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ORIGINAL ARTICLE

Resurrection and description of *Biscogniauxia pezizoides*, the phylogenetic sister of *B. repanda*

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Abstract
Phylogenetic and morphological analyses suggest that *Biscogniauxia repanda*, typified on the basis of a specimen from Europe, differs from the North American *B. pezizoides*, although the latter has been synonymized under *B. repanda* shortly after it was newly described in 1889. The here provided evidence is based on ITS sequences and morphological characters of the ascocarp. As a consequence, *B. pezizoides* is resurrected and both species are re-described. On the basis of earlier studies by others, it is inferred that *B. repanda* occurs mainly in Europe and Eastern Asia on *Sorbus aucuparia* and *B. pezizoides* mainly in North America and Eastern Asia on *Ulmus* spp. and *Acer* sp.

Keywords *Xylariales* · *Graphostromataceae* · 1 new taxon · Type specimens · *Camillea* · *Graphostroma*

Introduction

The genus *Biscogniauxia* Kuntze, family *Graphostromataceae* M.E. Barr, J.D. Rogers & Y.M. Ju, typically comprises facultative saprotrophs, endophytes or weak pathogens with a narrow host specificity. Bipartite stromata, developing underneath the bark of the host and breaking open when mature, are typical morphological features. *Biscogniauxia* species are described from all over the world, and it is suggested that they are adapted to dry or seasonally dry habits (Ju et al. 1998; Wendt et al. 2018).

In 1815 Fries described *Sphaeria repanda* Fr. (Fries 1815) from Europe. Later it was re-classified in the illegitimate genus *Nummularia* Tul. & C. Tul. (Nitschke 1867) and eventually placed in the new genus *Biscogniauxia*. As a result, the current name is *Biscogniauxia repanda* (Fr.) Kuntze (Kuntze 1891). Essentially in parallel, the species *Nummularia pezizoides* Ellis & Everh. (Ellis and Everhart 1884) was described on dead wood in North America and recombined as *B. pezizoides* (Ellis & Everh.) Kuntze (Kuntze 1891).

The original descriptions of *B. repanda* (Fries 1815) and *B. pezizoides* (Ellis and Everhart 1884) are quite general and do not provide any species-specific morphological characters. Therefore, *B. repanda* and *B. pezizoides* were considered synonymous (Ellis and Everhart 1889) and this concept was adopted by Jong and Benjamin (1971) and Ju et al. (1998) based on examinations of both type specimens. Even though Pouzar (1979) stated differences (like size of stroma, distribution, and host preference) between European and North American specimens (including type material), he did not consequently separate them into different species. Vasilyeva et al. (2007; 2009) once again stated the differences between the synonymised *B. repanda* and *B. pezizoides* with regard to their occurrence in eastern Russia without separating them. Today, *B. repanda* and *B. pezizoides* are listed as synonyms in the Index Fungorum (https://www.indexfungorum.org/, last accessed 16 April 2025), while MycoBank accepts both as separate species (https://www.mycobank.org, last accessed 16 April 2025).

This study examines specimens identified as *B. repanda* from Europe and North America to resolve segregation of *B. repanda* from *B. pezizoides*. DNA sequences of specimens from both regions were generated and phylogenetically analysed. Material of the specimens was also morphologically compared. Detailed descriptions are given, and pictures of important structures are presented.

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Material and methods

Collections

Loaned specimens were from herbaria WSP, PRM, and NY. Other collections were from Jiri Kout (University of West Bohemia, Czech Republic), Jürgen Peitzsch, and Till Lohmeyer (Germany). Newly collected specimens were deposited in herbarium KAS (acronyms follow Index Herbariorum, https://sweetgum.nybg.org/science/ih/).

DNA extraction, amplification, sequencing, and phylogenetic analyses

Small pieces (~ 1 mm^3) were cut from the herbarium specimens. The DNA extraction was conducted with E.Z.N.A.® Fungal DNA Mini Kit (Omega Bio-Tek, Georgia, USA) following the short protocol of the manufacturer's instructions. Instead of 5 µL RNase and 10 µL β-mercaptoethanol, 10 µL of Proteinase K (200 µg/ml) was added.

To amplify ribosomal internal transcribed spacer 1, 2, and 5.8S gene (ITS), polymerase chain reaction (PCR) was run with taq polymerase (HOT FIREPol® Blend Master Mix Ready to Load with 7.5 mM $MgCl_2$, Solis BioDyn, Estonia) and primers ITS1F and ITS4 (Gardes and Bruns 1993; White et al. 1990) by using an annealing temperature (AT) of 55 °C. When amplification of the whole ITS region was not possible (for specimens WSP72759, WSP72573, WSP73524), fragments with ITS1F/ITS2 (AT 59 °C), ITS1.2 (5′-TCC GTTGGTGAACCAGCGG-3′)/ITS2 (AT 63 °C) and ITS3/ITS4 (AT 58 °C), or ITS3/ALR0.2 (AT 63 °C) were amplified (Gardes and Bruns 1993; White et al. 1990; Riebesehl and Langer 2017). Alternatively, a nested PCR (for WSP73521, WSP73553, WSP72890) was conducted. Nested PCR was performed first with ITS1F/ITS4 and then with ITS5/ALR0.2 (AT 59 °C) (White et al. 1990). To amplify the beginning domains (D1-D2) of the 28S rRNA gene, the primer pairs NL1/NL4 (AT 58 °C) and LR0R/LR5 (AT 55 °C) were used (Bunyard et al. 1996; O'Donnell 1993; Vilgalys and Hester 1990). The PCR programme includes 240 s initial denaturation at 94 °C, followed by 35 cycles of 40 s at 94 °C, 40 s AT (see above), and 50 s at 72 °C, with a final 240 s extension at 72 °C. The DNA Clean and Concentrator®−5 kit (Zymo Research, Irvine, California, USA) was used for purification of PCR products, and sequencing was commissioned by Eurofins Genomics (Ebersberg, Germany). DNA sequences were edited manually with MEGA 11 (Tamura et al. 2021), under consideration of the five quality check guidelines (Nilsson et al. 2012), to assemble the forward and reverse sequence. The sequences were deposited in NCBI GenBank (Benson et al. 2018, https://www.ncbi.nlm.nih.gov/genbank; Tab. 1).

