

Surprising discovery of *Sedecula pulvinata* in Central Europe – is it really a species endemic to the western USA?

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Sedecula pulvinata (Basidiomycota: Boletales) is a hypogeous fungus reported as a rare and endemic species in the dry conifer forests of the western United States. Surprisingly, fruitbodies found in the Czech Republic, Central Europe, in 2011 match this species based on ITS rDNA sequences (99.3% sequence similarity) and morphology. Additional records attributable to this species based on sequence similarity were found in the GlobalFungi database of environmental metabarcoding data. This search expands the currently known geographical range in the western USA and adds new records from one Canadian and one Pakistani environmental DNA soil sample. These records challenge the assumption of its endemism in the western United States. The European find, along with some from the USA and one from Canada, which significantly differ in habitat, suggests a broader ecological flexibility of this species. Further investigations are needed to determine the relationships between North American and European populations. Additionally, historical records and potential synonymy with other fungal species from Europe warrant further research into the taxonomy and systematics of this genus and related taxa.

Key words: hypogeous fungi, endemism, *Boletales*, ecology, distribution, GlobalFungi.

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Valda S., Kolařík M. (2024): Překvapivý objev *Sedecula pulvinata* ve střední Evropě – je to skutečně endemický druh západních Spojených států? – Czech Mycol. 76(1): 33–44.

Sedecula pulvinata (Basidiomycota: Boletales) je podzemní houba, která byla známa jako vzácný a endemický druh v suchých jehličnatých lesích západních Spojených států. V roce 2011 byly překvapivě nalezeny plodnice v České republice, ve střední Evropě, které tomuto druhu odpovídají na základě sekvencí ITS rDNA (99.3% podobnost) a morfologie. Další nálezy, které lze připsat tomuto druhu na základě podobnosti sekvencí, byly nalezeny v GlobalFungi, databázi environmentálních dat z metabarcodingu. Výsledky hledání rozšiřují současný známý areál na západě USA a přidávají nové nálezy z environmentální DNA z jednoho kanadského a jednoho pákistánského vzorku půdy. Tyto nálezy kladou otazník nad předpokladem, že je tento druh endemický v západních Spojených státech. Evropský nález, stejně jako nálezy z Kanady a některých lokalit v USA, jejichž stanoviště se značně liší od dosavadních lokalit, naznačuje širší ekologickou flexibilitu tohoto druhu. Další výzkumy

budou potřebné k určení vztahů mezi severoamerickými a evropskými populacemi. Navíc historické záznamy a možné synonymie s jinými druhy hub z Evropy vyžadují další výzkum v oblasti taxonomie a systematiky tohoto rodu a jemu příbuzných taxonů.

INTRODUCTION

Sedecula Zeller (*Basidiomycota: Boletales*) is a monotypic genus of hypogeous fungi which significantly differs in its characteristics from other genera with underground or semi-subterranean fruitbodies (Zeller 1941, 1948, 1949). The only known species, *Sedecula pulvinata* Zeller, has been reported as a rare and endemic species in the dry conifer forests of the western United States. *Sedecula pulvinata* has been associated with conifers of the genera *Abies*, *Picea* and *Pinus* (Castellano et al. 1999). Phylogenetically, it is related to the genus *Coniophora* DC. within *Coniophoraceae* and represents a unique morphological transition between resupinate basidiocarp morphology (found in *Coniophora* and relatives) and hypogeous, sequestrate basidiocarp morphology (Trappe et al. 2015). Stable isotope analysis of nitrogen and carbon ratios in the fruitbodies has shown that *Sedecula* nutrition does not occur through mycorrhizal associations as is typical of most underground fungi, but rather through saprotrophic means, similar to the closely related genus *Coniophora* (Trappe et al. 2015).

During a particularly dry period in the summer of 2011, S. Valda found three fruitbodies in the Czech Republic, which were later identified as *S. pulvinata* based on morphology and ITS rDNA sequences. This marks the first record of this species outside its presumed distribution range in the western United States. This article provides a description of the discovered fruitbodies, their habitat, and a brief discussion on possible historical records of this taxon in Europe. Furthermore, we used the GlobalFungi database to search for this fungus in environmental DNA samples.

