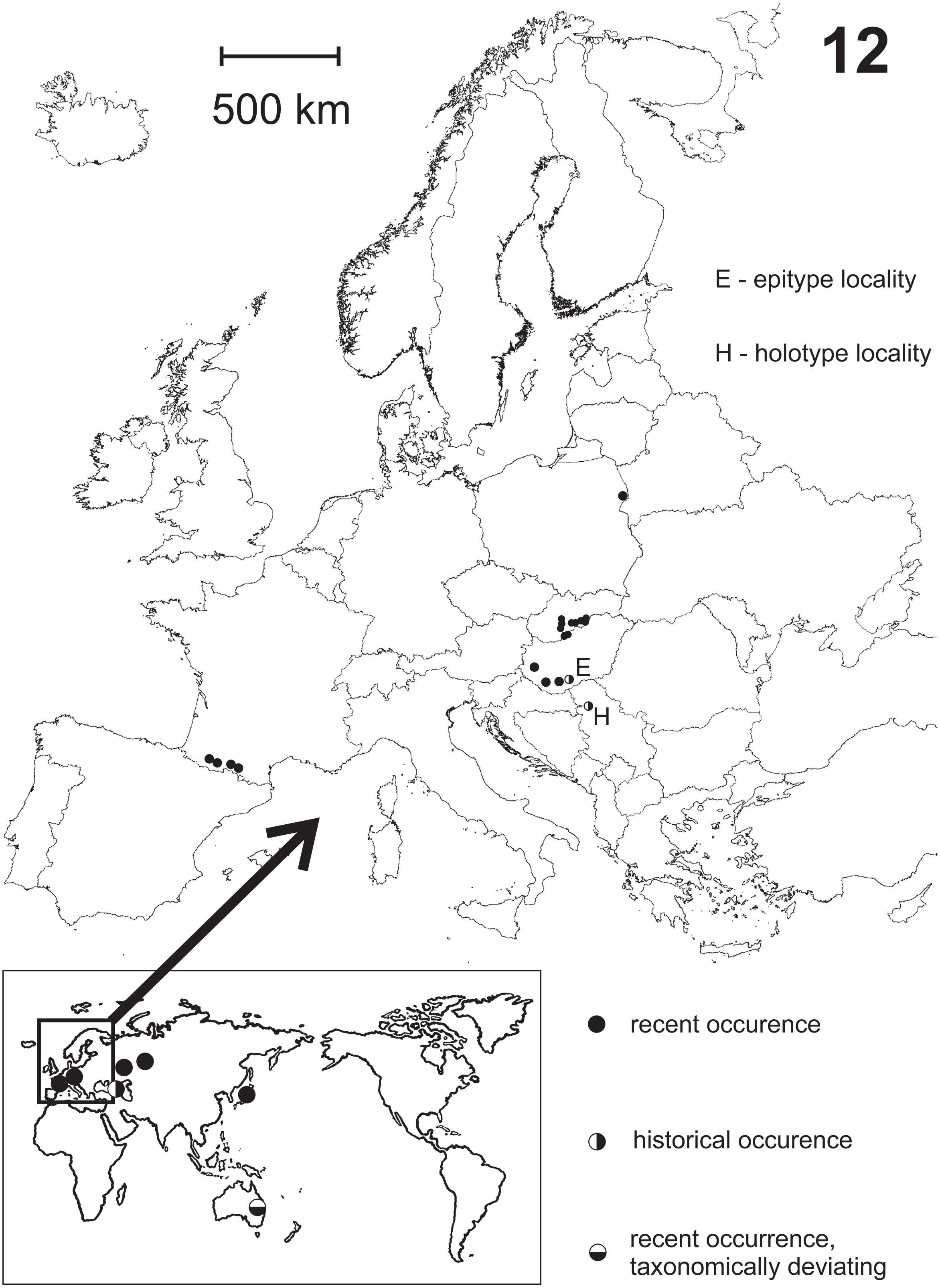


Fig. 12. *Pluteus fenzlii*, distribution. In detailed map of Europe, each dot represents one locality. Records from Novosibirsk and Krasnoyarsk regions (Siberia, Russia) published via the Internet are not shown in world map.

