

Geoglossum simile of North America and Europe: distribution of a widespread earth tongue species and designation of an epitype

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Received: 12 December 2013 / Revised: 28 January 2014 / Accepted: 12 February 2014 / Published online: 14 March 2014
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Abstract *Geoglossum simile* is a distinctive species of the earth tongue class *Geoglossomycetes*, first described in 1873. The taxonomic standing of this species has long been disputed, resulting in nearly 70 years of potential misdiagnoses. Although *G. simile* was originally described from North America, it has subsequently been reported from several European countries as well as Asia, Australasia, and India. In this study, we report the first records of *G. simile* from Slovakia and the Czech Republic, examine the morphological and molecular diversity of Northern Hemisphere collections, discuss the taxonomic history and current status of the species, and designate a recent North American collection as the epitype of this widely distributed and conservationally significant species.

Keywords *Ascomycota* · *Geoglossomycetes* · Fungal conservation · Phylogenetics · Systematics

Introduction

The fungal class *Geoglossomycetes* Schoch et al. (2009) has been a subject of study for mycologists for over three centuries (Hustad et al. 2013). This long history of research has yielded a complicated taxonomy with many synonyms and nomenclatural transfers, resulting in over two hundred published names (www.indexfungorum.org). Currently, the class contains six genera and an estimated fifty species (Kirk et al. 2008, Hustad et al. 2013). Fungi of the class *Geoglossomycetes* have been included in several studies on the evaluation of European grasslands (Rald 1985, Nitare 1988, Jordal 1997, McHugh et al. 2001, Adamčík and Kautmanová 2005) and are of conservation interest. The genus *Geoglossum* Pers. contains the earliest described species in the class and is also the most widespread genus with members reported from every continent except Antarctica.

Geoglossum simile Peck was described (Peck 1873) from specimens collected in Sand Lake (New York, USA) by Charles Horton Peck and Ft. Edward (New York, USA) by Elliot Calvin Howe. Peck did not designate either specimen as the holotype and because these specimens are the only ones listed in the protologue, they are regarded as syntypes. At that time Peck was under the erroneous assumption that *G. glabrum* possessed 3–4 septate ascospores (as reported by Cooke (1871)), and, thus, he believed that his specimen with 7-septate ascospores was a separate and undescribed species. Peck (1878) reconsidered his original diagnosis of a new species and placed *G. simile* as a synonym under *G. glabrum* Pers. Peck made no mention of the distinctive paraphyses in his collections of *G. simile* in either treatment and may not have compared them with authentic material of *G. glabrum* from Europe. He did

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admit (Peck 1878) the “application of the specific name *glabrum*” to his specimens was “unfortunate and liable to mislead the student, for the stem is covered by a kind of minutely-tufted tomentum of matted septate filaments, which, with the projecting masses of spores from the mature club, give the plant a scarcely less hairy aspect than that of *G. hirsutum*”. The squamulose stem composed of acute tufts of paraphyses is a characteristic morphological feature observed in dried specimens of *G. simile*, but is not found in *G. glabrum*.

Peck’s confusion over the identity of this species influenced subsequent authors for over 70 years. Massee (1897), Durand (1908), and Lloyd (1916) considered *Geoglossum simile* as a synonym of *G. glabrum* in their influential early monographs of *Geoglossaceae*. It was not until Imai (1941) that the species were again recognized as separate. With the exception of Seaver (1951), the concept of *G. simile* as a species separate from *G. glabrum* was subsequently accepted by the majority of researchers (e.g., Nannfeldt 1942, Mains 1954, Eckblad 1963, Maas Geesteranus 1965, Ohenoja 2000, Roobeek 2009, Hustad et al. 2011). *G. simile* is one of the most commonly occurring *Geoglossum* species in eastern North America (Mains 1954), but many collections made prior to the 1940s may be mislabeled as *G. glabrum*. Hustad et al. (2013) found *G. simile* to occur on a well-supported branch in the *Geoglossum* clade in a four-gene molecular phylogeny of Geoglossomycetes, separate from *G. glabrum* and sister to *G. sphagnophilum*.

Although *Geoglossum simile* was originally described from North America, it has subsequently been collected in Asia (Imai 1941), Australasia (Beaton & Weste 1979), Europe (Bille-Hansen 1954), and India (Batra & Batra 1963). Our assumption that the species may occur in Central Europe was confirmed by material collected in Slovakia and the Czech Republic in 2006 (Kučera & Lizoň 2012). Examination of these collections and other European material has raised the question of whether specimens of *G. simile* from Europe and North America represent the same species or discrete species with convergent morphologies. Members of the genus *Geoglossum* were thought to be quite rare in Slovakia and the Czech Republic with only a few taxa reported from these countries before recent collections (Kučera et al. 2008, 2010, 2013, Kučera & Gaisler 2012, Kučera & Lizoň 2012, Kučera 2012).

The goals of this study were to: 1) compare European and North American material using both morphological and molecular techniques, and 2) designate an epitype for *Geoglossum simile* from recently collected North American material to facilitate the interpretation of the lost and aging material examined by Peck.

Materials and methods

Specimens were identified based on morphological characters using pertinent literature and original species descriptions.