MATERIAL AND METHODS

Fungal material was collected on 19 June 2011 by S. Valda, at Milovická stráň, Pálava Protected Landscape Area, southern Moravia, Czech Republic (48°50'55.5" N, 16°41'35.2" E, elev. 220–250 m). The habitat is classified (Chytrý et al. 2010) as Pannonian woods with *Quercus pubescens* (91H0), featuring a layer of leaf litter and humus under *Quercus robur*, *Fraxinus excelsior*, and *Cornus mas*. The specimen is deposited in the National Museum, Prague under PRM 960012.

Microscopic features were examined in water, Melzer's reagent, lactophenol with Cotton Blue, 10% ammonia solution with Congo Red and 5% KOH solution with Congo Red at 1000× magnification under an oil immersion lens using an Olympus BX 43 microscope. For each fruitbody, 50 randomly selected spores and 10 other structures were measured in 5% KOH directly under the microscope using an eyepiece micrometer. For spores, the values are given as minimum, median range across three studied fruitbodies, and maximum value.

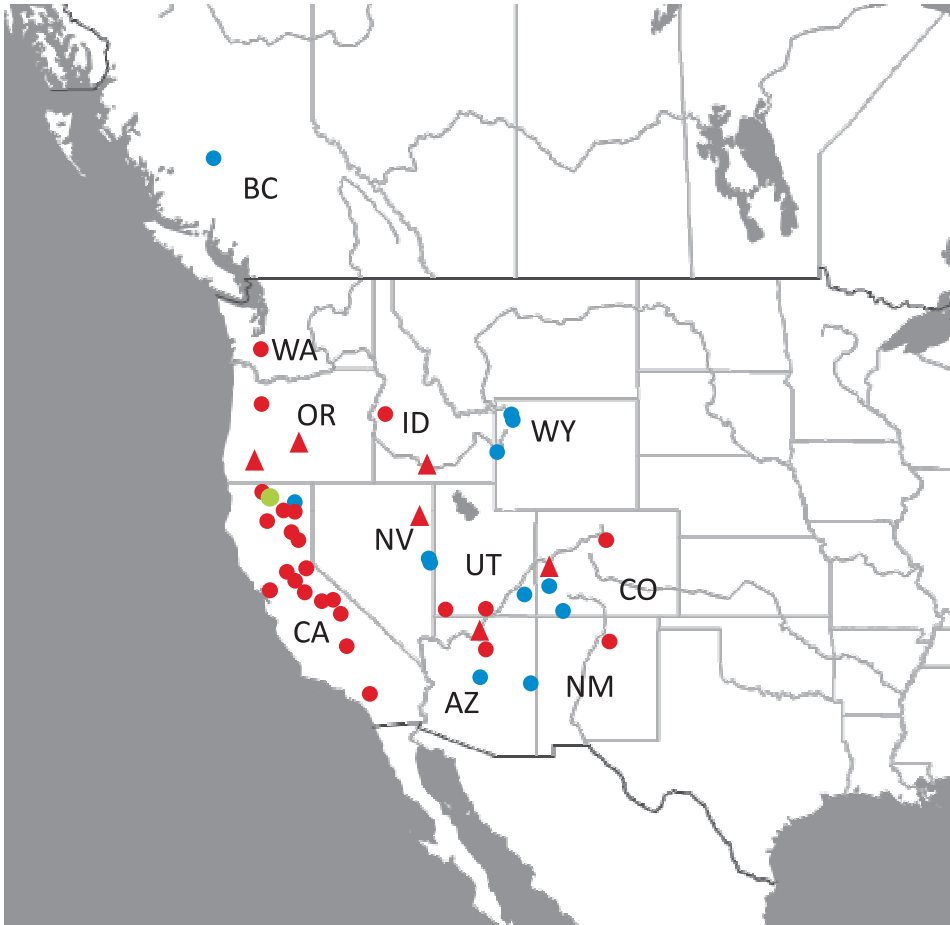


Fig. 1. Map of *Sedecula pulvinata* distribution in North America based on GlobalFungi (blue dots) and field collections (red and green dots). Observations from field collections are taken from Castellano et al. (1999), Trappe et al. (2015), Siegel et al. (2019), and references therein. Triangle symbols indicate locations for which exact coordinates were not provided. The type locality is marked in green. The other two locations represent the Czech Republic and Pakistan (see Results).