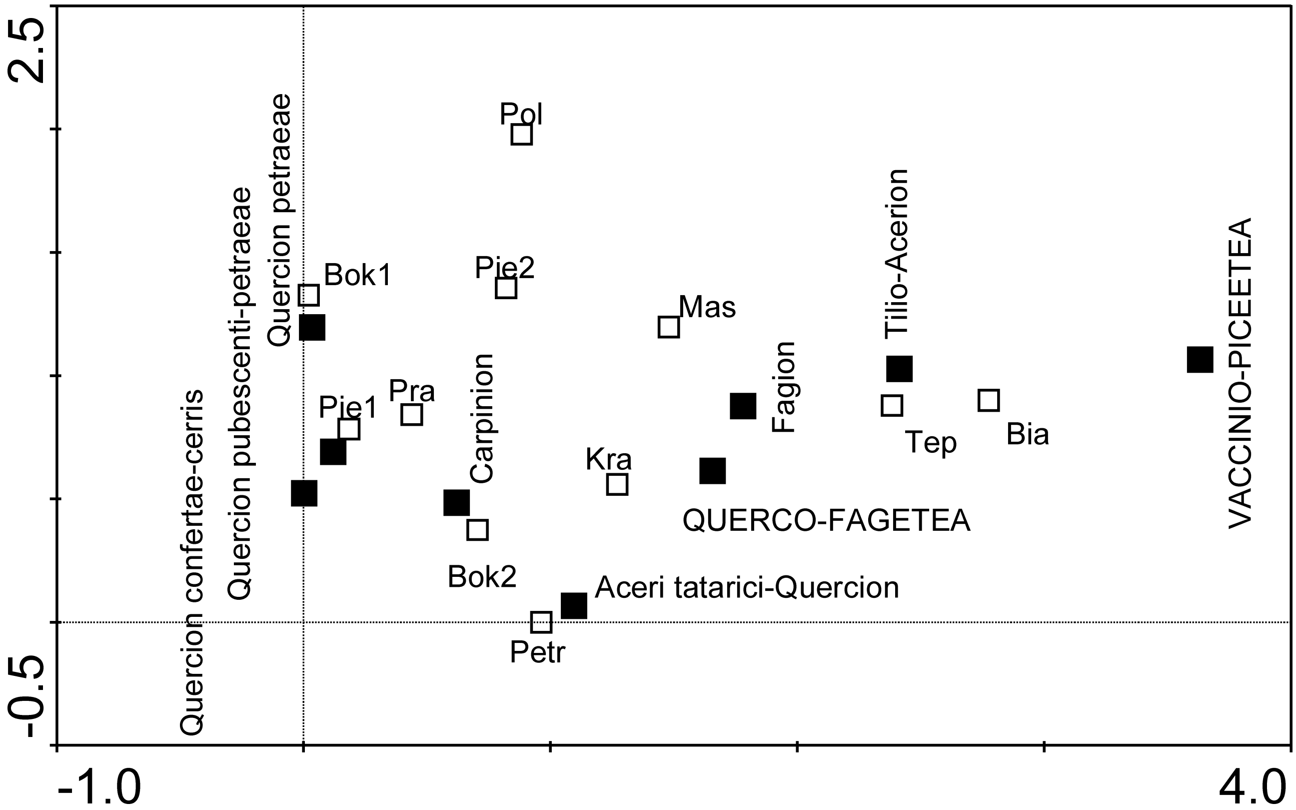


Fig. 13. Biplot diagram (DCA, axes explain 30 % of species variance) showing the position of vegetation composition on *P. fenzlii* localities (empty squares) in vegetation space. Higher vegetation units (black squares) are passively projected. Abbreviations of localities (for full data see Studied collections): Bia – Białowieża National Park; Bok1 – Boky 1; Bok2 – Boky 2; Kra – Kráľovce-Krnišov, Končitý vrch hill; Mas – Mäsiarsky bok; Petr – between Petrovce and Jestice villages; Pie1 – Piesok hill 1; Pie2 – Piesok hill 2; Pol – Poltár, Tri chotáre hill; Pra – Pravica, Háj hill; Tep – Teplý Vrch, Malá obora protected area. Full names of vegetation units: class QUERCO-FAGETEA Br.-Bl. et Vlieger in Vlieger 1937, subclass Fagetalia Pawłowski in Pawłowski et al. 1928: alliance Carpinion betuli Issler 1931, alliance Tilio-Acerion Klika 1955, alliance Fagion sylvaticae Luquet 1926; subclass Quercetalia pubescenti-petraeae Klika 1933: alliance Quercion pubescenti-petraeae Br.-Bl. 1932, alliance Quercion petraeae Zólyomi et Jakucs ex Jakucs 1960, alliance Aceri tatarici-Quercion Zólyomi et Jakucs 1957, alliance Quercion confertae*-cerris Horvat 1954 (*~petraeae).

was 2.0–2.5 % (14–17 nucleotide and indel differences). Thus, a clear barcoding gap exists that can unambiguously separate the two species. On infrageneric level, *P. fenzlii* formed a strongly supported clade with *P. mammillatus* (Fig. 11).