The macromorphological ascomatal characters were observed in fresh and dried material. Dried ascomata were hand-sectioned and fragments were examined in water and Melzer’s reagent or 5 % KOH using an Olympus BX51 compound microscope with differential interference microscopy. Permanent slides were made using PVLG (Omar et al. 1979) with material rehydrated in 5 % KOH. Images were captured with a QImaging QColor3 digital camera and processed using Adobe Photoshop v. 7.0 (Adobe Systems Inc., Mountain View California). A minimum of 30 measurements were made for each micromorphological character using NIH Image (National Institutes of Health, Bethesda, Maryland) and standard univariate statistics were performed on these measurements (Table 1). Acronyms for fungaria follow Index Herbariorum (Thiers 2013). Recent collections were georeferenced and the coordinates reported in WGS 84 format.

Total genomic DNA was extracted from dried ascomata using a QIAGEN DNeasy Plant Mini Kit (QIAGEN Inc., Valencia, California) and gene fragments were PCR amplified and sequenced using methods outlined by Promputtha and Miller (2010). The internal transcribed spacer (ITS) region of nuclear ribosomal DNA (nrDNA), consisting of the ITS1, 5.8S, and ITS2 regions, was amplified and sequenced using a combination of the primers ITS1, ITS4, and ITS5 (White et al. 1990). The 28S large subunit (LSU) nrDNA region was amplified and sequenced using primers JS1 (Landvik 1996) and LR3 (Vilgalys & Hester 1990).

Individual gene alignments were created manually in Sequencher v. 5.0.1 (Gene Codes Corp., Ann Arbor, Michigan) and optimized using Muscle v. 3.7 (Edgar 2004) in SeaView v. 4.2 (Galtier et al. 1996). Ambiguous regions were removed from each dataset using Gblocks v. 0.91b (Castresana 2000) under the following parameters: minimum number of sequences for both conserved and flanking regions=12, maximum number of contiguous non-conserved positions=4, minimum length of a block=4, and allowed gap positions in 12 sequences. GTR+I+G was determined by the Akaike Information Criterion (AIC) (Posada & Buckley 2004) to be the best-fit model of evolution by jModelTest v. 0.1.1 (Posada 2008) for both individual gene datasets. Maximum likelihood (ML) analyses were performed with PhyML (Guindon & Gascuel 2003) under the GTR substitution model with six rate classes and invariable sites optimized. An unrooted BioNJ starting tree was constructed and the best of nearest neighbor interchange (NNI) and subtree pruning and regrafting (SPR) tree improvement was implemented during the heuristic search. Nonparametric bootstrap support (BS) (Felsenstein 1985) was determined with 100 replicates. Clades with BS support ≥ 70 % were considered significant and highly supported (Hillis & Bull 1993).

Bayesian inference employing a Markov Chain Monte Carlo (MCMC) algorithm was performed using MrBayes

Table 1 Macromorphological and micromorphological characters of examined collections of *Geoglossum simile*, presented as mean ± standard deviation of 30 measurements for each microcharacter (with minimum/maximum values in parentheses). CA Canada, CZ Czech Republic, NL Netherlands, SK Slovakia, SW Sweden, UK United Kingdom, USA United States

Locality (# of specimens measured)	Spores (µm)	Asci (µm)	Paraphysis apical cell (µm)	Ascomata length (mm)	Fertile Hymenium (mm)	Sterile stem (mm)
CA (1)	(91-)96.94-108.58 (-112.91) × (5-) 6.58-8.52(-9.6)	(169-)169.55-205.83(-213.9) × (25.9-)26.5-29.94(-30.1)	(8.2-)9.5-13.6(-16.8) × (5.7-) 28.7.6(-8.34)	59	22 × 5	35 × 2.5
CZ (12)	(60-)73.1-89.9(-108) × (4.7-) 6.6-7.8(-11)	(155.8-)173.2-197.6(-221.8) × (16.5-)24.2-29.6(-36)	(7-)9.7-14.1(-20) × (4-)5.1-7.3 (-10)	(21-)38-64(-78)	(4-)11-19(-25) × (1-)2-4(-4)	(15-)26-48(-60) × 0-2(-3)
NL (1)	(80-)85-94.6(-100) × 6.9-7.7(-8)	(165-)171.4-194.4(-200) × 24.6-26.8(-27)	(7-)9.8-13(-15) × (5-)5.9-8.1 (-10)	(51-)50-58	11-13(3) × 2	39-45 × 1
SK (4)	(60-)75.1-90.5(-100) × (6-) 6.6-7.6(-8)	(167-)180-200.8(-210) × (23-) 25-28.8(-32)	(7-)9.7-12.9(-16) × (5-)5.4-7.4 (-9)	(30-)32-66(-80)	8-22(-35) × (2-)3-5(-7)	(20-)21-47(-52) × 1-3
SW (3)	(86-)88.7-93.9(-95) × (7-) 6.8-7.6(-8)	(185-)189.2-207.6(-210) × (26-) 26.9-30.9 (-33)	(10-)11.3-14.7(-15) × (6-) 6.6-8.2(-9)	70	30 × 4	40 × 1
UK (1)	(64.2-)71.4-86.9(-97.9)	(154-)171.3-200.7(-212) × (18.9-)19.9-22.4(-23.8)	(6.9-)8.4-9.8(-14.1) × (4.1-) 5.2-7.6(-9.2)	34	13.1 × 3	26.2 × 1.4
USA (8)	(84-)90.1-100.5(-105) × (6-) 6.9-7.9(-8)	(170-)178.6-196.2(-210) × (25-) 26.3-31.7(-35)	(8-)9-11.6(-14) × 5-6.8(-8)	(22-)45-62(-80)	(3.6-)5-9(-9) × 2-4	13-21(-22) × 1
Ft. Edward Lectotype (NYS #2797)	(80.2-)82.2-89.8(-94.4) × (7-) 6.8-7.6(-8)	(172.3-)178.1-199.3(-208) × (23.6-)25-29(-30.7)	(8-)9.5-13.3(-16.5) × (7-) 6.7-8.1(-9.4)	No data	No data	No data
Epitype (CORT 005220; ILLS 71160)	(75.6-)81-94(-102) × (6.5-) 7.1-8.0(-9.1)	(171.4-)180.1-194.8(-205) × (22.3-)24.1-27.6(-31.1)	(7.9-)9.0-13.6(-15.7) × (5.4-) 6.7-7.3(-9.5)	(35-)33-59(-75)	(6-)8.6-21(-26) × (3-) 5.1-7.4(-11)	(21-)30-39(-49) × (1.2-) 2.1-3.0(-4.4)