For phylogenetic study, DNA sequences (Table 1) were aligned with MAFFT v.7.526 (https://mafft.cbrc.jp/alignment/server/, Katoh et al. 2019) using the L-INS-i algorithm (for ITS) and the G-INS-i algorithm (for 28S rDNA) with default settings. The manually edited alignment is supplied as online source (Online Resource 1). The phylogenetic tree was calculated with MEGA 11, choosing the maximum likelihood (ML) analysis under the usage of a substitution model based on BIC. The MEGA 11 Model Selection tool was used to choose the substitution model. The following settings were applied for ML calculation: 1000 bootstrap replications, Kimura 2-parameter substitution model (Kimura 1980), Gamma distribution with five discrete categories, partial deletion of gapped positions, 95% site coverage cutoff, and otherwise default settings. Editing of the resulting phylogenetic tree was done with Microsoft PowerPoint 2016.

Morphological analyses

Freshly collected specimens were cultured by removing ascospores with tweezers from the perithecia and placing them on potato dextrose agar (PDA). They were subcultured at room temperature (approximately 21 °C) with daylight as light source until all contaminants were removed. The collected specimens were dried for 3 days at 30 °C for long-term storage.

For morphological investigation, strains were grown on potato dextrose yeast agar (PDYA) (Callan and Rogers 1986) at room temperature (approximately 21 °C) with daylight as light source.

Specimens and cultures were investigated with a Zeiss Discovery-V8 SteREO binocular and a light microscope Zeiss Axio Imager.M2 (Carl Zeiss Microscopy, Oberkochen, Germany). Measurements were conducted in tap water. For both species, at least 50 ascospores were measured. For the *B. repanda* cultures, 50 conidia were measured for each strain. For investigation and measurement of the apical aperture within the asci, Melzer's iodine reagent was used.

Photographs were taken by camera Axiocam 105 colour (R2) adapted to the microscopes.

Results

Phylogenetic analysis

In the phylogenetic analysis, DNA sequences of closely related *Biscogniauxia* species were compared with three sequences of *B. repanda* from Europe and three to four sequences of North American specimens (hitherto also determined as *B. repanda*, but within this study reassigned to *B. pezizoides*). The ITS dataset consists of 866

Table 1 Phylogenetically analysed ITS and 28S rDNA sequences and the corresponding specimens or isolates. Type status is identified with an asterisk, and newly generated sequences are in bold

Species	Specimen voucher/ isolate	GenBank accession numbers		Host plant	Country	Reference
		ITS	28S rDNA			
Biscogniauxia anceps (Sacc.) J.D. Rogers, Y.M. Ju & Cand.	123	EF026132	-	Unknown	France	Unpublished
	WSP73512	**PQ227779**	**PQ215671**	**Bark**	**Spain**	**This study**
Biscogniauxia arima F. San Martín, Y.M. Ju & J.D. Rogers	WSP:112/ WSP69713*	NR_167683	-	Wood	Mexico	Unpublished
			PQ215672			**This study**
Biscogniauxia atropunctata (Schwein.) Pouzar	YMJ 128	JX507799	-	Wood	USA	Mirabolfathy et al. 2013
	CBS 275.61	**PQ211043**	**PQ211079**	**Unknown**	**USA, West Virginia**	**This study**
Biscogniauxia bartholomaei (Peck) Lar.N. Vassiljeva	ATCC:38992	AF201719	-	Unknown	Unknown	Pinto-Sherer 2001
	WSP72759	**PQ227780**	**-**	***Alnus tenuifolia* Nutt., decayed wood**	**USA, Idaho**	**This study**
Biscogniauxia citriformis (Whalley, Hammelev & Talig.) Van der Gucht & Whalley	YMJ 129	JX507801	-	*Casuarina equisetifolia* L., wood	USA	Mirabolfathy et al. 2013
	WSP72573	**PQ227781**	**PQ215673**	***Casuarina equisetifolia* L.**	**USA, Hawaii**	**This study**
Biscogniauxia cylindrispora Y.M. Ju & J.D. Rogers	89092701/ WSP70164*	EF026133	-	*Cinnamomum* sp., bark	Taiwan	Unpublished
			PQ215674			**This study**
Biscogniauxia formosana Y.M. Ju & J.D. Rogers	YMJ 89032201/ WSP70165*	JX507802	-	Bark	Taiwan	Mirabolfathy et al. 2013
			PQ215675			**This study**
Biscogniauxia granmoi Lar.N. Vassiljeva	YMJ 135	JX507803	-	*Prunus padus* L., bark	Austria	Mirabolfathy et al. 2013
	JKI-GFF-2022–009/ TL 2022–004	**PQ227782**	**PQ215676**	***Prunus padus* L., dead wood**	**Germany**	**This study**
Biscogniauxia latirima Y.M. Ju & J.D. Rogers	YMJ 89101101/ WSP70167*	JX507804	-	bark	Taiwan	Mirabolfathy et al. 2013
			PQ215677			**This study**
Biscogniauxia marginata (Fr.) Pouzar	CBS 124505	KU684016	-	*Malus* sp. or *Pyrus* sp., bark of felled stem	Germany	U'Ren et al. 2016
	JKI-GFF-2022–006	**OR260269**	**PQ215678**	***Sorbus aucuparia* L.**	**Germany**	**This study**
Biscogniauxia mediterranea (De Not.) Kuntze	147 (JDR)	EF026134	-	Corticated wood	France	Unpublished
	CBS 259.63	**PQ211044**	**PQ211080**	**Unknown**	**USA, California**	**This study**
Biscogniauxia nummularia (Bull.) Kuntze	MUCL 51395 *	NR_153649	KY610427	*Fagus sylvatica* L.	France	Wendt et al. 2018
	JKI-GFF-2021–008	**OR260268**	**PQ215679**	***Fagus sylvatica* L.**	**Germany**	**This study**
Biscogniauxia pezizoides	**WSP73520**	**PQ227783**	**PQ215680**	**cf. *Quercus* twig**	**USA, Missouri**	**This study**

Table 1 (continued)