Substrates

Based on our data from Poland, Slovakia and Hungary, the most frequent substrate in this part of Europe is *Quercus cerris* (5 localities), followed by *Fagus sylvatica* (2), *Carpinus betulus* (1), *Populus tremula* (1), *Quercus petraea* (1), *Tilia platyphyllos* (1), *Tilia* sp. (1), and perhaps *Cerasus avium* (1). Basidiomata were observed on fallen trunks (including their branches), both thin and medium thick (10–55 cm diam.), and branches separated from old living trees and lying on soil (about 20 cm diam.). The basidiomata grew either from decorticated wood or cracks in the bark, often at sites covered by mosses. They appeared on upper or side parts of trunks and branches. The trunks were either in full contact with soil or more or less above the soil due to their curvature. In such cases, the percentage of air-exposed parts was 50–90 %. The wood was in decay stages 2–4.

Habitat and vegetation indication

In Poland, Białowieża National Park, closed canopy (70 %) formed by hornbeam (*Carpinus betulus*) altogether with pedunculate oak (*Quercus robur*) and additional occurrence of small-leaved lime (*Tilia cordata*) and Norway spruce (*Picea abies*) prevailed in the tree layer. In shrub undergrowth, only hornbeam was rarely present (3 %). Occurrence of nitrophytes (*Urtica dioica*, *Geranium robertianum*) and clear-cut species (like *Rubus idaeus*) shows concurrent human/animal influence on the forest composition and structure both in the past (coppicing, opening) and at present (grazing by wild game, e.g. European bison, elk, wild boar).

In southern Slovakia, the vegetation diversity and plant species richness was more complex. *Pluteus fenzlii* grew under closed canopy of broad-leaved forests (cover 60–80 %) dominated by Turkey oak (*Quercus cerris*) and hornbeam (*Carpinus betulus*), with adjacent pedunculate and sessile oaks (*Q. robur* agg., *Q. petraea* agg.) and small-leaved lime (*Tilia cordata*). Shrub layer varied from open to dense stands (cover 0–25 %). Cover of herb layer varied between 1–60 % with 25 species per sample on average. Mesophilous and meso- to eutrophic shade-tolerant hemicryptophytes were admixed in the undergrowth. Herb layer showed average habitat conditions without any group of diagnostic or differential species, significant for standard vegetation units (Fig. 13). Thermophilous acidophytes were sampled only in NNR Boky on shallow soil on raised elevation of andesitic bedrock. In Tri chotáre hill, forest spring and wet depression was indicated by hygrophilous species of open habitats. Well-preserved forest on deep scree slope is present in NNR Mäsiarsky bok, where except of nitrophilous plants also diagnostic species of hornbeem, scree and beech woods occur (alliances Tilio-Acerion and Fagion). Other nitrophilous species indicate higher content of nutrients and/or anthropogenic impact, additionally with *Impatiens parviflora*, a neophyte originating from central Asia.

Discussion

Morphological and molecular data

Pluteus fenzlii basidiomata are tough and compact at first, then expanding and fragile. These characters remain striking even in dry herbarium material. Basidiospores of the Hungarian collections (FP 2014-08-02, AL 15/133, AL 89/75, DB6233) are on average shorter and narrower, 5.42 × 4.73 µm, than those of the Slovakian ones (PVKU 1487, PVKU 1749, PRM 888602, BRNM 766999, BRNM 767000, BRNM 788131), 6.85 × 5.29 µm. Basidiospores of the Slovakian collections (average values) are the largest ones compared with the Polish, Hungarian (this paper) and the Russian ones (Malysheva et al. 2007). Moreover, their absolute size, (4.0)5.0–8.0(9.0) × 4.0–6.0 µm, is also larger than in the French ones (Corriol & Moreau 2007). Malysheva et al. (2007) mentioned that the basidiospore size is very variable within one collection. Concerning our collections, it is variable only in two of them (PVKU 1749, PRM 888602).