3.1.2 (Huelsenbeck & Ronquist 2001) on the CIPRES Science Gateway Teragrid (Miller et al. 2010) as an additional method of determining branch support. The GTR+I+G model with six rate classes was employed. Four independent chains of MCMC were run for 10 million generations. Clades with Bayesian posterior probability (BPP) of ≥95 % were considered significantly supported (Alfaro et al. 2003). Effective sample size (ESS) was estimated using Tracer v. 1.6 (Rambaut & Drummond 2009).

Individual datasets of ITS and LSU were examined for potential conflict before being concatenated into a single dataset for total evidence analysis (Kluge 1989, Eernisse & Kluge 1993). Individual gene phylogenies were considered to be incongruent if clades with significant ML BS and BPP were conflicting in the individual tree topologies (Wiens 1998, Alfaro et al. 2003, Lutzoni et al. 2004). Since no incongruencies were found among individual datasets, the ITS and LSU datasets were concatenated and final ML and Bayesian analyses were performed on the combined dataset. Alignments and trees are deposited in TreeBASE (<http://treebase.org>) under submission ID 15095.

A total of 32 specimens of *Geoglossum simile*, including the Fort Edward lectotype and the newly-designated epitype from Cortland County, New York were examined (Table 1). Twenty-two sequences were newly generated for this study (11 ITS, 11 LSU). These sequences were analyzed together with 20 sequences from previous studies (Hustad et al. 2011, 2013), along with four sequences from GenBank. Sequences from 23 collections, representing twelve collections of *G. simile* and eleven collections representing eight closely-related outgroup species (Hustad et al. 2013) were included in the analyses (Table 2).

Results

The final combined matrix had an aligned length of 1265 bp, which was reduced to 1173 after the removal of 92 ambiguous characters by Gblocks. Of the 1173 characters used in the phylogenetic analyses, 1019 of the sites were complete (no gaps or missing characters in any of the sequences), 221 of the complete sites were variable across the dataset, and 110 (10.8 %) of these variable sites were informative. We estimated burn-in of 10 % was sufficient to remove the pre-stationary posterior probability distribution using Tracer v.1.6, resulting in an ESS of 212.5797. The most likely tree produced by the PhyML analysis of the concatenated ITS and LSU dataset is shown in Fig. 1. Sequences from *Geoglossum simile* form a strongly supported clade (BS=100 %, BPP=1.0) with *G. sphagnophilum* occurring as a sister species to *G. simile*.

Table 2 List of taxa, collection numbers, fungarium accession numbers and GenBank accession numbers for specimens used in this study

Taxon Name	Coll/Strain #	Fungarium ID	ITS	LSU
<i>Geoglossum barlae</i>	Moingeon s.n.	ILLS 61034	JQ256416	JQ256433
<i>Geoglossum difforme</i>	V. Hustad 25	ILLS 67348	KC222123	KC222136
<i>Geoglossum difforme</i>	A. Methven 10498	ILLS 67349	KC222124	KC222137
<i>Geoglossum fallax</i>	J. Gaisler s.n.	ILLS 61037	JQ256419	JQ256435
<i>Geoglossum glabrum</i>	A. Miller 22257	ILLS 61035	JQ256417	JQ256434
<i>Geoglossum glabrum</i>	J. Gaisler s.n.	ILLS 67347	KC222122	KC222135
<i>Geoglossum glabrum</i>	OSC 60610	GenBank	AY789318	AY789317
<i>Geoglossum simile</i>	A. Miller 2171	ILLS 61039	JQ256421	JQ256437
<i>Geoglossum simile</i>	A. Methven 10528	ILLS 67350	KC222125	KC222138
<i>Geoglossum simile</i>	M. Melicharová s.n.	SAV 10129	KF854286	KF854294
<i>Geoglossum simile</i>	V. Kučera, J. Gaisler, V. Kautman s.n.	SAV 10730	KF854287	KF854295
<i>Geoglossum simile</i>	V. Kučera, J. Gaisler, V. Kautman s.n.	SAV 10731	KF854288	KF854296
<i>Geoglossum simile</i>	J. Gaisler s.n.	SAV 10691	KF854289	KF854297
<i>Geoglossum simile</i>	V. Kučera s.n.	SAV 10587	KF854290	KF854298
<i>Geoglossum simile</i>	I. Kautmanová s.n.	SAV 9063	KF854291	KF854299
<i>Geoglossum simile</i>	V. Kučera s.n.	SAV 9069	KF854292	KF854300
<i>Geoglossum simile</i>	M. Zajac s.n.	SAV 10136	KF854293	KF854301
<i>Geoglossum simile</i>	T. Baroni 9613	CORT 005220; ILLS 71160	KF944381	KF944383
<i>Geoglossum simile</i>	T. Galante 9	CORT 005221	KF944382	KF944384
<i>Geoglossum sphagnophilum</i>	Poumarat s.n.	ILLS 67351	KC222126	KC222139
<i>Geoglossum uliginosum</i>	V. Kučera s.n.	SAV 10162	KJ152695	KJ152696
<i>Geoglossum umbratile</i>	Mycorec 1840	GenBank	AY789304	AY798303
<i>Glutinoglossum glutinosum</i>	J. Gaisler s.n.	ILLS 67353	KC222129	KC222142

Taxonomy

Geoglossum simile Peck.