Species	Specimen voucher/ isolate	GenBank accession numbers		Host plant	Country	Reference
		ITS	28S rDNA			
Biscogniauxia pezizoides	**WSP73521**	**PQ227784**	**-**	**Dead wood**	**USA, Wisconsin**	**This study**
Biscogniauxia pezizoides	**WSP73553**	**PQ227785**	**PQ215681**	**Unknown**	**USA, Illinois**	**This study**
Biscogniauxia pezizoides	ATCC 62606	KY610383	KY610428	Unknown	USA	Wendt et al. 2018
Biscogniauxia repanda	**KAS-JKI-GF-2023–003**	**PQ586672**	**PQ586673**	***Sorbus*, twig**	**Germany**	**This study**
Biscogniauxia repanda	**KAS-JKI-GF-2023–009**	**PQ227787**	**PQ215683**	**Lying trunk of hardwood**	**Czech Republic**	**This study**
Biscogniauxia repanda	**WSP72890**	**PQ227788**	**PQ215684**	***Sorbus aucuparia* L.**	**Czech Republic**	**This study**
Biscogniauxia simplicior Pouzar	136	EF026130	-	**Unknown**	France	Unpublished
	WSP73524	**PQ227789**	**PQ215685**	***Rhamnus cathartica* L.**	**France**	**This study**
Jackrogersella cohaerens (Pers.) L. Wendt, Kuhnert & M. Stadler	agrD458/CBS 114744	AY616688	-	*Fagus sylvatica* L.	Germany	Triebel et al. 2005
Hypoxylon pulicicidum J. Fourn., Polishook & Bills	MUCL49879/CBS 122622	JX183075	KY610492	Rotten wood	France, Martinique	Bills et al. 2012, Wendt et al. 2018

positions, of which 454 positions were used in the final data set. The results of the ITS analysis (Fig. 1) show more than 3.4% genetic distance between the European and North American specimens. Relatedness of both species is moderately supported (bootstrap value 74). The 28S rDNA dataset consists of 552 positions in the final dataset, and the phylogenetic analysis (Fig. 2) shows a similar topology as the ITS phylogeny. The branch accommodating *B. repanda* and *B. pezizoides* is supported by a bootstrap value of 91.

Taxonomy

The morphological study contains the analysis of six specimens from Europe, including the isolectotype specimens of *B. repanda*, and five specimens from North America, including the lectotype and paralectotype specimens of *B. pezizoides*.

Biscogniauxia repanda (Fr.) Kuntze, Figs. 3 and 4
MB 438113

Diagnosis: Differing from *B. pezizoides* by having larger ascocarps and larger ascocarp margins, which are more enhanced and strongly fringed.

Type: Fries Scleromyceti Sueciae 1 (K, lectotype of *Sphaeria repanda*, designated in Miller (1961)); SWEDEN: on wood, leg. E. Fries, Scleromyceti Sueciae Exs. 1 (UPS, isolectotype of *Sphaeria repanda*); leg. E. Fries (PRM 718926, isolectotype of *Sphaeria repanda*); leg. E. Fries (PRM 801263, isolectotype of *Sphaeria repanda*).

Sexual morph: **Stromata** raised-discoid, oval with minor irregularities in outline, covering an area of 0.7–2.5 × 0.6–1.8 cm near surface, 0.5–0.9 × 0.5–0.8 cm near base, 0.4–0.9 cm high (with margin), surface wavy to slightly uneven; mature surface dark grey to black; margins slightly brighter, distinctly raised, strongly fringed or perforated, 0.5–2.9 mm broad, 0.8–1.8 mm high; dark brown and hard immediately beneath surface and between perithecia; tissue beneath perithecia 1.1–5.1 (avg. 3.2) mm, dark brown to light brown, woody, mixed with small pieces of blackish material. **Perithecia** black, shiny, oblong, encased by carbonaceous, darker tissue, 1.2–1.9 (avg. 1.5) mm high, 0.3–0.6 (avg. 0.4) mm wide. **Ostioles** individually encased by carbonaceous, darker tissue, with openings visible on stroma surface, papillate, higher than stroma surface, with broad ring around openings, 129–258 (avg. 190) µm diam., often cracked around the elevations, colour usually the same as stromata. **Asci** in total 90–125 (avg. 110) µm long, 5.3–7.2 (avg. 6.3) µm wide, spore bearing part 81.5–97.5 (avg. 88.5) µm long, proximal part without ascospores 9.3–31.6 (avg. 22.3) µm long; apical ring bluing in Melzer's iodine reagent, shape discoid, 0.9 µm high, 3.1 µm wide. **Ascospores**