In most collections studied by us, cheilocystidia and pleurocystidia are variable in size and shape. The same fact was observed by Malysheva et al. (2007) in Russian collections (each collection had different size and shape of cystidia, but, generally, there was no difference among group of collections from central Russia and western Siberia). Some of our collections clearly differ in shape of cystidia. Pleurocystidia of Slovakian collections PVKU 1859, PVKU 1487, and PVKU 1749 are frequently ventricose to fusiform-ventricose (Figs. 8, 9), whereas such pleurocystidia are rare in other collections. The collection PRM 888602 has lageniform to fusiform pleurocystidia with two constrictions at apex (Fig. 10). This type of pleurocystidia was not mentioned by Malysheva et al. (2007) and Corriol & Moreau (2007). Generally, variability within one collection, among collections from one region and among different regions is flexible. Some characters are unique for one collection or for one region. However, it is not possible to conclude that the differences of microscopic characters are regional-based.

Altogether, there are now 19 ITS sequences of *Pluteus fenzlii* available (15 newly generated in this study) from a broad geographic sampling of Eurasia plus one sequence from Autralia (Tab. 1). Based on the ITS data available we did not observe any pattern of genetic differentiation in terms of geographical distribution of *P. fenzlii*, except that the Southern Hemisphere (Australian) sequence differed by 4–5 substitution or indel positions from the rest of the *P. fenzlii* sequences. The variation within Northern Hemisphere sequences was maximally 2 substitution or indel positions. On the other hand, the morphologically very similar North American species *Pluteus mammillatus* differs from *P. fenzlii* by constant 14–17 substitution and indel positions in the ITS region. Our conclusion is that the implication of the ITS barcode region followed by the geographical distribution (Eurasia/Australia vs. North America) seem to be the best characters to recognize and separate *Pluteus fenzlii* and *P. mammillatus*.

On infrageneric level, *P. fenzlii* and *P. mammillatus* formed a strongly supported clade (Fig. 11). This relationship agrees well with results of previous studies (e.g. Menolli et al. 2015, Malysheva et al.

2016). This clade seems to belong to *Pluteus* sect. *Celluloderma* based on the most recent phylogenetic survey of Menolli et al. (2015).

Substrates

In Europe and Asia, *P. fenzlii* has been reported from wood of the following trees (Schulzer et al. 1866, Kalchbrenner 1873, Singer 1929, Kotlaba 1981, Corriol & Moreau 2007, Malysheva et al. 2007, Gierczyk et al. 2015, Karasiński 2014, 2016): *Acer campestre*, *Betula* sp., *Fraxinus excelsior*, *Hedera helix*, *Juglans* sp., *Quercus petraea*, *Quercus* sp., *Tilia tomentosa*, *Tilia* sp. Based on our data from Slovakia and Hungary, we add the following species: *Carpinus betulus*, *Fagus sylvatica*, *Populus tremula*, *Quercus cerris*, *Tilia platyphyllos* and probably also *Cerasus avium*.

Substrates of *P. fenzlii* differ in various regions. *Fraxinus excelsior* prevails in French Pyrenees. *Quercus cerris* is the main host in southern Slovakia even if other known host trees – *Acer campestre*, *Carpinus*, *Fraxinus*, *Tilia* – occur in the same area. *Tilia* and *Fraxinus* are substrates in Białowieża, Poland even if *Quercus* (but *Q. robur*, not *Q. petraea* or *Q. cerris*) and *Carpinus* are very common there. In European Russia, *Tilia* and *Acer platanoides* are preferred substrates. In Siberia, *P. fenzlii* was found only on wood of *Betula*. Generally, the simple hypothesis that *P. fenzlii* grows on dominant tree of each region is true only for South Slovakia (*Quercus cerris*). The observed discrepancy could be connected with different composition of mycobiota in host trees in different regions. In such situation, mycelium of *P. fenzlii* is probably exposed to different competition forces under different combination of environmental variables, especially the climatic ones.