ITS rDNA sequences were obtained from the fruitbody using ITS1 and ITS4 primers following the method by Kolařík et al. (2021), and the complete ITS region sequence was deposited in the NCBI GenBank database under accession number PP140383. The distribution in published environmental DNA data was determined using the GlobalFungi database Release 5 (globalfungi.org) following the procedure described by Réblová et al. (2022). The search was particularly conducted using separate ITS1 and ITS2 spacers through the Exact hit and BlastN functions. Haplotypes from our collection and GenBank accession no. KJ882287 were used for the search. The current geographical distribution, based on field collections (Fig. 1), is derived from localities mentioned by Castellano et al. (1999), Trappe et al. (2015), and Siegel et al. (2019). Additionally, the Mycology Collections Data Portal

(Anonymus on-line) contained 63 *S. pulvinata* entries, but these entries did not expand the geographical area covered by the three aforementioned studies and were not used further.

The phylogenetic relationships of all published *S. pulvinata* sequences (USA), Czech sequences, and short reads (ITS2) from the GlobalFungi database (USA, Pakistan, Canada) (Tabs 1, 2) were studied using the Maximum likelihood (ML) method. The sequence alignment was performed in MAFFT 6 using the G-INS-i strategy (Katoch et Standley 2013). ML analysis was performed in PhyML 3.1. (Guindon et al. 2010) using 1000 bootstrap replicates, the GTR substitution model, and default settings. *Coniophora* species, known as a sister to *Sedecula* (Trappe et al. 2015), were used as an outgroup. The alignment had 11 sequences, 593 sites, 59 variables, and 8 singletons.

Tab. 1. *Sedecula pulvinata* sequences obtained from vouchers and used in the phylogenetic analysis.

Sequence accession	Voucher	Location	Reference
KJ882286	MICH 26633	Boulder, Colorado, USA	Trappe et al. (2015)
KJ882285	MICH 26608	Washington, Utah, USA	Trappe et al. (2015)
KF021224	OSC 39125	Yuba Pass, California, USA	Frank J.L. et Trappe M.J., unpubl.
KF021225	OSC 39125	Yuba Pass, California, USA	Frank J.L. et Trappe M.J., unpubl.
KJ882287	MICH 67760	San Miguel, New Mexico, USA	Trappe et al. (2015)

Tab. 2. Records of *Sedecula pulvinata* found in the GlobalFungi database based on 99.0–100% sequence similarity. The localities are shown in Fig. 1, and the phylogenetic position of the ITS2 sequences obtained from these samples is depicted in Fig. 2. The linkage between sample numbers and ITS2 sequences is apparent from Fig. 2.

Location	Longitude, latitude	Elevation (m)	SampleID	Habitat	Reference
Canada, British Columbia, Teardrop Muskeg Road, Prince George	-123.267, 54.3333	852	3753	boreal coniferous forest dominated by <i>Picea glauca</i> × <i>engelmannii</i> and <i>Pinus contorta</i>	Sukdeo et al. (2018)
Pakistan, Naltar Valley	74.11, 36.22	3282	59674	montane coniferous forests	Tedersoo et al. (2021)
USA, Arizona, Oak Creek	-111.736, 35.0241	1723	20478	forest with <i>Populus angustifolia</i>	Van Nuland et al. (2021)
USA, Arizona, Blue River	-109.087, 33.668	1830	36509	forest with <i>Populus angustifolia</i>	Van Nuland et al. (2021)
USA, California, Adin	-120.9, 41.08	1390	50943	forest with <i>Populus angustifolia</i>	Tedersoo et al. (2021)
USA, Colorado, San Juan River	-107.139, 37.049	1944	6626	forest with <i>Populus angustifolia</i>	Van Nuland et al. (2021)
USA, Colorado, San Juan River	-106.885, 37.4602	2738	7145	forest with <i>Populus angustifolia</i>	Van Nuland et al. (2021)
USA, Colorado, San Miguel River	-108.15, 38.0557	2113	12406	forest with <i>Populus angustifolia</i>	Van Nuland et al. (2021)
USA, Nevada	-114.131, 38.9191	1881	13766	forest with <i>Populus angustifolia</i>	Van Nuland et al. (2021)
USA, Nevada	-114.175, 38.8638	2121	34860	forest with <i>Populus angustifolia</i>	Van Nuland et al. (2021)
USA, Nevada	-114.083, 38.9232	1713	13540	forest with <i>Populus angustifolia</i>	Van Nuland et al. (2021)
USA, Wyoming	-110.002, 44.4899	2118	23202	forest with <i>Populus angustifolia</i>	Van Nuland et al. (2021)
USA, Wyoming	-110.583, 43.6405	2053	6690	forest with <i>Populus angustifolia</i>	Van Nuland et al. (2021)
USA, Wyoming, Snake River	-110.984, 43.1786	1755	31231	forest with <i>Populus angustifolia</i>	Van Nuland et al. (2021)
USA, Wyoming	-109.625, 44.4669	1814	7566	forest with <i>Populus angustifolia</i>	Van Nuland et al. (2021)