= *Geoglossum glabrum* var. *simile* (Peck) S. Imai, Trans. Myc. Soc. Jap. 3: 52. 1962.

Mycobank MB 162582.

Syntype: USA, New York, Rensselaer County, Sand Lake [as ‘Sandlake’], Adirondack Mountains, C.H. Peck, September 1873 (NYS, lost).

Lectotype: USA, New York, Washington County, Fort Edward, E.C. Howe, 1873 (NYS f2797) – designated here. Fig. 2.

Epitype: USA, New York, Cortland County, Kennedy State Forest, Scutt Hill Road, T.J. Baroni [TJB 9613], 10 August 2003 (CORT 005220; isoepitype ILLS 71160) – designated here. Fig. 3.

Emended description

Ascomata (21-) 39-65 (-80) mm high, solitary, club-shaped, stipitate. Fertile part lanceolate, more or less compressed, (4-) 9.7-19.2 (-35) mm long, (1-) 2-4 (-7) mm thick, apex usually subacute to obtuse, blackish-brown, differentiated from the sterile stipe, sometimes with a narrow median groove. Stipe

gracile, cylindrical above, terete, minutely pubescent or glabrous when fresh, forming acute tufts and squamulose when dried (Fig. 3a and c), brownish-black with dark cinnamon brown base, (15-) 26-48 (-60) mm long, 0.5-2 (-3) mm thick. Asci (155-) 175-200 (-220) × (16.5-) 24.5-29.5 (-36) μm, 8-spored, clavate or lanceolate to narrowly tapered towards the apex, the pore bluing in Melzer’s reagent. Ascospores (60-) 74-91 (-108) × (4.7-) 6.6-7.8 (-11) μm, in parallel fascicle, 7-septate (though 8- and 9-septate ascospores rarely seen), dark fuliginous, cylindrical to clavate or slightly narrower at one end, slightly curved (Figs. 2b and 3b). Paraphyses filiform, pale brown in upper part, straight or curved, (though often sigmoid at the terminal end) moderately to closely septate in the upper part constricted to form barrel-shaped segmented cells resembling didymospores (often forming chains of three or more such cells in sequence at the terminal end), protruding beyond the asci, the apical cell (7-) 9.7-13.9 (-20) × (4-) 5.3-7.3 (-10) μm (Figs. 2c and 3d).

Habitat

Geoglossum simile occurs in Europe most commonly in peat bogs and wet meadows among mosses. In North America the species is commonly found on moss-covered soil and humus

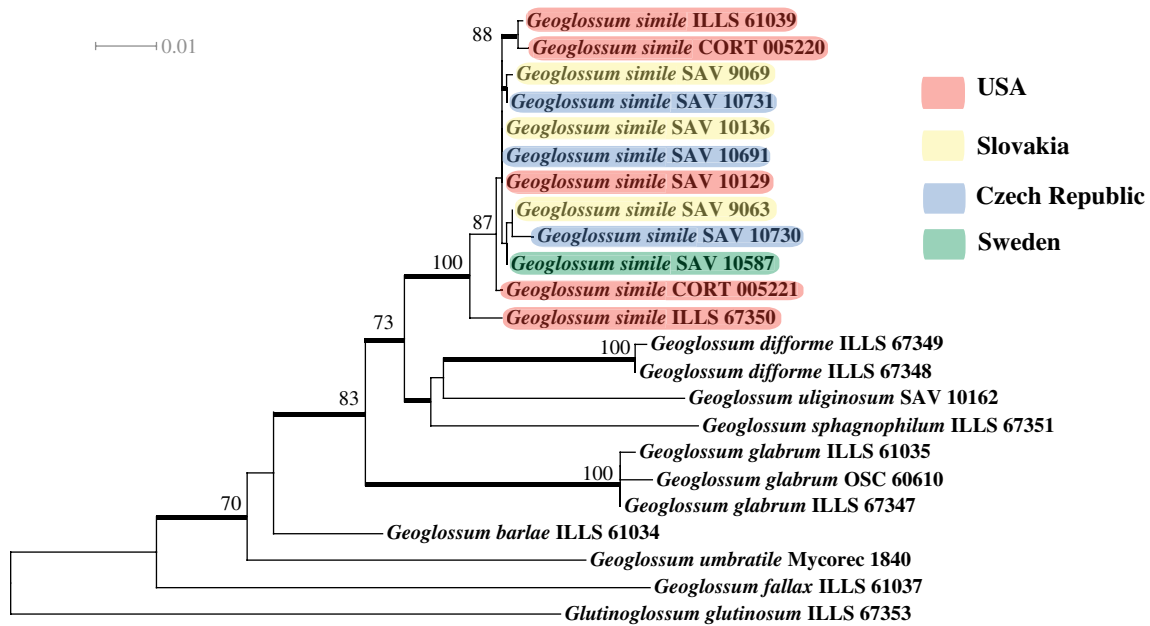


Fig. 1 PhyML maximum likelihood phylogeny showing the position of *Geoglossum simile* based on a combined dataset (1173 bp) of ITS and LSU DNA sequences ($(-\ln)L$ score=3866.3). Numbers at nodes indicate significant BS values (≥ 70 %) based on 100 replicates; thickened

branches indicate significant BPP (≥ 95 %). Several species of *Geoglossum* and *Glutinoglossum glutinosum* are included as outgroups. Numbers associated with taxon names are fungarium accession numbers or strain numbers obtained from GenBank

