

Noteworthy record of *Gymnopilus stabilis* (Fungi, Agaricales) from a burnt area after a great fire in Bohemian Switzerland National Park, Czech Republic

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A new record of the rare agaric species *Gymnopilus stabilis* from the Czech Republic is described morphologically and genetically. The basidiomata show good agreement with the recently published epitype and diagnostic characters of the species. While the robustness of the basidiomata, the presence of a pink hue, and a distinct sweetish aromatic smell are typical characters, though not always present, the predominantly warm orange colour of adult pilei seems to be stable character. The combination of fleshy basidiomata and typical pileus colour distinguishes *G. stabilis* from *G. penetrans/hybridus* and *G. decipiens*, which are taxa sometimes confused with *G. stabilis*. Comparison of the nearest ITS rDNA sequences from GenBank confirmed the identity of our record and showed that the species is distributed not only in Europe and Siberia, but also in Pakistan and India. The ecological characterisation of *G. stabilis* is updated, showing that it is a saprotrophic species on dead wood of conifers, both *Pinus* and *Picea*, but also a facultative anthracophilous fungus able to grow on burnt wood and ash.

Key words: Basidiomycota, Hymenogastraceae, morphology, ITS rDNA, taxonomy, ecology, distribution.

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Nový nález vzácného druhu lupenaté houby *Gymnopilus stabilis* z České republiky je popsán morfologicky a molekulárně. Plodnice vykazují dobrou shodu s nedávno publikovaným epitypem a diagnostickými znaky druhu. Zatímco robustnost plodnic, přítomnost růžového odstínu a zřetelná nasládlá aromatická vůně jsou typické, ale ne vždy přítomné znaky, převládající teple oranžová barva dospělých klobouků se zdá být stabilním znakem. Kombinace masitých plodnic a typické barvy klobouku odlišuje *G. stabilis* od druhů *G. penetrans/hybridus* a *G. decipiens*, jejichž jména se někdy mylně používají pro *G. stabilis*. Porovnání nejbližších sekvencí ITS rDNA z GenBank potvrdilo

identitu našeho nálezu a ukázalo, že druh je rozšířen nejen v Evropě a na Sibiři, ale také v Pákistánu a Indii. Ekologická charakteristika *G. stabilis* je inovována tak, že se jedná o saprotrofní druh na odumřelém dřevě jehličnanů, jak borovice, tak smrku, ale také o fakultativně antrakofilní druh schopný růst na spáleném dřevě a popelu.

INTRODUCTION

The taxonomy of the agaricoid genus *Gymnopilus* P. Karst. (*Basidiomycota*; traditionally *Cortinariaceae*, then *Strophariaceae*, now *Hymenogastraceae* according to Kalichman et al. 2020) has recently been summarised by Holec et al. (2022), showing that in spite of the great progress connected with the use of molecular methods in the last three decades, the delimitation of many species still remains unclear. The best way to improve this is a morphological and molecular-genetical study of a large number of well-documented collections from different parts of the world, followed by a critical selection of diagnostic characters and fixing the species name by typification, either using existing holotypes or by designation of a neotype or epitype for older taxa lacking a well-preserved type material.

The species *Gymnopilus stabilis* (Weinm.) Kühner et Romagn. ex Bon, described from Europe (Weinmann 1836), has already passed through this process (Holec et al. 2022). It is characterised by robust, firm and thick-fleshed basidiomata covered by a white to creamy cobwebby to silky general veil when young; a yellow-ochre, ochre-orange to orange-brown pileus, a thick stipe (10 mm and more) and a conspicuous aromatic smell. However, its basidiomata are found so rarely that each additional collection can contribute to the understanding of its morphological and genetic variability and to a better designation of its key characters. We found the species accidentally in 2023 during a detailed survey of a burnt site after a great forest fire in Bohemian Switzerland National Park (České Švýcarsko), Czech Republic in summer 2022 (Kudláčková et al. 2024). In this article, we provide detailed information on the morphology, anatomy, ITS DNA sequence and ecology of this collection. The record is further compared with similar finds from around the world. The aim is to improve our insight into the variability, taxonomy, ecology and distribution of *Gymnopilus stabilis*.