RESULTS

Molecular analysis

Comparison with published DNA data was problematic due to the variable length of ITS sequences from previous studies. The Czech sequence showed a similarity of 98.9–99.3% with various reference vouchers of *S. pulvinata*, specifically voucher MICH 67760 (GenBank accession no. KJ882287, 537/543 bp), MICH 26608 (KJ882285, 270/272 bp), OSC 39125 (KF021225, 286/288 bp), MICH 26633 (KJ882286, 267/272 bp). Other best hits exhibited a similarity below 89% (*Coniophora cystidiophora* CBS 153.33, MH855390).

Global distribution of *S. pulvinata* was studied using separated ITS1 and ITS2 spacers in the GlobalFungi database. Based on ITS2, ten amplicon sequence variants with a similarity of 99.0–100% to KJ882287, originating from 17 samples,

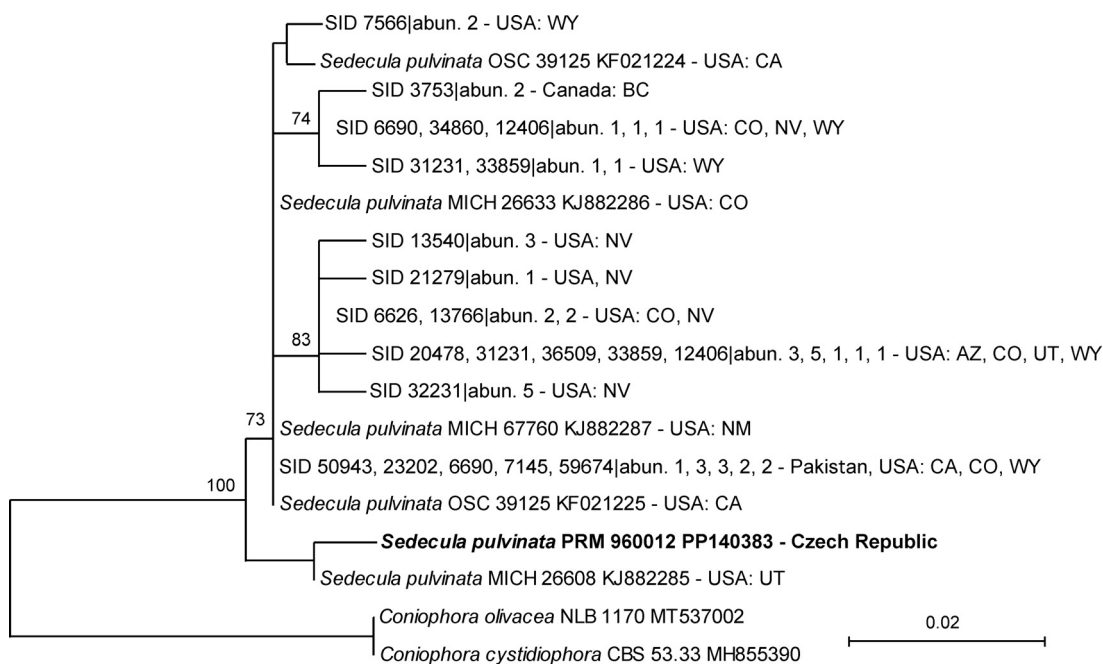


Fig. 2. Maximum likelihood tree of *Sedecula pulvinata* based on the ITS region showing relatedness of the Czech specimen, other collections and environmental sequences from GlobalFungi. Bootstrap values ≥ 50 from 1000 replicates are shown. The tree is unrooted and the branch leading to the outgroup (*Coniophora*) was reduced to half. Sequence labels of ITS2 short reads from GlobalFungi database contain sample codes (SID) and information about the number of observed reads in a particular sample (abundance). Details of the sequences and samples are provided in Tabs 1 and 2.

were found. They originated from Canada, USA and Pakistan (Tab. 2, Fig. 1). The next closest hit was 94.6%. Based on the ITS1 marker, two hits of 99.0–100% similarity to KJ882287 were found. They originated from the samples already identified by the ITS2 marker. Phylogenetically, sequences from the USA, Canada, and the Czech Republic form a well-supported (bootstrap support, BS 100%) group within which no other groups are statistically better supported. The Czech entry formed a weakly (BS 48%) supported branch with specimen MICH 26633 from Colorado (Fig. 2).

Morphological features