Pluteus fenzlii was found on fallen decaying trunks and their branches, sometimes lying apart. It was able to produce basidiomata on rather dry wood as considerable parts of the trunks and branches (50–90 % of their length) were not in contact with soil but air-exposed. The wood was in decay stages 2–4 (Heilmann-Clausen 2001), i.e. from partly decorticated trunks and branches with rather hard wood (starting decay only) to decayed soft wood (but still in the form of trunks and branches, not completely destroyed ones).

Habitats

In Europe, *Pluteus fenzlii* occurs in heterogeneous habitats dominated by various trees. Although beech (*Fagus sylvatica*) plays a major role in European deciduous forests (Ellenberg 1988, Bohn et al. 2004), we register only two records of *P. fenzlii* on beech wood (Hungary). The most frequent habitats of *P. fenzlii* are thermophilous oak forests in hilly regions composed of a mixture of xero- and mesophilous species. Their species composition changes along the environmental gradients (altitude, bedrock and soils, acidity, nutrients, moisture, etc.) and geographic regions (dispersal trails: Carpathian, Pontic-Pannonian, subcontinental, submediterranean). Southern Slovakia represents a transitional zone among Pontic, Matra and Carpathian biogeographical areas where different mesophilous and thermophilous forests merge continuously (Bohn et al. 2004). It represents a northern border of distribution of the Illyrian-Balkan vegetation group distinguished from the Central European one by geographically differential species (e.g. *Quercus cerris*, *Q. frainetto*, *Fraxinus ornus*, *Castanea sativa*, *Acer tataricum*; Horvat et al. 1974). The exact determination of vegetation associations on individual localities of *P. fenzlii* in Slovakia was difficult to impossible (Fig. 13). The average number of observed herb layer diagnostic species was lower when compared with phytosociological literature (Roleček 2005, Purger et al. 2014).

In Białowieża, thermophilous stands covered by open oak woodlands (association Potentillo albae-Quercetum) were much more widespread in the past (Kwiatkowski 1994). A comparative long-term study of permanent plots (Kwiatkowska et al. 1997) highlighted expansion of shade-loving trees, like hornbeam (*Carpinus betulus*), which occupy fertile, not too wet soils. Interestlingly, our record of *P. fenzlii* originates just from the hornbeam-dominated stand.

Open and light habitats are typical for *P. fenzlii* records from European Russia. Localities in Middle Volga Biosphere Reserve are open Pine forests with *Pinus sylvestris* alternating with broadleaved forests with *Tilia cordata*, *Acer platanoides*, *Quercus robur*, and *Ulmus glabra* (Malysheva et al. 2007) on background of carbonate rocks covered by loam. This area has continental climate with annual precipitation of ca. 500 mm. The western Siberian locality has vegetation formed by coniferous forests (*Pinus sibirica*, *Abies sibirica*, *Picea obovata*) in contact with secondary deciduous-coniferous forests (with *Populus tremula*, *Betula pendula* – substrate of *P. fenzlii*) with mossy or grassy undergrowth mixed with different types of swamps. The area has moderately continental climate with ca. 650 mm of annual precipitation and its bedrock consists of Quaternary deposits, covered by loamy and clay soils (Malysheva et al. 2007).

In Hungary, *P. fenzlii* occurs in several hilly regions. The sites are either mesophilic or thermophilic. The locality in Börzsöny Mts. in northern Hungary (near the border with southern Slovakia) is covered by acidophilous beech forest (association Luzulo-Fagetum) on andesite bedrock. The other localities (in Börzsöny Mts., Bakony Hills, Zselic Hills, Mecsek Mts.) are basically *Quercus-Carpinus* dominated forests, on different background (sandstone, andesite, alluvial deposits: slightly acidic loess and clay). The localities of *P. fenzlii* in South Hungary belong to sub-Mediterranean *Ruscus aculeatus* type, similarly like the type locality in Serbia (Fig. 1B in Purger et al. 2014).

In foothills of French Pyrenees, *P. fenzlii* was found in (i) north oriented deep limestone ravines: calcicolous mountain beech forests composed of *Tilia platyphyllos*, *Fagus sylvatica*, *Buxus sempervirens*, with rich herb layer, phytosociologically belonging to suballiance Scillo lilio-hyacinthi-Fagenion sylvaticae, (ii) similar habitat composed of *Fraxinus excelsior*, *Buxus sempervirens*, *Tilia platyphyllos*, *Fagus sylvatica*, belonging to alliance Fraxino-Quercion roboris, (iii) calcareous terrace along a stream, colonized mainly by *Fraxinus excelsior*, belonging to association Isopyro thalictroidis-Quercetum roboris (alliance Fraxino-Quercion roboris) (Corriol & Moreau 2007).