MATERIAL AND METHODS

Morphology. The description of macromorphological characters is based on fresh basidiomata. Micromorphological characters of dried material were studied by J. Holec in a 5% KOH solution using an Olympus BX 43 microscope with high-quality planapochromatic oil immersion lens (magnification 1000×), based on 20 randomly selected spores and 5 cells for basidia, cystidia, etc. All structures were measured directly under the microscope using an eyepiece micrometer. Basidia were measured without sterigmata, basidiospores without ornamentation. Spore size is presented as

the main data range (10–90 percentile values), flanked by limit values in parentheses, of all spores measured. Q = quotient of length and width in any one basidiospore, Q_{av} = mean of basidiospore Q values. L = number of lamellae reaching the stipe, l = number of lamellulae between each pair of lamellae. Morphological terminology follows Vellinga (1988). Voucher specimen is deposited in the Mycological Department of the National Museum, Prague (herbarium PRM).

Molecular genetic study. For chromosomal DNA extraction, an extraction buffer with cetyltrimethylammonium bromide (CTAB) was used. The buffer was freshly prepared according to the CSH Protocols published by the Cold Spring Harbor Laboratory Press (cshprotocols.cshlp.org; doi.org/10.1101/pdb.rec11984). A small amount (1–5 mg) of the dried basidioma was disrupted using a Dremel rotary tool with a diamond wheel point (∅ 1.5 mm) for 1 min at 12,000 rpm. The crude extract of chromosomal DNA was purified using the High Pure PCR Template Preparation Kit (Roche Diagnostics, Mannheim, Germany). Because of the high amounts of inhibitors (secondary metabolites, proteins, polysaccharides, polyphenolic compounds, etc.) in fungal fruit bodies, the washing step with Inhibitor Removal Buffer was repeated twice. Quality and quantity of the DNA extracts were checked with agarose gel electrophoresis. The amplification and sequencing reactions of the ITS rDNA region were performed with the primer set ITS1F and ITS4 (White et al. 1990, Gardes et Bruns 1993) under the usual ITS PCR conditions. The purified PCR product was sequenced from both directions with the primers mentioned above using BigDye fluorescent chemistry (Applied Biosystems, Foster City, USA) on an ABI PRISM 3130xl genetic analyser (Applied Biosystems). All reactions were carried out at the Centre of DNA Sequencing at the Institute of Microbiology of the Czech Academy of Sciences, Prague (IM CAS). The generated sequences were edited in Geneious Prime software (version 2024.0.3, Biomatters, Auckland, New Zealand) and compared with the eight most similar ITS sequences of *Gymnopilus stabilis* available in GenBank, selected with the BLAST tool (Altschul et al. 1990). The threshold was similarity over 99% and included the epitype of the species designated by Holec et al. (2022). Comparison of these sequences was performed by means of aligning using Geneious alignment algorithms included in Geneious Prime (version 2024.0.3, Biomatters).

RESULTS

Gymnopilus stabilis (Weinm.) Kühner et Romagn. ex Bon, Doc. Mycol. 16 (no. 61): 16, 1985 Figs 1–3

= *Agaricus stabilis* Weinm., Hymen. Gasteromyc.: 210, 1836

Morphology and ecology

Macromorphology. The description is based on one record (see Collection studied) consisting of three mature basidiomata growing in a group, two of them fused at the base, found after rain and light frosts. *Pileus* 45–70 mm, fleshy, convex with broad umbo and inflexed margin, veil almost indistinct, probably washed off by rain, present only at margin as fine, whitish, cobwebbed fibrils, surface smooth, not slimy, slightly hygrophanously marbled, warmly orange-ochre ('apricot'), towards margin paler and more yellow. *Lamellae* moderately dense, L = 56–60, l = 1–3, about 5 mm high, slightly ventricose, adnate with decurrent tooth, warmly ochre-yellow, at maturing rusty yellow, edge slightly and



Fig. 1 (above), Fig. 2 (below). *Gymnopilus stabilis*, Černý důl valley, Czech Republic (PRM 960872, for details see Collection studied). Fresh basidiomata in situ, just removed from substrate. The white coating on the surface of the pilei in Fig. 1 is not the pileus colour, but hoarfrost formed by morning frost. On the pileus margins in Fig. 2, whitish fibrillose remains of the cobwebby veil can be seen. Photo J. Holec.

irregularly undulate, concolorous. Stipe 60–70 mm long, cylindrical and 8–11 mm broad in upper half, subclavate and 16–20 mm wide towards base, dry, mat, pale to deep yellow but yellow-ochre towards base, in the upper part with indistinct ring-like cortina, below it covered by yellowish whitish velvety fibrils with pinkish tinge. Context pale yellow in pileus, watery orange-yellow under pileipellis, deep yellow to rusty yellow-ochre in stipe. Taste neutral at first, distinctly bitter after about 30 seconds. Smell fine and sweetish aromatic-fruity in lamellae, more distinct in context when cut, sweetly cocoa, just like in some *Hebeloma* species. Spore print rusty.