Macroscopic description (Fig. 3). The three Czech fruitbody collections grew together in a cluster, in the upper humus layer and partially decomposed leaf litter, with only half of the largest fruitbody protruding above the surface. They reached sizes of 15 mm (youngest fruitbody), 35 mm, and 60 mm (most mature fruitbody) in diameter, respectively, and heights of 8–25 mm. The fruitbodies were irregular, flattened, cushion-shaped, growing underground to semi-underground, with their upper surface exhibiting irregularly undulated and occasionally slightly lobed areas covered by a thin cottony layer of cream to light orange-ochre mycelium. On the lower side, the fruitbodies were not covered by a false peridium (see below), and among remnants of the substrate (soil, plant roots) adhered by whitish mycelial strands, a visible exposed part of the gleba can be seen. The gleba was composed of irregularly protruding rounded ridges of a dark reddish brown to dark brown-black colour. The fruitbodies did not have a developed true peridium like other underground fungi. The cottony layer on the surface is essentially the subiculum within which an irregular basic matter of the fruitbody gradually grows in the form of veined, labyrinthically undulating, and branching thick rounded ridges growing downward, gradually merging and creating very irregular, closed or open chamber-like structures. The young fruitbodies are therefore not firm and compact. They gradually gain greater cohesion due to a thin, approximately 2–3 mm thick, sterile part of the gleba at the upper edge of the fruitbody, which eventually forms a tough shell (false peridium) covering and simultaneously holding up the fertile part of the gleba.

The subiculum is formed by a cottony layer of loosely interwoven fine hyphae penetrating the substrate. In older fruitbodies, it is compressed into a thin leathery layer on their upper side. In young fruitbodies, the subiculum has a whitish to cream colour with ochreous orange tones. In older fruitbodies veined surfaces of dark ochre to orange glebal parts are visible through this layer, especially when bruised. Occasionally, a greenish tint on the surface of the subiculum can be observed, likely due to algal growth. The gleba is composed of highly contorted and occasionally branched thick and firm ridges growing from the upper, arched edge