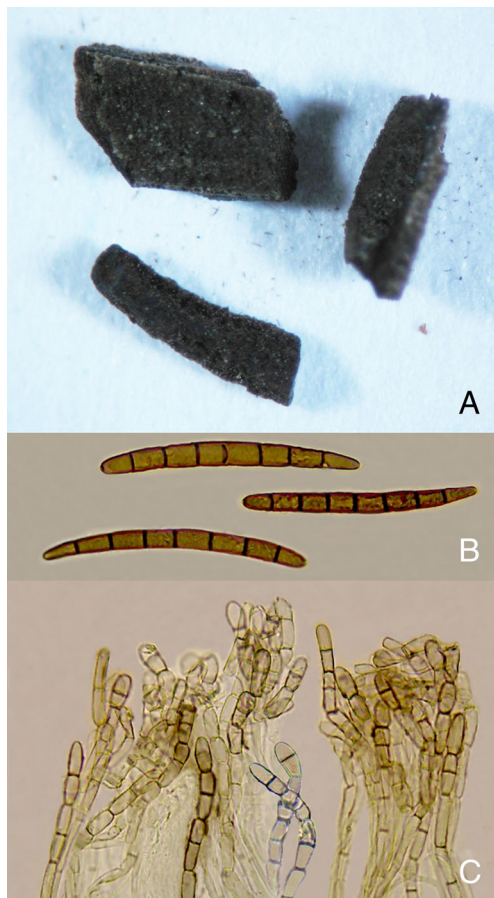


Fig. 2 Images of material from Ft. Edward lectotype of *Geoglossum simile*. **a** Macroscopic image of collection (total magnification=24 \times), **b** Ascospores (total magnification=400 \times), **c** Paraphyses (total magnification=400 \times)

in mixed deciduous forests. According to the literature, it also is found on soil (Nannfeldt 1942, Zhuang and Wang 1997), as well as in swamps, bogs and well-drained soil (Mains 1954), damp pasture (Jørgensen & Vevle 1968, Ohenoja 2000), soil in *Cedrus* or *Quercus* forest (Maas Geesteranus 1965), on rotten logs (Nannfeldt 1942), and among *Sphagnum* (Nannfeldt 1942, Mains 1954) and other mosses (Mains 1954).

Conservation

Earth tongues are widely collected and studied in North America and Europe and their presence in a particular habitat often indicates limited human disturbance. Earth tongue species diversity has been used as a proxy for grassland health in conservation value assessments (Newton et al. 2003, Genney et al. 2009). *Geoglossum simile* is present on several Red Data Lists throughout Europe, listed as *threatened with extinction* in Austria (Aron et al. 2005) and Germany (Sonneborn et al. 2005), *critically endangered* in Denmark (Stoltze & Pihl 1998), *vulnerable* in The Netherlands (Arnolds & Veerkamp 2008), and *near threatened* in Norway (Fandnes 2011). In Sweden, *G. simile* is listed as *not threatened* (Gärdenfors 2010), even though the species is often found in the same habitat as *G. uliginosum*, a very rare and endangered species in Sweden according to a National Biodiversity Action Plan from 2007-2011 (Nitare 2007). The species was listed as one of three Ascomycetes believed to be extinct in the provisional Red Data List of British fungi (Ing 1992), although Mackey et al. (2011) recognized *G. simile* as a characteristic species of

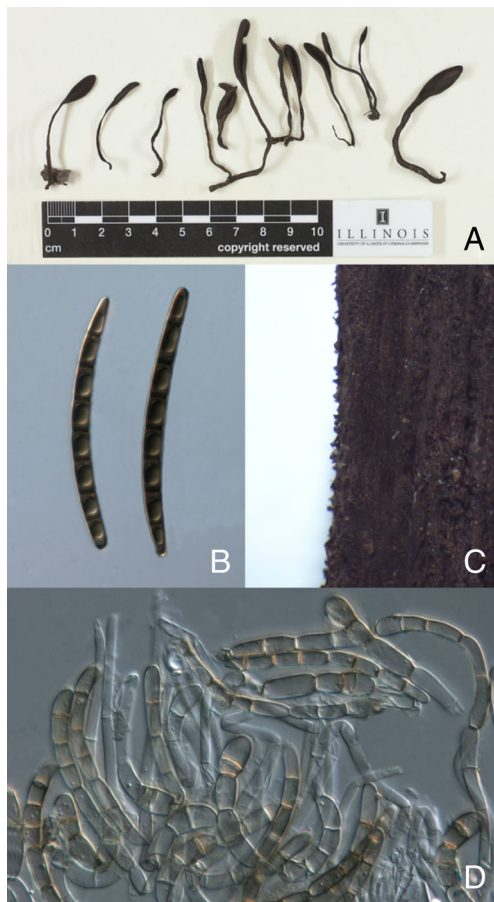


Fig. 3 Images of newly designated epitype of *Geoglossum simile* (CORT 005220; ILLS 71160). **a** Dried ascomata of the epitype collection; **b** Ascospores (total magnification=320×); **c** Stipe showing characteristic squamulose tufts (total magnification=12.5×); **d** Paraphyses (total magnification=400×)

High Nature Value Farmland. Though the conservation status of *G. simile* has not been formally assessed in eastern North America, it should likely be regarded as *least concern* due to the abundance of the species in second-growth forests.