Micromorphology. Basidiospores (7.5)8.0–8.5(9.0) × 5.0–5.5 μm, Q = 1.5–1.7, Qav = 1.59, ellipsoid to ellipsoid-amygdaliform, some with slight suprahilar depression in side view, basically yellow-ochre but finally rusty brown with very distinct ornamentation, verrucose to verrucose-rugulose, individual verrucae irregular, 0.5–2.0 μm long and about 0.5 μm high. Basidia 23–26 × 7–8 μm, cylindrical to clavate-cylindrical, with median constriction and attenuated base, 4-spored. Basidioles 18–21 × 7–8 μm, cylindrical to narrowly clavate. Lamellae edge heterogeneous, composed mostly of cystidia, but also basidia, basidioles, and cylindrical hyphidia 3–4 μm wide. Cheilocystidia 28–40 × 6–9(10) μm, cylindrical to narrowly lageniform, rarely utriform, mostly subcapitate to capitate with globose head 6–10(11) μm broad, thin-walled, wall yellow, interior hyaline or with homogeneous or granular yellow-rusty pigmentation. Pleurocystidia not observed. Lamellae trama regular, consisting of parallel to subparallel hyphae 2–12 μm wide, cells hyaline with pale yellow wall. Pileipellis (in section) a yellow-brown to rusty brown cutis of densely arranged parallel to subparallel hyphae 2.5–7.0 μm wide, coarsely rusty brown encrusted, covered by a thin, pale yellow, slightly gelatinous layer of subparallel to interwoven hyphae 2–7(9) μm wide, mostly hyaline, with yellow membranal or intracellular pigment, some also encrusted, forming a sparse net when seen from above (in scalp), terminal cells narrowly clavate, up to 11 μm wide. Pileocystidia not observed. Stipitipellis very similar to pileipellis, also 2-layered, but upper pale layer not gelatinous, made up of densely arranged parallel to subparallel hyphae, in places covered by nests of densely arranged, interwoven, mostly upwardly directed, arcuate, rusty brown encrusted hyphae, with narrowly clavate terminal cells up to 11 μm wide. Caulocystidia not observed. Veil cells not studied (veil almost completely washed off by rain). Clamp connections present in all tissues.

Substrate. On burnt wood chips and ash of *Picea abies*, among the pyrophilous moss *Funaria hygrometrica*, 16 months after the fire (see next paragraph).

Habitat. Burnt clearing after man-made *Picea abies* forest. Based on time-lapse aerial photographs available at www.mapy.cz, the original man-made spruce