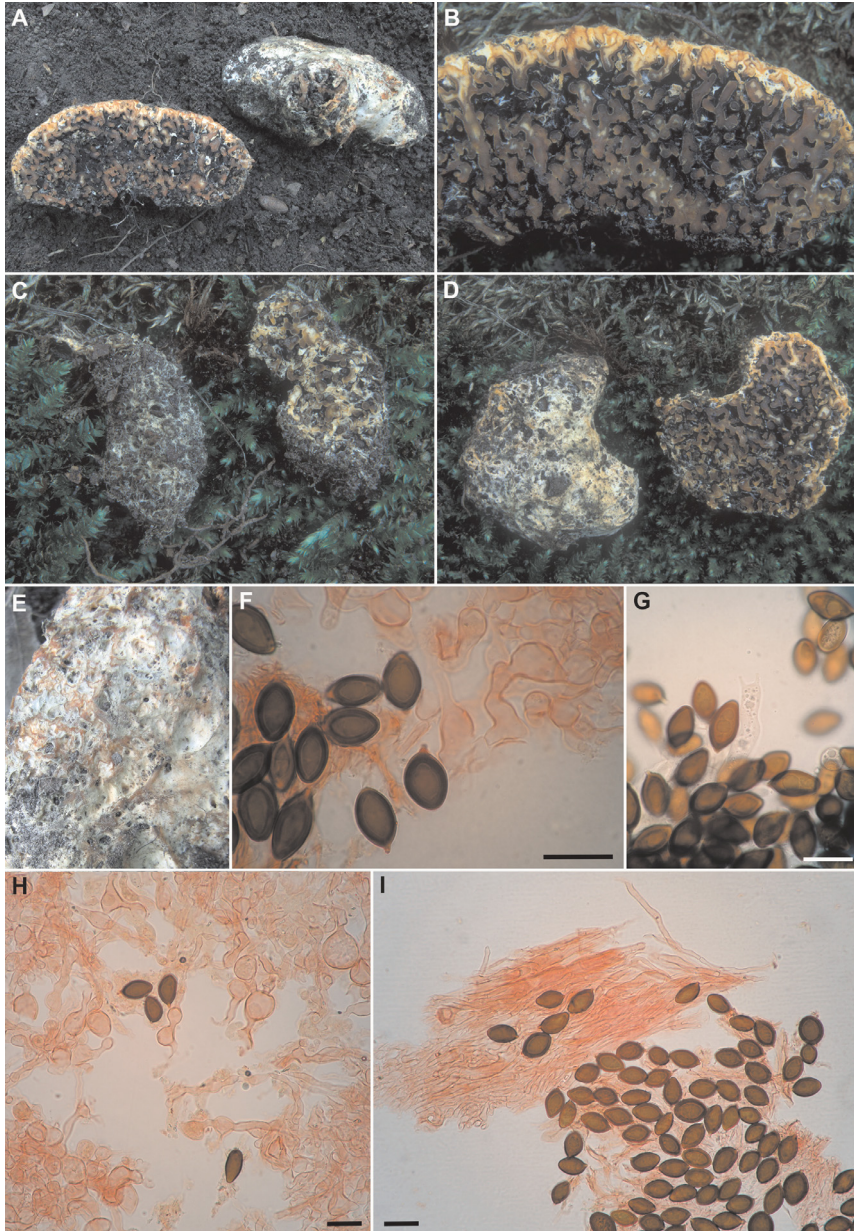


Fig. 3. Morphology of *Sedecula pulvinata* (PRM 960012). **A** - cross-section of the ripest fruitbody (in situ); **B** - detail of cross-section of the ripest fruitbody; **C** - cross-section of the youngest fruitbody (ex situ); **D** - horizontal section of moderately mature fruitbody (ex situ); **E** - detail of surface of the ripest fruitbody; **F** - spores and cells forming gleba crust in Congo Red 5% KOH; **G** - spores and bisporic basidia in water; **H, I** - spores and cells of upper peridium layer in Congo Red 5% KOH. Bars = 20 μ m. Photos S. Valda.

of the fruitbody downward, where they slightly converge. Among them, very irregular to labyrinthine thin chambers open at the base of the fruitbody, some of them possibly completely closed. The ridges (walls of the chambers) are initially light ochre to orange-yellow and gradually darken from the edge to rusty orange or dark reddish brown. Sometimes, various shades of colours from very dark at the edge to light cream in the centre are visible in cross-section. At the upper edge of the fruitbody, the walls are thinner, lighter, and more closely spaced; they are not covered by a hymenium and form a thin shell supporting the arched fertile part. The surface of the walls is covered by a dark red to blackish brown hymenium which has a velvety appearance due to the spore mass. Remnants of the whitish subiculum are sometimes enclosed in the chambers. The smell is pronounced, strangely spicy, not unpleasant. The taste has not been determined.