Distribution

Asia: China (Zhuang and Wang 1997, Zhuang 1998), India (Batra & Batra 1963, Thind & Sing 1964, Maas Geesteranus 1965, Prasher & Sharma 1997), Japan (Imai 1941); Australasia: Australia (Beaton & Weste 1979); Europe: Austria (www.gbif.org), Czech Republic (this paper), Denmark (Bille-Hansen 1954, Ohenoja 2000), Estonia (www.gbif.org), France (Priou 1992, Moingeon & Moingeon 2003), Germany (Benkert 1976, www.gbif.org), Norway (Eckblad 1963, Jørgensen & Vevle 1968, Olsen 1986), Slovakia (this paper), Sweden (Hakelien 1964, Nitare 1988, Turander 2012), Switzerland (www.gbif.org), United Kingdom (www.gbif.org); North America: Canada (Nannfeldt 1942, Mains 1954, Voitk 2013),

Greenland (Petersen & Korf 1982), USA (Peck 1873, Nannfeldt 1942, Mains 1954).

Specimens examined

CANADA: Nova Scotia, Annapolis County, Melvern Square Vault, 3. IX. 1973, K.A. Harrison (ILLS 71106).

CZECH REPUBLIC: Jizerské hory Mountains, Nature Reserve “Jizerka peat bog” 500 m N from “Pešákovna” chalet, Q 5158c, 50°49'45.6" N, 15°20'12.6" E, 882 m, at the margin of peat bog with *Molinia caerulea* and *Sphagnum* sp., 25. VIII. 2012, J. Gaisler (SAV 10689), (SAV 10686), (SAV 10681), (SAV 10682). – 380 m NW from “Pod Bukovcem” chalet in Jizerka settlement, Q 5158c, 50°48'52.9" N, 15°20'59.1" E, 891 m, moist meadow with *Sphagnum* sp., *Carex* spp., *Juncus* spp., 25. VIII. 2012, J. Gaisler (SAV 10687). – 280 m NE from “Pyramida” chalet in Jizerka settlement, Q 5158c, 50°49'11.2" N, 15°20'58.8" E, 856 m, in peat bog with *Pinus mugo* and *Molinia caerulea*, 9. VIII. 2012, J. Gaisler (SAV 10685), (SAV 10679), (SAV 10680). – 50 m N from “Granit” chalet, Horní Černá Studnice village, Q 5257c, 50°42'38" N, 15°13'08" E, 760 m, in moist meadow with *Sphagnum* sp., *Carex* spp. and *Juncus* spp., 29. VII. 2009, Z. Egertová, M. Kříž s.n. (SAV 10683) – 270 m NE from “Pyramida” chalet in Jizerka settlement, in ditch near road, 50°49'10.2" N, 15°21'0.5" E, 857 m, in *Sphagnum* sp. and *Molinia caerulea*, V. Kučera, J. Gaisler, V. Kautman (SAV 10731). – 320 m SE from “Javor” chalet in Jindřichov village, Q 5257c, 50°44'47.8" N, 15°11'54.4" E, 581 m, in moist meadow with *Sphagnum* sp., *Carex* spp., *Juncus* spp. and *Cirsium palustre*, 7. VIII. 2011, J. Gaisler (SAV 10671). – Horní Maxov, 300 m E from “U náhonu” chalet and 40 m from a small pond, Q 5257a, 50°45'59.8" N, 15°11'59.5" E, 711 m, in wet meadow with *Sphagnum* sp., *Carex* spp. and *Juncus* spp., 7. VIII. 2011, J. Gaisler (SAV 10955).

NETHERLANDS: Gelderland, Lochem, in old meadows with *Carex* sp. and *Juncus* sp., 28. VII. 2012, C.F. Roobeek (SAV 10956).

SLOVAKIA: Laborecká vrchovina Mts., Natural Reserve Haburské rašelinisko peat bog, ca 5 km NNE from the Habura village, Q 6697a, 49°22'11" N, 21°53'09" E, 682 m, in *Sphagnum* sp., 20. IX. 2006, V. Kučera (SAV 9061), (SAV 9070). – Nízke Tatry, village Liptovská Teplička, in peat bog pod Sol'ankou“, 48°58'44" N, 20°02'52" E, 920 m, 9. IX. 2006, V. Kučera, I. Kautmanová (SAV 9063). – Kysuce, village Raková, peat bog with *Sphagnum* sp., 42°29'18.59" N, 18°40'44.2" E, 677 m, 10. IX. 2009, M. Zajac (SAV 10136).

SWEDEN: Närke, Sköllersta, ca 1 km S of Hälla, drained swamp, 06. IX. 1964, N. Hakelien (UPS F-122051). – Värmland, Övre Ullerud, slightly damp pasture, 22. VIII. 1991, Bo Jansson (UPS F-599179). – Vadkärn, municipality of Varberg, pasture, in grass, 57°16'23.5" N, 12°23'08.3" E, 16. IX. 2012, V. Kučera (SAV 10587).

UNITED KINGDOM: England, Dunsop Valley, Forest of Bowland, wet, acid soil, associated with *Poaceae* and short grass, 5. X. 1997, I. Ridge (ILLS 71105).