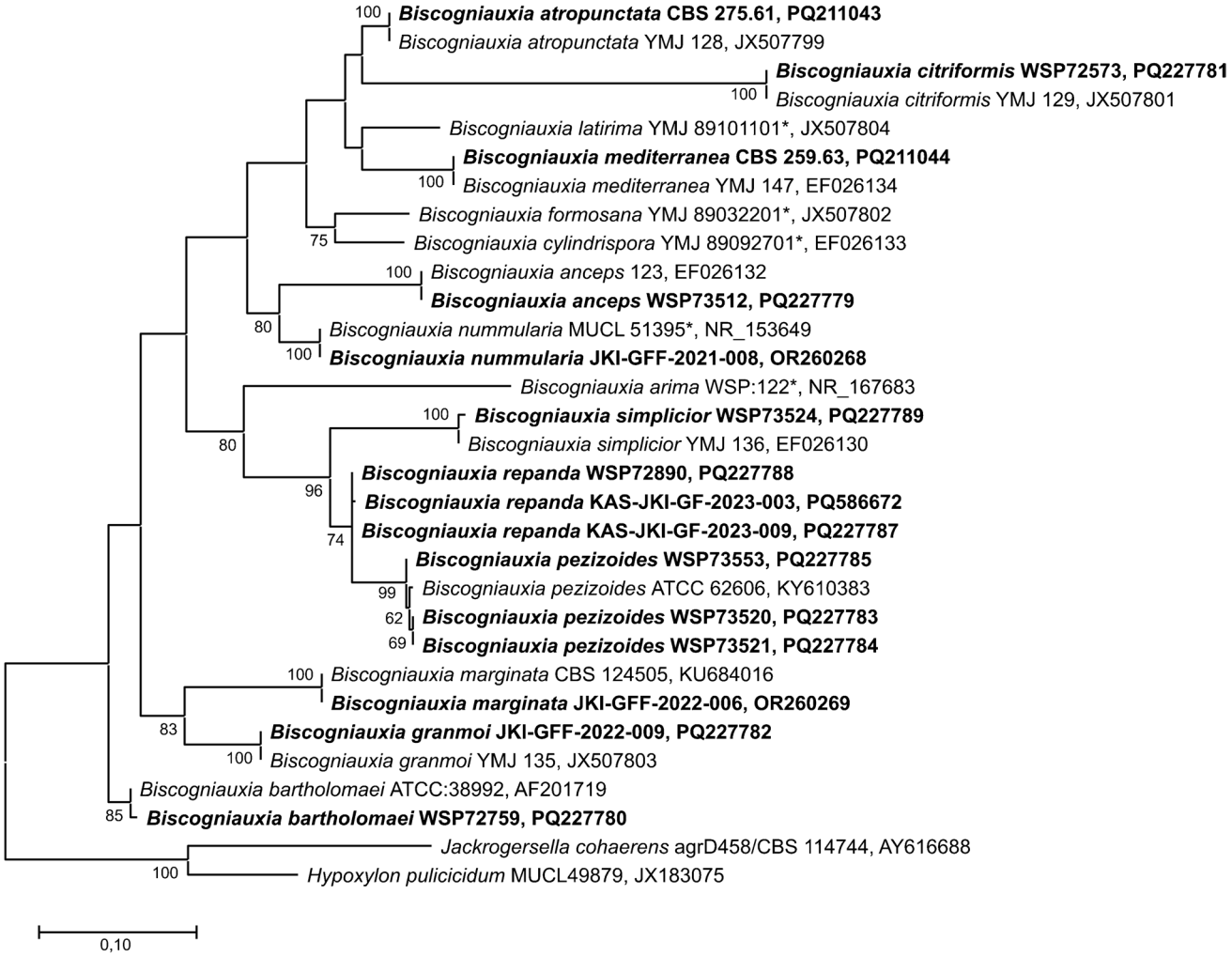


Fig. 1 Phylogeny of *Biscogniauxia* with regard to *B. repanda* and *B. pezizoides* based on ITS sequences. Calculations are made with the maximum likelihood method. Bootstrap values are provided if they are higher than 50. The species name is followed by the specimen number and the sequence accession number (GenBank, NCBI). Asterisks mark sequences deriving from type material. Sequences generated in this study are marked in bold. The scale bar indicates the estimated number of substitutions per nucleotide position

unicellular, ellipsoid, equilateral to slightly inequilateral, 10.8–14.3 (avg. 12.8) µm × 3.4–6.8 (avg. 5.6) µm, brown to dark brown, with rounded ends, smooth surface and two germ slits across spore length. **Paraphyses** copious, hyaline, thin (~ 1.5 µm wide), longer than asci, unbranched, with oily or granular content.

Colonies reaching 2–4.5 cm diameter on PDYA in 4 weeks at room temperature (approximately ~ 21 °C); mycelium first hyaline, airy and floccose, later light reddish-brown with some parts dark-brownish, and dark reddish-brown drops on top; with dark reddish-brown pigment visible in the media beyond colony margin.

Asexual morph: **Conidiophores** randomly scattered over colony surface, branching nodulisporium-like, at least 150 µm long, hyaline or brown, smooth or rough. **Conidiogenous cells** sympodially proliferating, 12.4–23.8 (avg. 18.3) µm long, 1.8–3.8 (avg. 2.8) µm wide, apex distinctly swollen, pitted, 3.3–6.6 (avg. 4.8) µm wide; conidia production holoblastic. **Conidia** hyaline to faintly light brown, 4–7.7 (avg. 5.6) × 2.4–3.3 (avg. 2.8) µm, ovoid (subglobose to oblong) to amygdaloid with small hilum at one end; attached to conidiogenous locus by up to 1.5 µm long, non-persistent, connective structures in early stage.

Habitat: Examined specimens in this study are found on *Sorbus aucuparia*. In literature, *S. aucuparia*, *S. pohuashanensis* Hedl., *S. sibirica* Hedl., and in some exceptional cases *Ulmus* spp. and *Malus silvestris* are listed as habitat for *B. repanda* s.s. (or the "European population") (Eckblad and Granmo 1978; Pouzar 1979; Vasilyeva et al. 2009; Vasilyeva and Stephenson 2010).

Distribution: Present in Germany and the Czech Republic according to the here examined specimens.

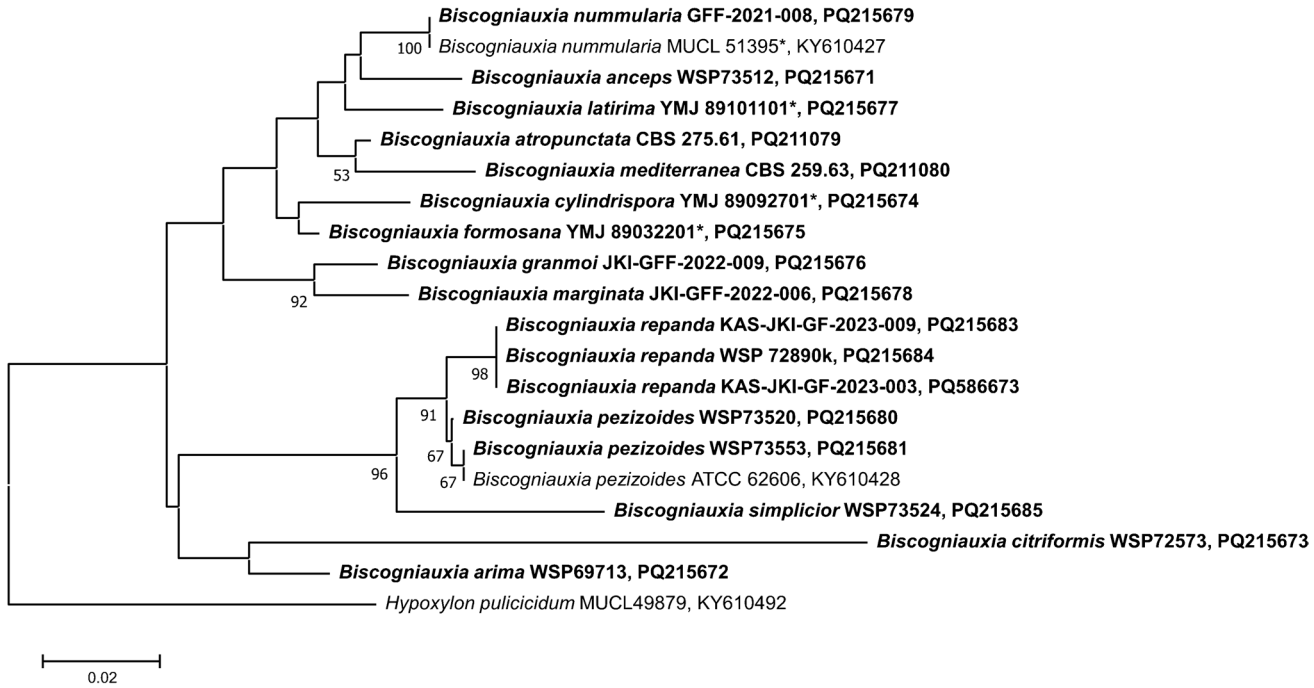


Fig. 2 Phylogeny of *Biscogniauxia* with regard to *B. repanda* and *B. pezizoides* based on 28S rDNA sequences. Calculations are made with the maximum likelihood method. Bootstrap values are provided if they are higher than 50. The species name is followed by the specimen number and the sequence accession number (GenBank, NCBI). Asterisks mark sequences deriving from type material. Sequences generated in this study are marked in bold. The scale bar indicates the estimated number of substitutions per nucleotide position