Microscopic description. The subiculum is composed of loosely interwoven thin-walled hyphae with a thickness of (2)3–6 μm . The hyphae are irregular, smooth, often swollen (inflated) in many places, with septa not observed. In the upper layer (towards the surface of the fruitbody), the hyphae have variously shaped terminations (tapered, club-shaped, headed, and branched), reaching a diameter of up to 14 μm . The lower layer of the subiculum is formed by irregular shorter cells (pseudoparenchyme). The gleba consists of 3–5 μm wide, loosely interwoven hyphae and irregular oval cells of various sizes (4)10–20 μm , which are occasionally irregularly swollen (inflated), reaching a diameter of 28–70 μm . Basidia consist of an irregularly cylindrical, slightly bent part with dimensions of 43–52 \times 7–10 μm , sharply transitioning into a 7–9 μm long narrowed base (stalk). They bear two prominent sterigmata measuring 5–7(9) \times 1.5 μm . In the hymenium, very numerous cylindrical basidioles, 23 \times 10–11 μm in size, are also present. They are sometimes slightly constricted in the middle and also have a stalk-like narrowed base (10 \times 3 μm). Occasionally, in the hymenium, long, narrowly cylindrical structures similar to basidioles exceeding the basidia by 5–10 μm are visible. The spores are irregularly almond-shaped, sometimes egg-shaped, rarely triangular with rounded corners, (18)20–22(23.5) \times (11.5)12–13.5(15) μm in size. At the base of the spore, often an eccentrically positioned short stalk with a hilar appendix can be observed, measuring 1.8–2 μm in width and 1–2 μm in length. In water, individual spores are yellow-brown to brown, with a dark, reddish brown, 1–2 μm thick wall. Inside the spore, one large or occasionally two smaller droplets are often visible. In Melzer's reagent, the spores have a darker rusty brown colour, while they appear very dark blue to bluish-black (cyanophilic) in cotton blue.

DISCUSSION

Comparison of European and North American collections

The European specimen exhibits a remarkable sequence similarity of over 99% in its ITS barcode, which is generally considered indicative of species identity. Despite the significant genetic similarity, certain differences are evident. The most prominent is the striking colouration of the fruitbodies, which becomes even more pronounced upon bruising or upon oxidation during cross-sectioning. The original description and photographic documentation of recent finds in the United States (Anonymus on-line) only depict a whitish to greyish colour, without any hints of ochre or even orange tones. Thiers (1977), based on his own observations, additionally reports occasional light yellow hues in the peridium of fresh, young fruitbodies in American collections. Simultaneously, he states that there is no change in colour following bruising or oxidation. Additionally, the spore length in the European collection is slightly smaller ($18\text{--}23.5 \times 11.5\text{--}15 \mu\text{m}$) compared to the measurements by Zeller (1941), which are $23\text{--}26 \times 13\text{--}16.2 \mu\text{m}$, or those mentioned by Thiers (1977), which are $(22)25.5\text{--}28.5 \times (12)13.3\text{--}14.3 \mu\text{m}$ in size. However, Trappe et al. (2015), based on a study of numerous American collections, reported a broader range of values, $(18)23\text{--}26(27) \times (12)13\text{--}16(20) \mu\text{m}$, which aligns more closely with the European collection. Consequently, we consider the European collections to be identical to the American ones, but further studies involving multiple variable genetic markers may shed more light on the relationship between these two populations. Concerning the morphology, we would like to add that there are still uncertainties about the ontogenesis of the fruitbody. As noted by Zeller (1948), the formation of *Sedecula* fruitbodies appears to be centripetal (developing from the edge towards the centre), although he did not have access to younger stages of fruitbodies to confirm this definitely. Even more recent literature, which mostly reiterates the original description of the fruitbody, lacks to mention the appearance of younger or even primordial fruitbodies.