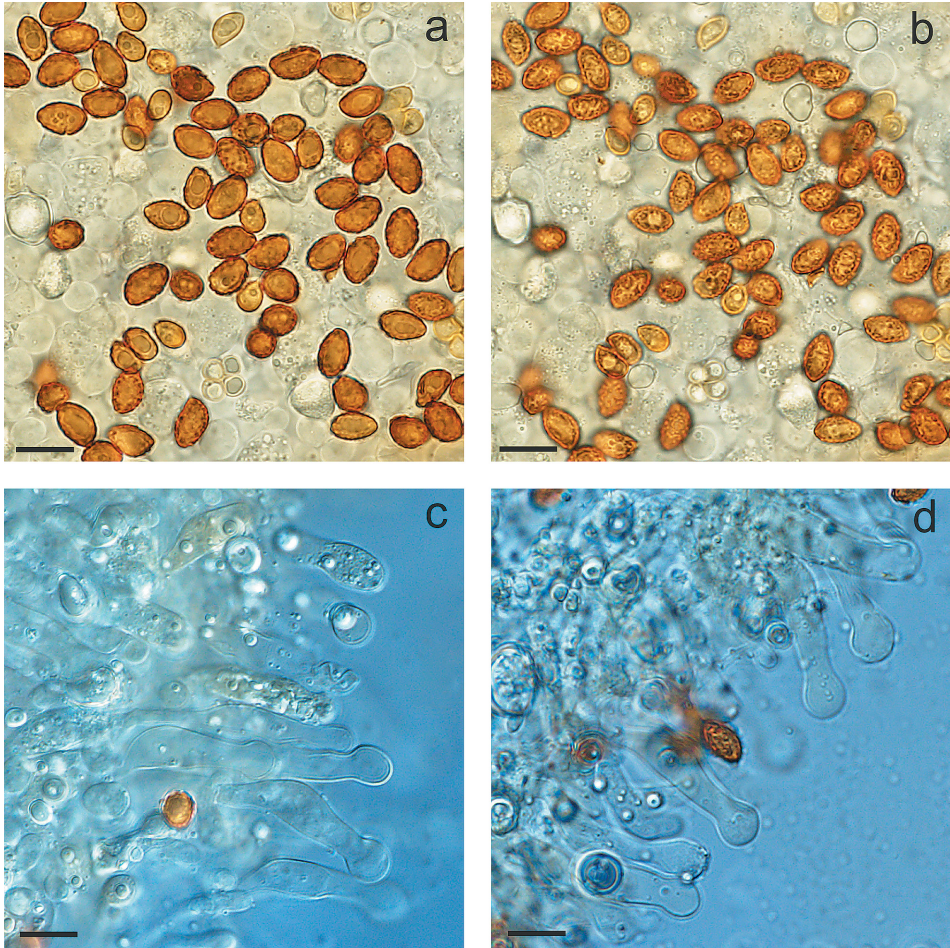


Fig. 3. Micromorphological characters of *Gymnopilus stabilis*, Černý důl valley, Czech Republic (PRM 960872, for details see Collection studied). **a** – basidiospores, outline; **b** – basidiospores, ornamentation; **c**, **d** – cheilocystidia. Scale bars = 10 μ m. Photo J. Holec.

forest was destroyed by bark beetle sometime after 2015, then completely felled by summer 2019, and finally destroyed by fire at the turn of July and August 2022 during the greatest fire in the modern history of the area (e.g. Boháč et Drápela 2023, Kudláčková et al. 2024).

Collection studied

Czech Republic. Northern Bohemia, Bohemian Switzerland National Park, ca 4 km E of the village of Hřensko, Černý důl valley, 250 m a.s.l., 50°52'46.0" N, 14°18'10.7" E, 22 Nov 2023 leg. J. Holec, det. J. Holec et P. Zehnálek, JH 149/2023 (PRM 960872).

Molecular genetic study

The single sequence received (GenBank no. PP732200) with a length of 528 bp was obtained from the forward read (primer ITS1F). The reversed read (primer ITS4) lacked sufficient quality. The obtained sequence differs from the epitype sequence (Holec et al. 2022: MW750182) in two substitutions (transitions). Differences from other nearest sequences (BLAST search, see Methods) are quantified in Tab. 1. For completeness, we also include a comparison of all selected sequences against the epitype (Tab. 1, last column). They differ from the epitype in 0–4 bp (0.00–0.65%) except for the USA sequence MT371762 (7 bp, 1.02%).

DISCUSSION

Morphology

Holec et al. (2022) delimited *Gymnopilus stabilis* based on morphological and phylogenetic analysis and fixed the name by epitype designation using a collection from the Czech Republic. Most of the diagnostic characters are present in the collection described here: thick-fleshed basidiomata with remains of whitish cobwebby general veil on pileus margin and stipe surface, pileus with a predominant orange colour, rather distinct smell, in our case sweetish aromatic with fruity and cocoa admixture. Although the basidiomata were smaller than usually reported for this species, we tentatively identified them to be *G. stabilis* already in the field based on the mentioned characters, which was confirmed by subsequent analyses. We were mainly guided by the robustness of the basidiomata, the warm (apricot) pileus colour and the pink (salmon) tinge of the veil remains. This pink tinge seems to be a characteristic feature of the species, being observed either in flesh (Holec et al. 2022), or, as in the described collection, on veil remains. However, while the size of the basidiomata, the presence of a pink hue, and the distinct smell are characters that (even if typical) are not evident in all collections of *G. stabilis*, the predominant warm orange colour of the adult pilei seems to be a stable character.