Specimens examined: CZECH REPUBLIC: Sumava mountains, in Vydra river valley, at Cenkova Pila, 49.1061N–13.493176W, 700 m, on branches of *Sorbus aucuparia*, 8 October 1997, leg. Z. Pouzar (WSP72890); West Bohemia, Pilsen, Kamenný rybník Nature reserve, lying trunk of hardwood, 1 April 2011, leg. J. Kout (KAS-JKI-GF-2023–009); GERMANY: Saxony-Anhalt, Sangerhausen, dead wood of *Sorbus aucuparia*, 25 January 2022, leg. J. Peitzsch (KAS-JKI-GFF-2022-005; GenBank, ITS: PQ227786, 28S: PQ215682); ibid. (specimen KAS-JKI-GF-2023-003/culture DSM 119972, resampled one year later, 23 March 2023, from the same location and substrate, supposedly the same organism); SWEDEN: leg. E. Fries (PRM 718926, isolectotype of *Sphaeria repanda*); leg. E. Fries (PRM 801263, isolectotype of *Sphaeria repanda*).

Notes: Besides *B. repanda*, seven other *Biscogniauxia* species, *B. albosticta* (Ellis & Morgan) Y.M. Ju & J.D. Rogers, *B. ambiens* Y.M. Ju & J.D. Rogers, *B. cinereolilacina* (J.H. Mill.) Pouzar, *B. nawawii* M.A. Whalley, Y.M. Ju, J.D. Rogers & Whalley, *B. querna* Pouzar, *B. schweinitzii* Y.M. Ju & J.D. Rogers, and *B. pezizoides*, have two germ slits. However, *B. albosticta*, *B. ambiens*, *B. cinereolilacina*, *B. nawawii*, and *B. schweinitzii* have applanate (not raised-discoid) stromata (Ju et al. 1998). *Biscogniauxia querna* can be distinguished by its larger, laterally compressed ascospores, approximately 17–22 × 11–14 × 9–10 µm (Pouzar 1986; Ju et al. 1998), and *B. pezizoides* has smaller ascocarps with inconspicuous broad, flat margins.

The geographical distribution of *B. repanda* s.s. is not known. Eckblad and Granmo (1978) described a species from Norway matching *B. repanda* as described here. Authors who state morphological differences within *B. repanda* s.l. (calling them the "European or North American populations," Pouzar 1979) or even support the separation of *B. repanda* and *B. pezizoides* on species level (Vasilyeva et al. 2007, 2009; Vasilyeva and Stephenson 2010) reported *B. repanda* s.s. (or the "European population") from Europe, eastern Asia, and in some exceptional cases, from North America.

Compared to *B. pezizoides* (Callan and Rogers 1986, therein called *B. repanda*), conidiogenous cells of *B. repanda* are shorter. The conidia of both species are difficult to separate, though the conidia of *B. repanda* tend to have a broader size range (3.9–7.7 × 2.4–3.3 µm) than the conidia of *B. pezizoides* (4.0–6.0 × 2.0–2.5(3.0) µm). We did not observe "botryoid clusters" of conidia in *B. repanda* that Callan and Rogers (1986) specified for *B. pezizoides*. However, the general appearance of the cultures of *B. repanda*, like the reddish brown colour, is similar to the described appearance of *B. pezizoides* (Callan and Rogers 1986). The observed branching pattern of the conidiophores is nodulisporium-like, as defined by Ju and Rogers (1996).

Biscogniauxia pezizoides (Ellis & Everh.) Kuntze, Fig. 5

MB 438116

Diagnosis: Differing from *B. repanda* by having smaller ascocarps and smaller ascocarp margins, which are less enhanced and not obviously fringed.

Type: CANADA: Ontario, Ottawa, host unknown, October 1883, leg. J. Macoun, 228 (NY 01013358, lectotype of *Nummularia pezizoides*, designated in Ju et al. (1998); BPI 738910, isolectotype); UNITED STATES: Kansas, Shawnee Co., Topeka, 39.048334N–95.678037W, host unknown, 15 April 1884, leg. Cragin, 345 (NY 03390737, paralectotype of *Nummularia pezizoides*).

Sexual morph: **Stromata** raised-discoid, covering an area of 0.2–0.7(1.1) × 0.2–0.6 cm, 0.1–0.25 cm high; almost always round to oval in outline, with irregular outline when fused together; with black or brownish-black surface, and slightly brighter and browner at margins when mature; margins slightly raised at some parts (up to 370 µm), broad and crumbly; stromata immediately beneath surface and between perithecia dark brown and hard; tissue beneath perithecia light brown, woody; base of stroma is reached 200–640 (avg. 370) µm below perithecia; in some cases stroma is delimited at the base by a black line. **Perithecia** black, shiny, tubular, encased by carbonaceous, darker tissue, 0.9–1.5 (avg. 1.1) mm high, 0.2–0.5 (avg. 0.3) mm wide. **Ostioles** individually encased by carbonaceous, darker tissue, with openings visible on stroma surface, papillate, higher than stroma surface, visible as small rounded mounds, colour same or slightly darker than stromata, 108–247 (avg. 168) µm diam. Asci 97–110 (104) µm long, 5.8–10.3 (7.2) µm wide, spore bearing part 71.6–95.1 (avg. 85.9) µm long, proximal part without ascospores 9.7–28.3 (avg. 18.5) µm long; apical ring not or only slightly bluing in Melzer's iodine reagent, shape discoid or slightly bent, 0.6 µm high, 2.62 µm wide. Ascospores unicellular, ellipsoid, equilateral to slightly inequilateral, 10.3–15.1 (avg. 12.6) × 4.4–6.3 (avg. 5.3) µm, brown to dark brown, with rounded ends, smooth surface, and two germ slits across spore length. **Paraphyses** copious, hyaline, thin (~ 1.5 µm wide), longer than asci, unbranched, with oily or granular content.