Habitat differences

To date, *Sedecula pulvinata* is known from ca 32 locations in the western United States, specifically from dry coniferous forests at elevations around 2,000 metres above sea level. Within the USA, the presence of *S. pulvinata* has been confirmed in Arizona, California, Colorado, Nevada, and Utah, regions where this fungus is known from direct finds (Castellano et al. 1999, Trappe et al. 2015, Siegel et al. 2019). Additionally, we report several sites in Wyoming (Tab. 2, Fig. 1), calling for verification by field study. Our study has shown that its distribution and ecology may be broader, including boreal Canada, montane coniferous forests

in Pakistan, and the relatively warm part of Central Europe. In the USA, the species is known exclusively from coniferous forests, namely under *Abies concolor*, *A. lasiocarpa*, *A. magnifica*, *Picea engelmannii*, and *Pinus contorta* (Castellano et al. 1999). Nevertheless, based on our envDNA datamining, the fungus also occurs in deciduous forests dominated by *Populus angustifolia* in the USA. The soil samples were collected directly beneath *Populus angustifolia* trees during a study by Van Nuland et al. (2021) across many states (AZ, CA, CO, NV, UT, WY). This indicates that this fungus also occurs in unexpected habitats in the USA. Canadian location falls within the boreal coniferous forest biome, dominated by species of the genera *Picea* and *Pinus*. The site of the European find is located in the warm Pannonian biogeographic region, in the habitat of Pannonian woods with *Quercus pubescens*. It is at a relatively low elevation, and only deciduous trees grow there. Since *Sedecula* is not associated with any mycorrhizal partner, it may be expected to have a relatively broad ecological range.

During the fruiting of the Czech specimen, the weather was consistently moderate, with no significant temperature or precipitation extremes. The fruiting of common fungal species was rather moderate but typical of the summer season in this region. In the following years, no additional specimens were found at this location despite visits in different seasons and under varying moisture and temperature conditions.

Possible relations with old taxa

It is currently uncertain whether the occurrence of *S. pulvinata* in Europe is natural or whether it was anthropogenically introduced in the past. The mere fact that the species was first discovered and described in North America does not provide insight into its origin or possible endemism. This species may have been discovered and described in Europe earlier, and possibly multiple times. Some morphological characteristics (colour, structure) bear some resemblance to the original illustrations of *Ceratomyces fischeri* Corda (1837). Although the genus name *Ceratomyces* is now considered synonymous with several common genera of lignicolous fungi, it is mainly due to the lack of any type material available for revision. A mere comparison of Corda's illustrations could cast doubt on the assumptions of some authors (e.g. Saccardo 1888, de Seynes 1888) that *Ceratomyces fischeri* is identical to the species *Ptychogaster albus* Corda (1838), which is generally considered the anamorphic stage of *Postia ptychogaster* (F. Ludw.) Vesterh. Pilát (1927) even believed that *Ceratomyces fischeri* was synonymous with *Trametes odorata* (Wulfen) Fr., now *Gloeophyllum odoratum* (Wulfen) Imazeki. However, Donk (1960) pointed out that the species *C. fischeri* had not been identified unequivocally and satisfactorily.

Some morphological characteristics resembling those of the genus *Sedecula* are also found in the illustrations of fruitbodies of *Fibrillaria subterranea* Pers., as published by Tulasne et Tulasne (1851), who initially believed them to be the conidial form of the oak bracket fungus *Daedalea quercina* (L.) Pers. De Seynes (1888) claimed that Tulasnes' *Fibrillaria* fruitbodies belonged to Corda's genus *Ceratomyces* and specifically particularly observed similarities with the species *C. terrestris* Schulzer (Schulzer 1874), which is now referred to as *Sporotrichopsis terrestris* (Schulzer) Stalpers (Stalpers 2000). The species *Fibrillaria subterranea* was originally described by Persoon (1822) based on fruitbodies found underground on a dead tree trunk. However, due to the brief description and lack of a holotype, the true nature of this species remains unknown. Interestingly, another species originally described in the genus *Fibrillaria*, *F. ramosissima* Sowerby (1803), is now considered synonymous with *Coniophora puteana* (Schumach.) P. Karst. (Index Fungorum on-line). It appears that some species initially described in the ambiguous genus *Fibrillaria* are closely related to the genus *Sedecula*. The taxonomy and systematics of these genera and species are shrouded in many uncertainties but offer ample room for further study, particularly revision of the type material.

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