Microscopically, the collection described here agrees in most characters with the collections studied by Holec et al. (2022). This applies in particular to the size and appearance of the spores, which fall within the ‘diagnostic’ range (7–9 × 4–5.5 µm) and have a typical, distinctly verrucose to rugulose-verrucose ornamentation. The only major difference is the presence of a slightly gelatinous layer on the pileus surface. It is possible that this layer was more prominent before the basidiomata were collected due to wet weather. In any case, this is not a character questioning the identity of the collection. In addition, caulocystidia rarely observed by Holec et al. (2022) were absent in the collection described here.

Tab. 1. Sequences discussed in this paper. The newly generated sequence is in bold. Species names in quotation marks indicate original identification as given in GenBank, which in many cases has been corrected here or in a previous publication (Holec et al. 2022). These revisions are shown in brackets.

Species name	Voucher	Sequence accession number (GenBank)	Country, locality (if given)	Sequenced by	Reference	Length of compared sequence, difference from PP732200 in bp (with %)	Length of compared sequence, difference from the EPTYPE in bp (with %)
<i>G. stabilis</i>	PRM 960872	PP732200	Czech Rep., Černý úhl	Felsberg J. in IM CAS	this paper	–	528 bp, 2 substitutions (0.38%)
<i>G. stabilis</i> EPTYPE	PRM 954258	MW750182	Czech Rep., Písty, Písečný přesp	Holec J. et al.	Holec et al. (2022)	528 bp, 2 substitutions (0.38%)	–
<i>G. stabilis</i>	STU 403802 = SMNS-STU-F. 0900412	MF039261	Germany, Neubulach	Eberhardt U. et al.	Eberhardt et al. (2018)	528 bp, 4 substitutions, 2 indels (1.14%)	683 bp, 2 substitutions, 2 indels (0.59%)
<i>G. stabilis</i>	M-0159312 (= herb. Ludwig 1106)	MW750189	Germany, Fürstenwalder Stadtluch	Holec J. et al.	Holec et al. (2022)	528 bp, no difference	683 bp, no difference
' <i>G. penetrans</i> ' (= <i>G. stabilis</i>)	4653	MH930170	Russia, Siberia, Krasnoyarsk	Vaishlya O. et al.	Holec et al. (2022: 336)	528 bp, no difference	683 bp, 1 substitution (0.15%)
' <i>G. decipiens</i> ' (= <i>G. stabilis</i>)	GYMDEC1	MH930904	India, Kashmir Himalaya	Sajad S.	unpublished	528 bp, no difference	624 bp, 3 substitutions (0.48%)
' <i>G. decipiens</i> ' (= <i>G. stabilis</i>)	RKUDNC06	OM666727	India	Mayimao H.S. et al.	unpublished	528 bp, no difference	627 bp, 3 substitutions, 1 indel (0.64%)
' <i>G. penetrans</i> ' (= <i>G. stabilis</i>)	MAK:UTK26	OR782951	Pakistan	Azeem M. et Ahmad I.	unpublished	500 bp, 1 indel (0.2%)	611 bp, 3 substitutions, 1 indel (0.65%)
<i>G. cf. stabilis</i>	ARIZ AN 043729	MT371762	USA, Apache National Forest	Clements T.A.	Clements et Fulton (2018)	528 bp, 3 substitutions (0.57%)	683 bp, 7 substitutions (1.02%)

The combination of fleshy basidiomata and a predominantly warm orange pileus distinguishes *G. stabilis* from *G. penetrans/hybridus* and *G. decipiens*, which are taxa sometimes confused with *G. stabilis* (Holec et al. 2022). Representatives of the *G. penetrans/hybridus* lineage can also produce robust fleshy basidiomata (although they are typically rather slender), but their pileus colour is yellow-ochre, ochre-brown to rusty brown, without a warm orange tinge (Holec 2005). *Gymnopilus decipiens* in its original sense (Smith 1869) and modern interpretations (e.g. Høiland 1990, Orton 1993, Ludwig 2000, 2001, Holec 2005, 2012) is a small fungus with a pileus up to 30 mm in diameter, dirty yellow-brown, rusty brown to greyish brown, fibrillose-tomentose to tomentose-scaly. However, the delimitation of *G. decipiens* is still unclear (Hughes et al. 2020, Holec et al. 2022).

Interestingly, both typical *G. penetrans* and a fungus corresponding to the aforementioned characteristics of *G. decipiens* occur on burnt substrates in the Černý důl gorge. We can state with certainty that their basidiomata look completely different than the described collection of *G. stabilis*.