Habitat: Examined specimens in this study are found on not further specified dead wood. In one case, *Quercus* sp. is supposed. In literature, *Ulmus* spp., *Acer* sp., and in some exceptional cases, *Acer mono* Maxim., are listed as habitat for *B. pezizoides* (or the "North American population") (Pouzar 1979; Vasilyeva et al. 2007, 2009; Vasilyeva and Stephenson 2010).

Distribution: Species examined within this study are reported from North America (United States: Illinois, Missouri, and Wisconsin).

Specimens examined: CANADA: Ontario, Ottawa, host unknown, October 1883, leg. J. Macoun, 228 (NY 01013358, lectotype of *Nummularia pezizoides*); UNITED STATES: Kansas, Shawnee Co., Topeka, 39.048334N—95.678037W, host unknown, 15 April 1884, leg. Cragin, 345 (NY 03390737, paralectotype of *Nummularia pezizoides*); Illinois, Jo Daviess county, Tupperly Conservation Area, host unknown, 13 April 1983, leg. Dean A. Glawe, 83–11 (WSP73553); Missouri, Pike, DuPont Nature Preserve (Reservation Conservation Area), 39.557036N—91.186744W, twigs of cf. *Quercus* sp., 15 April 1983, leg. Dean A. Glawe, 86–34 (WSP73520); Wisconsin, near Monroe, 42.601119N—89.642916W, dead wood, 13 June 1962, leg. Jack D. Rogers (WSP73521).

Notes: As mentioned above, besides *B. pezizoides*, seven other *Biscogniauxia* species have two germ slits. However, *B. albosticta*, *B. ambiens*, *B. cinereolilacina*, *B. nawawii*, and *B. schweinitzii* have applanate (not raised-discoid) stromata (Ju et al. 1998). *Biscogniauxia querna* can be separated by its larger, laterally compressed ascospores, approximately 17–22 × 11–14 × 9–10 µm (Pouzar 1979; Ju et al. 1998) and *B. repanda*, as mentioned above, has larger ascocarps and more expansive, conspicuous margins.

We did not observe an asexual morph on the fungarium specimens, and cultures were not isolated. However, Callan and Rogers (1986) described a culture of the specimen WSP73553.

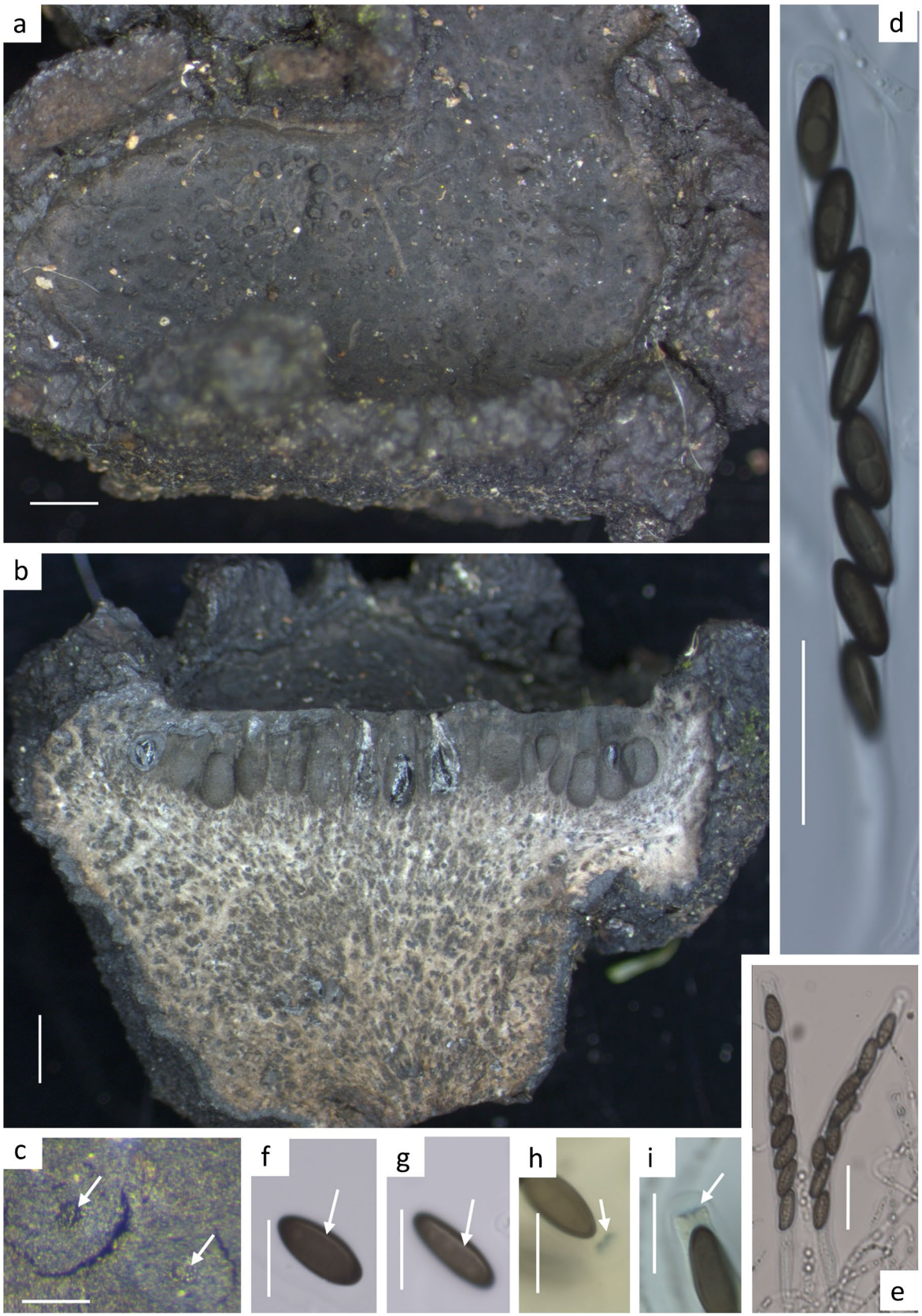
The distribution of *B. pezizoides* s.s. is not exactly known. Authors who state morphological differences within *B. repanda* s.l. (calling them the "European or North American populations," Pouzar 1979) or even support the species separation of *B. repanda* and *B. pezizoides* (Vasilyeva et al. 2007, 2009; Vasilyeva and Stephenson 2010) reported *B. pezizoides* (or the "North American population") from North America, eastern Asia, and in some exceptional cases, from Europe.