Generally, average habitat conditions prevail in niche selected by *P. fenzlii* and specialist plant species having higher ecological indication value are absent. Moreover, *P. fenzlii* sites have often been extensively managed, exploited or influenced by humans. Considerable spatial variation caused that plant species of different communities are mixed in a single plot, especially at the border of hornbeam and thermophilous oak woods.

Distribution

To date, *Pluteus fenzlii* is known from the following countries and regions:

– France: foothills of central Pyrenees, 400–740 m a.s.l. (Corriol & Moreau 2007)

– Poland: NE part, Białowieża National Park (Gierczyk et al. 2015, Karasiński 2014, 2016, this paper)

– Slovakia: thermophilic hills of central southern Slovakia (Singer 1979, Kotlaba 1981, this paper)

– Hungary: some mountain and hilly regions – Börzsöny Mts., Bakony Mts., Mecsek Mts., Szekszárdi-dombság Hills – locality of the epitype, Zselic Hills (Corriol & Moreau 2007, this paper)

– Serbia: Fruška Gora Hills, type locality, currently preserved as Fruška Gora National Park (Schulzer et al. 1866)

– Russia: area of Volga river: Samara bend, Zhigulevsky State Nature Reserve, today a part of the UNESCO Middle Volga Biosphere Reserve (Malysheva et al. 2007); several localities in western Siberia: Tyumen region (Malysheva et al. 2007, 2016)

– Georgia: Abkhazia, southeastern foothills of Caucasus Mts. – valley of Kodori river (Singer 1929)

– Japan: collection cited by Justo et al. (2011a,b), Hokkaido, Iwamizawa, Tonebetu, decaying tree in deciduous forest, 24 September 2005, leg. et det. S. Takehashi as *P. leoninus*, rev. A. Justo and H. Ševčíková as *P. fenzlii* (TNS-F 12376).

– Australia: Queensland, Bunya Mountains National Park, Munro Camp track; Queensland, Main Range National Park, Mt. Cordeaux (Leonard 2015).

We can conclude that *Pluteus fenzlii* is basically a Eurasian species with a distribution hot-spot in Central Europe (Fig. 12). Currently, Slovakia and Hungary are countries with the highest number of *P. fenzlii* localities (Fig. 12). There is also an increasing number of records from Siberia (Malysheva et al. 2007, Bulyonkova www.mycology.su: Novosibirsk region, www.mycoweb.ru: Krasnoyarsk region). Molecularly, Australian collection from Bunya Mountains National Park slightly deviates from the rest of *P. fenzlii* sequences (see Results). Further studies are necessary to evaluate the taxonomic status of the Australian subpopulation.

Andrej Piltaver (Slovenia) and Armin Mešić (Croatia) confirmed us (pers. comm., 2017) that *P. fenzlii* is not known in their countries, both in literature, databases, herbaria and unpublished records of amateur mycologists. Mešić contacted mycologists from Serbia and people from the Fruška Gora National Park who confirmed that there are no recent collections.

Corriol & Moreau (2007) epitypified *P. fenzlii* based on a historical collection of L. Hollós from a locality in Tolna County, near to Szekszárd which is a town situated rather close to the type locality in Serbia. They also cited another collection of L. Hollós on the page 239 as identical to the first one. In contrast, on the page 243, the two collections were assigned to different locality names as showed in the map (Carte 1.) too. The second locality name was given as "Sregzár" probably partly based on the database of the Stockholm herbarium (S), where the specimen is labelled as "Sregzard". However, "Sregzár" is an old name of Szekszárd, leaving the dots on the eastern part of the Hungarian map as a non-existent locality of *P. fenzlii*. Hollós collected both specimens in the surroundings of Szekszárd (situated in the Szekszárdi-dombság Hills) in the same year (1896) and on the same substrate (*Tilia tomentosa*).