Molecular genetic study

We do not include a phylogram in this article, because it would differ from our previously published tree-graph (Holec et al. 2022) only by four newly obtained sequences of *G. stabilis*, not by its topology.

The described collection shows full identity or very high ITS sequence similarity (99.62%) to three *Gymnopilus stabilis* collections mentioned by Holec et al. (2022: MW750189, MH930170, MW750182), including the epitype. Two sequences from India, newly added to GenBank and labelled *G. decipiens*, are also 100% identical (OM666727, MH930904). To verify if the sequenced basidiomata represent the robust fungus (*G. stabilis*) or the small one (*G. decipiens* group, see above), we contacted the authors/teams mentioned in GenBank. Unfortunately, they did not reply. However, the ITS rDNA identity with our sequence and high similarity with the epitype sequence (99.36% and 99.52%, respectively) show that they represent *G. stabilis*.

The *G. stabilis* sequence MF039261 (Neubulach, Germany) comes close to the epitype (Tab. 1) but is rather far from the sequence described here (difference in 6 bp, 1.14%). This could mean that within the range of the variability of *G. stabilis*, the Neubulach collection probably stands on the opposite side of the collection that we studied.

Sequence OR782951 labelled *G. penetrans* was obtained from a Pakistani collection. It shows a similarity of 99.80% to the sequence published here and 99.35% to the epitype. However, the sequence is shorter and the comparison is based on only 500 bp and 611 bp long parts, respectively (Tab. 1). One of its authors, I. Ahmad, kindly sent us a photograph of his find. The basidiomata are rather old

and partly dried (without veil, possessing raised pilei margins and a pileipellis disrupted by dryness), but show the typical robustness of *G. stabilis* and traces of orange colour at pileus centre. They are definitely closer in appearance to *G. stabilis* than to typical *G. penetrans*. We believe that this collection can also be identified as *G. stabilis*.

The American sequence MT371762, formerly labelled *G. cf. decipiens* in GenBank, is currently labelled *G. cf. stabilis* (GenBank) or considered a member of the *G. stabilis* lineage (Holec et al. 2022, <https://mushroomobserver.org/observations/327185>). Due to a lack of detailed morphological data and difference of 1.02% from the epitype (Tab. 1), it cannot be considered a true *G. stabilis*. It is perhaps its American sibling species, not yet described. The smaller difference from the sequence published here (Tab. 1: last line) has a methodological reason (missing part of the ITS1).

All other GenBank sequences have a BLAST similarity lower than 99%. In agreement with this, they are mostly labelled by other names than *G. stabilis* (*G. penetrans*, *G. sapineus*, *Gymnopilus* sp., but also *G. turficola*, *G. decipiens*, *G. odini*, i.e. species of the *G. sapineus* clade sensu Moser et al. 2001 and Holec et al. 2022). Generally, *Gymnopilus* species have relatively low divergence in the ITS rDNA region (Moser et al. 2001, Holec et al. 2022), which makes it difficult distinguish them on a molecular-genetic basis.

Ecology and distribution

Most of the reliable finds of *G. stabilis* come from “forests or sand dunes populated by pine. Basidiomata occur either on pine wood or on soil, however, it is likely that mycelium might grow in buried wood” (Holec et al. 2022). Our collection originates from a burnt area created by a great forest fire, growing on charcoal and ash from stumps and roots of *Picea abies* on a former clearing. However, records of *G. stabilis* from environments affected by fire are also known (Holec et al. 2022), see e.g. the epitype collection (where fire is indicated by the co-occurring *Pholiota highlandensis*) or the macro- and micromorphologically perfectly fitting record by Galeotti et Lezzi (2020: “growing on stumps and at the base of trunks, saprophytic on coniferous wood, typically in an environment with forest fires, often associated with *Pholiota h.*”). In summary, *G. stabilis* is a saprotrophic species on dead wood of conifers, both *Pinus* and *Picea*, also a facultative anthracophilous species able to grow on burnt wood and ash. Finds from deciduous forests (Kühner et Romagnesi 1957, Bon et Roux 2002) are debatable because their identity has not been verified molecular-genetically.

The Pakistani and Indian records/sequences (see previous section) extend our knowledge of the distribution range of *G. stabilis* to South Asia. The occurrence in North Asia is documented by a sequenced collection from Krasnoyarsk,

Siberia (Holec et al. 2022: MH930170). According to the current state of knowledge, *G. stabilis* appears to be a Eurasian species.

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