Specimen number NY 01013358 was called in Ju et al. (1998) a "holotype." However, the exact term is to our opinion "lectotype," wherefore, we corrected it here.

Discussion

The phylogenetic and morphological analyses in this study have shown that the investigated North American and European specimens of *B. repanda* s.l. should be separated into two distinct species: *B. repanda* and *B. pezizoides*. The included representatives of the two species differ by more than 3% genetic distance in the ITS region. Observed morphological character patterns of phylogenetically analysed specimens are congruent with those of the observed type materials. The description shows that the species can also be unambiguously separated based on morphology.

In the past, however, publications did not separate these species and certain specimens cited in literature cannot be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◂**Fig. 3** *Biscogniauxia repanda* (KAS-JKI-GF-2023-003): **a** ascocarp from above; **b** ascocarp cross section, with visible perithecia; **c** ostiolar openings on stromata surface from above; **d**, **e** asci with ascospores; **f**, **g** ascospores, arrows indicate germ slits; **h**, **i** ascus tip, arrow indicate dyed apical apparatus; scale bars: **a**, **b** = 1000 µm, **c** = 100 µm, **d**, **e** = 20 µm, and **f**–**i** = 10 µm

undoubtedly identified. Furthermore, statements about geographic occurrence and hosts are often inconsistently specified and can only be presumed.

For example, Jong and Benjamin (1971) only cited North American locations, but parts of the morphological characters they describe resemble those of the European species, *B. repanda*. *Biscogniauxia repanda* seems to occur in some rare cases also in North America (Pouzar 1979), which is probably why specimens of both species (*B. repanda* and *B. pezizoides*) were included in the morphological description of Jong and Benjamin (1971). Unfortunately, it is not documented in Jong and Benjamin (1971), which specimens they examined.

Pouzar (1979) states differences between European and North American specimens. In North America, he mainly observed specimens on *Ulmus* spp. Furthermore, he described smaller stromata and their margins were described as less developed. By contrast, the European specimens were almost always found on *Sorbus aucuparia*. This aligns with the observations within this study. Interestingly, though, Pouzar (1979) studied the same type specimens from both species, but did not separate them into different species. Rather, he explicitly adhered to the description of Jong and

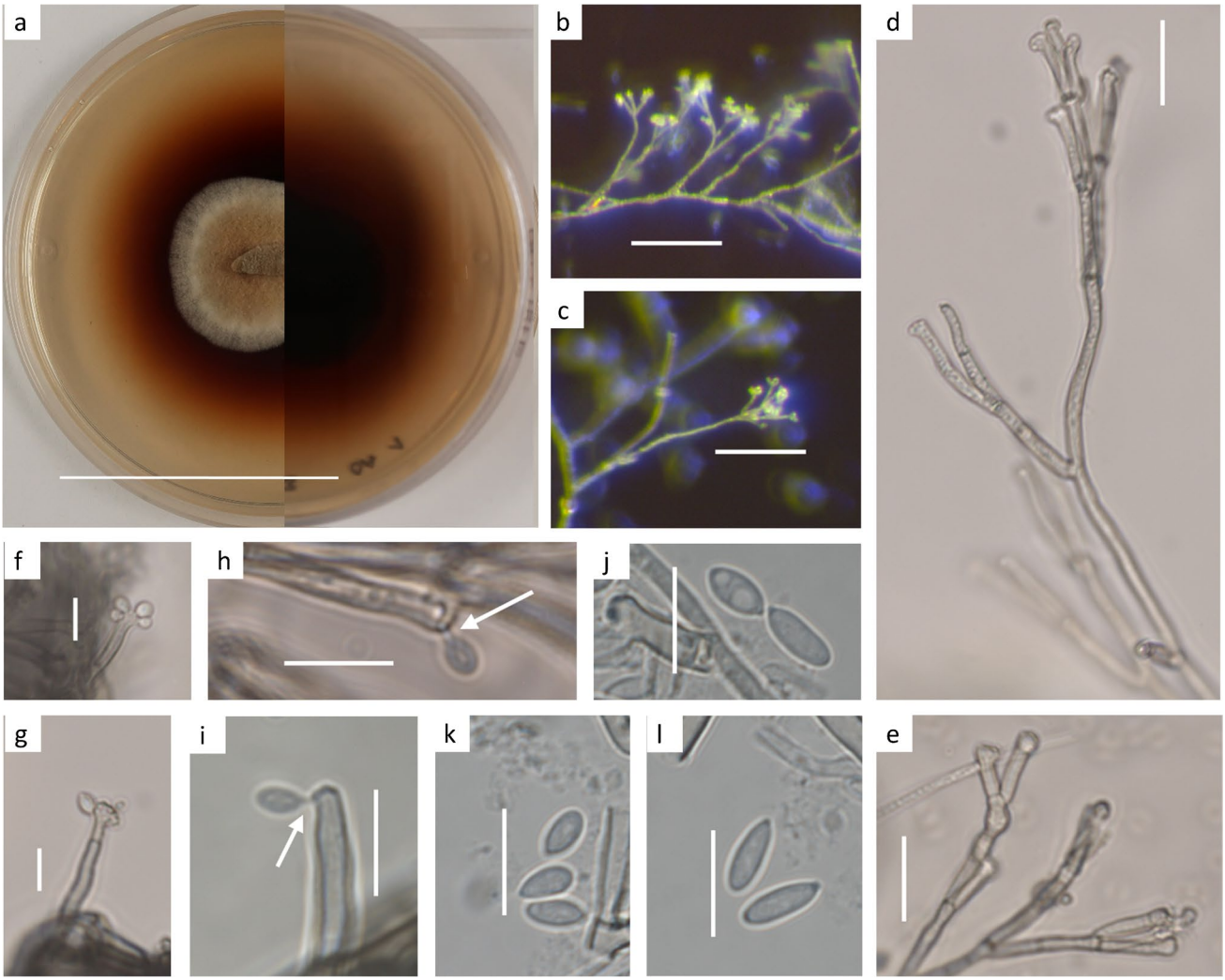
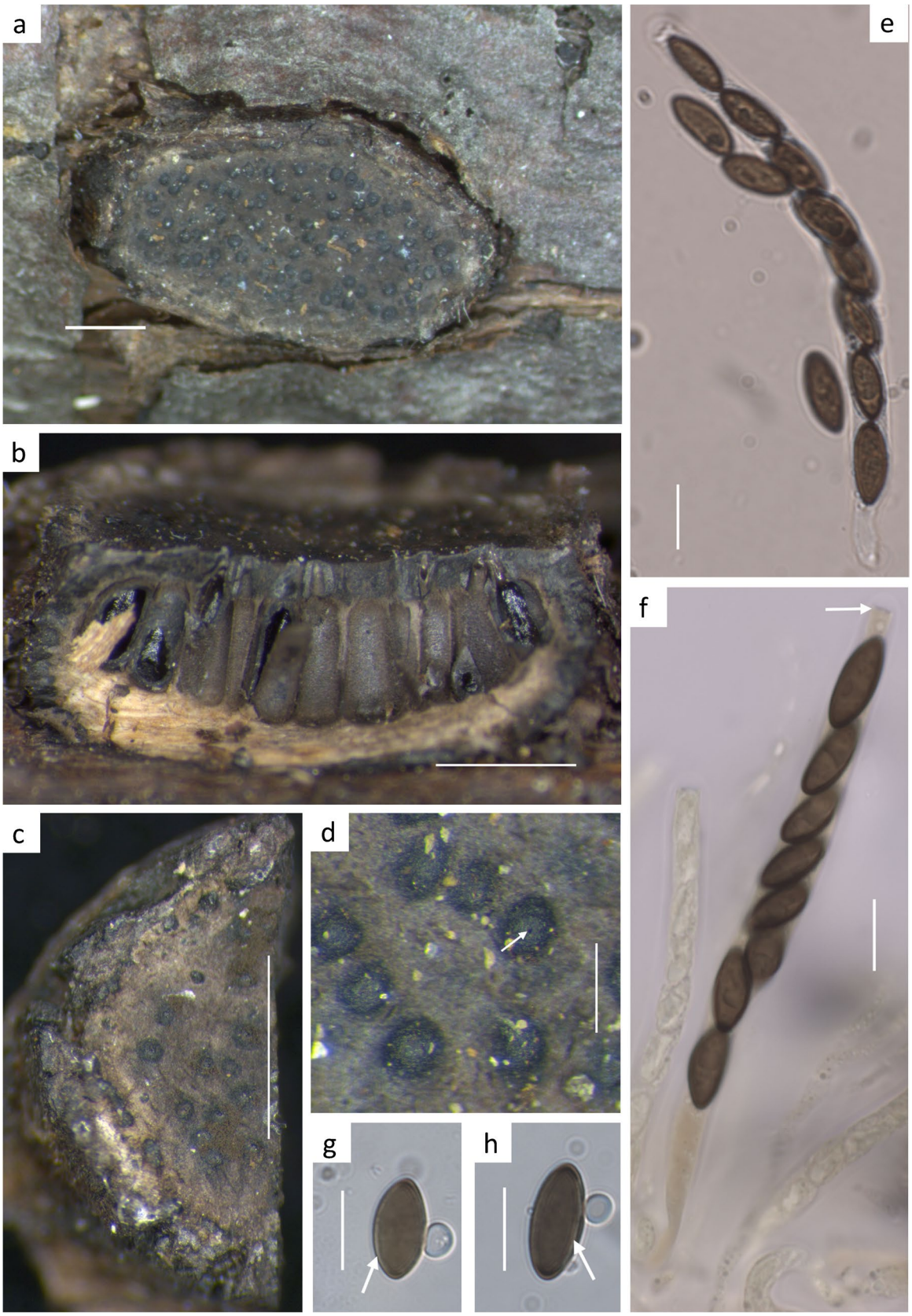