Concluding remarks

Collections of *P. fenzlii* from various countries are somewhat different microscopically. However, their variability overlaps within the whole distribution range of *Pluteus fenzlii*. The shape and size of cheilocystidia and pleurocystidia is variable both within one collection and between collections. The size of basidiospores differs in specimens from different countries (Poland, Slovakia, Hungary). The basidiospores of Slovakian collections are the largest. Our data show that the basidiospore size range of *P. fenzlii* is higher [(4.0)5.0–8.0(9.0) × 4.0–6.0 µm] than published before. Further studies are necessary to evaluate the variability of microcharacters and its possible relation to the population structure of this species.

Pluteus fenzlii occurs in hilly regions (altitude 230–425 m in Slovakia and France, with exceptional site at 740 m in France) mostly adjacent to higher mountain ranges (Pyrenees, the Carpathians, Caucasus). Exceptions are the hilly country of the Zhigulevsky State Nature Reserve in Middle Volga region (no mountain range in the vicinity) and the Białowieża National Park (lowland forest on glacial deposits, about 150 m a.s.l.). Another feature common for all localities is the more or less natural broadleaved (or mixed) vegetation, often protected in nature reserves of various rank (see Studied collections). Detailed vegetation data from Poland and Slovakia (Tab. 2) show that some of the localities are more or less influenced by man (clearing, cutting, grazing from unnaturally high populations of wild game) but the substrate of *P. fenzlii* is always represented by trees which are native and natural part of vegetation in the area. Therefore, we can consider *P. fenzlii* a species of ancient broadleaved forest (for concept of these forests and relation of fungi to them see e.g. Hofmeister et al. 2014).

The localities in Slovakia, South Hungary and Serbia are distinctly thermophilic, situated on more or less sunny slopes, often on background of volcanic rocks (e.g. andesite), or sediments like loess, clay or sandstone, i.e. both basic and acidic. They are represented by mesophilous and thermophilous vegetation on both convex and concave shapes of relief, on plains and slopes. In the European as well as regional context *P. fenzlii* is not strictly linked to a particular vegetation type. The localities are often situated in the transition zone between hornbeam (alternatively beech) and oak woods, which suggests habitat instability expressed by change of dominant trees during the long-term forest development.

The Central European and Russian localities are situated in clearly continental regions typical by low precipitation and hot summer. The climate of Białowieża National Park is less continental but much colder due to its northern position. On the other hand, the Pyrenean localities are situated in clearly oceanic area, with mild temperature and high annual precipitation (1000–1500 mm). They are represented by gorges, which are influenced by accumulation of cold air (Corriol & Moreau 2007). It is hard to explain such diverse habitat requirements in various parts of Europe. It is also noticeable that the distribution of *P. fenzlii* is limited to several regions which are distant hundreds to thousands kilometres.

The recent increase of *P. fenzlii* localities might be connected also with the global warming (Boddy et al. 2014). An indication of this is the fact that there are no recent records in Balkan countries (Serbia – country of type locality, Croatia, Slovenia; too hot for *P. fenzlii* at present?) but the species is found in regions located more north (Hungary, Slovakia, Poland, continental Russia).

Acknowledgements

We thank the following people for providing data on records of *P. fenzlii*: Libor Hejl (Nezvěstice, Czech Republic), Milan Macalák (Poltár, Slovakia), Pavol Smik and Emília Smiková (Poltár, Slovakia), Peter Nociar (Lučenec, Slovakia), Stanislav Glejdura (Kováčová, Slovakia), László Albert, Lajos Boros, Sándor Farkas, Péter Finy, Gergely Kutszegi, Viktor Papp (all Budapest, Hungary), Andrej Piltaver (Dol pri Ljubljani, Slovenia), and Armin Mešić (Zagreb, Croatia). We cordially thank Matthew Barrett (Kings Park, Perth, Western Australia) for providing us his sequence of *P. fenzlii* from Australia and curators of TNS herbarium (Tsukuba, Japan) for loan of their *P. fenzlii* collection.

The study of Jan Holec and Martin Kříž was financially supported by Ministry of Culture of the Czech Republic (DKRVO 2017/08, National Museum, 00023272). The research of Vladimír Kunca was financially supported by the Scientific Grant Agency of the Ministry of Education, Science, Research and Sport of the Slovak Republic (VEGA 1/0664/17). The study of Hana Ševčíková was enabled by support provided to the Moravian Museum by the Ministry of Culture of the Czech Republic as a part of its long-term conceptual development programme for research institutions (DKRVO MK000094862).

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(Manuscript accepted 14 December 2017; Corresponding Editor: I. Krisai-Greilhuber)