UNITED STATES: Kansas, Sedgwick County, Derby, City Park, 18. VI. 2010, M. Melicharová (SAV 10129). – Michigan, Chippewa County, Detour, Hardwoods, 20. VIII. 1949, H.A. Imshaug (ILLS 3768). – New York, Cortland County, Kennedy State Forest, Scutt Hill Road, 10. VIII. 2003, T.J. Baroni (TJB 9613) (CORT 005220; ILLS 71160). – Hamilton County, Raquette Lake, Long Point, 21. VII. 2007, T. Galante (TG 9) (CORT 005221) – North Carolina, Macon County, Nantahala National Forest, Standing Indian Campground, 35°04'33.79" N, 83°31'42.45" W, mixed deciduous forest, 3. XIII. 2004, A.S. Methven (ASM 10528) (ILLS 67350). – Haywood County, Great Smoky Mountains National Park, Cataloochee, Rough Fork Trail, 35°37' N, 83°7'15.8" W, 850 m, 14. VIII. 2009, R.E. Baird (ILLS 71108). – South Carolina, Ocone County, Walhalla Fish Hatchery, 34°59.155' N, 83°04.374' W, 14. VII. 2008, G. Presley, (ILLS 71104). – Tennessee, Blount County, Great Smoky Mountains National Park, Cades Cove, Junction of Sparks Lane and Cades Cove Loop Trail, on rotten wood, 35°36'23.5" N, 83°47'19.6" W, 533 m, 13. VIII. 2009, V.P. Hustad (ILLS 61039). – Cocke County, Great Smoky Mountains National Park, near Cosby, Madron Bald Trail 35°45'42.1" N, 83°16'15.7" W, 549–914 m, 21. X. 2009, V.P. Hustad (ILLS 71109).

Discussion

Sequences from twelve collections of *Geoglossum simile* from throughout Europe and North America were shown to be conspecific, occurring in a well-supported clade (100 % BS, 1.0 B.P. in our analyses. Furthermore, all sequenced collections of *G. simile* possess less than 3 % ITS sequence divergence across the entire ITS region (data not shown), further supporting our hypothesis that these collections are the same species (Hughes et al. 2009). Interspecific ITS variation between *G. simile* and *G. glabrum* was 10–11 % (data not shown), further casting doubt on the synonymy of these species.

We have chosen to make our typological changes in *Geoglossum simile* (designation of Ft. Edward syntype as the lectotype and designation of new material as the epitype for the species) for several reasons: 1) Peck's original collection of *G. simile* from Sand Lake has been lost, leaving only the syntype collection by Howe from Ft. Edward as the only known extant material that had been examined by Peck and this collection is designated here as the lectotype; 2) due to the age and deteriorating condition (Fig. 2a) of the Ft. Edward lectotype collection, molecular sequence data cannot be obtained and morphological study is limited, necessitating the designation of material of later provenance as

the epitype pursuant to Article 9.8 of the International Code of Nomenclature for algae, fungi, and plants (McNeill 2012); 3) the epitype collection is from New York and from similar forest as Peck's original material; and 4) the epitype collection consists of several ascomata in good condition (Fig. 3a).

The erroneous synonymy of *Geoglossum simile* under *G. glabrum* has likely resulted in inaccurate distribution records of *G. simile* as the species was not recognized as separate from *G. glabrum* until 1941, with Seaver considering the species synonymous as late as 1951. Imai later (1962) considered *G. simile* to be a variety of *G. glabrum* and designated the species as *G. glabrum* var. *simile*, although this synonymy was not accepted in subsequent taxonomic works on *Geoglossaceae* (Eckblad 1963, Hakelier 1964, Maas Geesteranus 1965, Benkert 1976, Ohenoja 2000, Roobeek 2009). Imai reasoned that the characteristic barrel-shaped terminal cells of the paraphyses of *G. simile* were also present in *G. cookeanum* Nannf., *G. glabrum* var. *americanum* Mains, *G. glabrum* var. *glabrum* sensu Mains, *G. glabrum* var. *inflatum* Mains, *G. glabrum* var. *sphagnophilum* (Ehrenb.) Fr., and *G. japonicum* S. Imai. Imai (1962) did not see enough dissimilarity in the varieties of *G. glabrum* described by Mains to be significantly distinguishable from one another and held to a broad taxonomic concept of *G. glabrum* with eight varieties of the species.

Geoglossum glabrum and *G. simile* are distinctive both macroscopically and microscopically. *G. glabrum* is characterized by a glabrous stipe, ascospores (55–) 65–80 (–90) × 6–8 μm, and paraphyses slightly longer than the asci with short chains of adherent darkened inflated globose cells toward the tips (Imai 1941, Nannfeldt 1942, Mains 1954). *Geoglossum simile* has a more gracile stem roughened with acute tufts or squamules of paraphyses on the stipe (especially when dry), slightly longer ascospores ((70–) 75–85 (–100)), though the ascospores of the Ft. Edward lectotype were even longer (80–) 82–90 (–94)), and paraphyses characterized by barrel-shaped elements at the terminal cells. Lastly, the habitats of the two species are different with *G. glabrum* nearly always found associated with *Sphagnum*, whereas *G. simile* is found in a diversity of habitats ranging from soil, humus, rotten logs, and associated with *Sphagnum*.