Fig. 4 *Biscogniauxia repanda* (KAS-JKI-GF-2023-003): **a** culture on PDYA after four weeks, front and back side of petri dish; **b**–**d** conidiophores formed by aerial mycelium; **e**–**g** conidiophores; **h**–**i** conidiogenous cells with attached conidia, arrows indicate short, non-persistent connective structures between conidia and conidiogenous cell; **j**–**l** conidia; scale bars: **a** = 5 cm, **b, c** = 100 µm, **d**, **e** = 20 µm, and **f**–**l** = 10 µm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◂**Fig. 5** *Biscogniauxia pezizoides* (WSP73520): **a**, **c** ascocarp from above; **b** ascocarp cross section, with perithecia; **d** ostiolar openings on stroma surface from above; **e**, **f** asci with ascospores, arrow indicates dyed apical apparatus; **g**, **h** ascospores, arrows indicate germ slits; scale bars: **a**–**c** = 1000 µm, **d** = 200 µm, and **e**–**h** = 10 µm

Benjamin (1971). In rare cases, *B. repanda* like specimens may occur on *Ulmus* spp. and *B. pezizoides* like specimens may occur on *Sorbus* spp. Likewise, Ju et al. (1998) examined the lectotype of *Nummularia pezizoides* and one more specimen from North America, as well as European specimens including the isolectotype of *Sphaeria repanda*. However, they did not note conspicuous differences within the examined specimens and agreed with the species concept of Jong and Benjamin (1971).

The specimens examined by Eckblad and Granmo (1978) align with our observations of the European material, denoted here with the name *B. repanda*. Only specimens from Norway were examined. The host was almost always *Sorbus aucuparia*, though one specimen was on *Ulmus glabra* Huds. (and one on *Malus sylvestris* (L.) Mill.). Vasilyeva et al. (2007; 2009) and Vasilyeva and Stephenson (2010) stated (like Pouzar 1979) the differences of both species with regard to their occurrence in eastern Russia. Unfortunately, however, these statements cannot be verified because examined specimens were not specified.

Based on the small number of examined specimens within this study, *B. repanda* is present in Europe (Germany, Czech Republic), while *B. pezizoides* is present in North America (Canada: Ontario, USA: Kansas, Illinois, Missouri, Wisconsin). However, based on the information of the above-mentioned previous publications, it is possible that, in rare cases, *B. repanda* might be found in North America and *B. pezizoides* in Europe. Furthermore, both species seem to be present in eastern Asia. For a clear assignment to one species or the other, specimens should be re-investigated.

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Data availability The datasets generated and/or analysed during the current study are available as online source.

Declarations

Ethics approval The authors assure that the manuscript complies with the guidelines of good scientific practice.

Consent to participate Not applicable.

Consent for publication All authors agreed with the content of the manuscript and gave explicit consent to submit it. The authors obtained consent from the responsible authorities at the institute where the work has been carried out, before the work was submitted.

Competing interests The authors declare no competing interests.

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