Durand undertook the most significant study of the original syntype material collected at Sand Lake by Peck. Although he considered Peck's material to represent *Geoglossum glabrum*, his illustration of the paraphyses of the Sand Lake collection (Fig. 53, Durand 1908), clearly shows the characteristic barrel-shaped terminal cells of the paraphyses in *G. simile*, a character that is not depicted in other illustrations of *G. glabrum* (or any other *Geoglossum*) in his monograph. Mains (1954) also examined Peck's Sand Lake collection and reported similar measurements and morphologies to both the Ft. Edward lectotype and our designated epitype.

Other species of *Geoglossum* have been placed in synonymy with either *G. glabrum* or *G. simile*. *G. cookeanum* is morphologically similar to *G. glabrum*, with the major distinction being the lack of dark pigmentation at the terminal cells of the paraphyses, weaker adherence of paraphyses, and greater variation in size of the terminal cells. These characters were considered distinctive enough for Nannfeldt (1942) to separate *G. cookeanum* from *G. glabrum*, and the treatment of this taxon as a separate species was accepted in nearly every subsequent publication on *Geoglossaceae* (Bille-Hansen 1954, Maas Geesteranus 1964, Benkert 1976, Ohenoja 2000), with the notable exception of Mains (1954), who believed the differences to represent simple variation and placed *G. cookeanum* as a synonym under *G. glabrum*. Spooner (1987) listed *G. glabrum* as a synonym under *G. cookeanum* based on the lack of reliable type material for *G. glabrum* from Persoon's collections. The validity of synonyms of *G. glabrum* is of taxonomic relevance and will be addressed in a future study.

Geoglossum japonicum was accepted by Imai (1962) as another variety under *G. glabrum*. The paraphyses of *G. japonicum* are more similar to *G. cookeanum* and differ from *G. simile* in having end cells which are irregularly and strongly-curved to circinate. The ascospores of *G. japonicum* were reported by Imai (1941) as $60\text{--}97.5 \times 6\text{--}8 \mu\text{m}$, well within the range of *G. simile*. Although we have not examined the type material of *G. japonicum*, the distinctive paraphyses of this species seem sufficient to separate this species from both *G. simile* and *G. glabrum*.

Imai (1962) also specifically mentioned three other varieties of *Geoglossum glabrum* (*G. glabrum* var. *americanum*, *G. glabrum* var. *inflatum*, *G. glabrum* var. *sphagnophilum*) as showing the characteristic paraphyses of *G. simile*. *Geoglossum glabrum* var. *americanum* is the most distinct of the three varieties with paraphyses strongly constricted at the septa and producing globose upper cells, which bear little resemblance to *G. simile*. *Geoglossum glabrum* var. *inflatum* has paraphyses that are rarely constricted at the terminal septum, but also rarely produce two-celled elements, a common and often noticed character in nearly all collections of *G. simile*.

Geoglossum glabrum var. *sphagnophilum* (= *G. sphagnophilum*) is currently regarded as a synonym of *G. glabrum*, based on similarities of paraphyses, ascospores, and habitats for both taxa. However, as indicated in Fig. 1, the specimen identified as *G. sphagnophilum* does not group with either *G. glabrum* or *G. simile* in our analyses. Our data supports the treatment of these taxa as two separate species. The validity of the name *G. sphagnophilum* and a phylogenetic treatment of this species and other synonyms of the *G. glabrum* group will be addressed in a future publication.

Confusion over the identity and taxonomical status of *Geoglossum simile* has resulted from the variability that occurs in its paraphyses and the inadequate amount of material

that has been studied. Measurements of asci and ascospore sizes are very similar in all studied specimens, with no significant differences observed between Slovak and Czech specimens, other European material, or from the lectotype specimen and other North American material. Minor differences were observed in the shape of paraphyses and in the size of apical cells of the paraphyses, with variation occasionally noticed in different ascomata of the same collection. Thinner apical cells were observed in collections from the Czech Republic (SAV 10686) and USA (SAV 10126): $8\text{--}14 \times 5\text{--}7 \mu\text{m}$ and $9\text{--}11 \times 5\text{--}6 \mu\text{m}$, respectively, while thicker apical cells ($7\text{--}12 \times 9\text{--}10 \mu\text{m}$) were observed in a collection from Sweden (SAV10587). In one collection from Slovakia (SAV 9063) we observed variable apical cells in the paraphyses, both thin ($9\text{--}10 \times 5\text{--}6 \mu\text{m}$) and thick ($10\text{--}15 \times 7\text{--}10 \mu\text{m}$), in the same ascoma. This variability in apical cell diameter appears to be normal variation within the species.

Conclusions

Our analyses indicate that all collections of *G. simile* we examined from Europe and North America represent a single, widespread species. We observed strong uniformity in morphological characters, which overlapped within one standard deviation of one another, among most European and North American collections. Although variation was observed in the morphology of the paraphyses, specifically the size of the apical terminal cells, there was no correlation between these characters and molecular data. Molecular evidence generated in this study further indicates that all collections of *G. simile* sampled are conspecific, with less than 3 % intraspecific sequence divergence observed in the ITS gene.

Acknowledgments The authors wish to thank the following for graciously providing specimens for study and analysis: RE Baird, AS Methven, I Ridge, CF Roobeek, and the fungaria ILLS, MICH, NYS, and SAV for the loan of specimens and assistance. Lastly, we acknowledge the following sources of funding: American Society of Plant Taxonomists, Discover Life in America, Mycological Society of America, Slovak Academy of Sciences (grants VEGA 2/0150/12 and VEGA 2/0088/13), and a grant from the Czech Republic Ministry of Agriculture (MACR 0002700604).

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