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The Caucasian corticioid fungi: level of endemism, similarity, and possible contribution to European fungal diversity

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Abstract We assess the composition of corticioid fungi in the Caucasus region for the first time. The Caucasian corticioids were compared with those of well-documented areas in the Northern Hemisphere using the Tripartite similarity index and cluster analysis. To investigate the significance of the Caucasus region as a possible contributor to the colonization of wood-inhabiting basidiomycetes in Europe, DNA sequences of nuclear ribosomal internal transcribed spacers (ITS1 and ITS2) belonging to the corticioid fungus *Peniophorella praetermissa* were analysed for comparisons of genetic diversity within and differentiation between geographical regions. Putative species endemism and disjunction of corticioids in the Caucasus region is also discussed. The composition of corticioid fungi in the Caucasus region was found to be

distinctly more similar to Europe and North America than to East Asia and India. Similarity tests and molecular *Fst*s both point to a strong connection between the Caucasus and Europe. The highest molecular diversity in *P. praetermissa* was in the Caucasus and East Asia as compared with other regions studied. The Caucasus and East Asia were significantly differentiated from each other, and unlike Caucasian samples, East Asian sequences were highly divergent from the European ones. This result suggests that the Caucasus might have been a source of colonization for Europe. Endemism is very low, possibly a common feature for wood-inhabiting saprotrophic fungi.

Keywords Basidiomycota · Checklists · Genetic diversity · Glacial refugia · Saprotrophic wood-inhabiting basidiomycetes · Tripartite similarity index

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Introduction

Due to the repeated Pleistocene glaciations, the biota in many parts of the Northern Hemisphere diminished or drastically changed. The present temperate forest vegetation in the Northern Hemisphere was mostly in the form of interrupted and sparse forest cover, steppes, tundra or otherwise under ice only 20,000 years ago during the Last Glacial Maximum (LGM; Ray and Adams 2001; Svenning et al. 2008). However, the severe cold periods were interrupted by more favourable climatic conditions that enabled biota to reclaim the areas without ice-cover (Huntley and Webb 1988). Based on pollen records, it can be concluded that vegetation within the same area differed between different interglacial periods (Cheddadi et al. 2005), which emphasizes the importance of ‘source’ areas and refugia in development of the biota in the areas devoid

of vegetation. Such relict areas are found today with vegetation that has persisted since the time of the LGM (Taberlet et al. 1998; Tarasov et al. 2000; Milne 2006), and a few of them are in the Caucasus region (Tarasov et al. 2000; Tumajanov 1971; see Suppl. Fig. 1).

The Caucasus region is one of the hotspots of biodiversity (Myers et al. 2000), with considerable species richness as well as a high number of endemic, rare and threatened species (Kremer et al. 2001). The region is categorized among the IUCN's recognized centres of plant diversity and endemism (Davis et al. 1995). With its western Palearctic glacial refugia, collectively known as Colchis and Hyrcan (Tumajanov 1971; Volodicheva 2002), the region has been shown as a contributor to the European recolonization of biota after retreat of glaciers, documented through recent palynological and phylogeographical studies (e.g., Tarasov et al. 2000; Brunhoff et al. 2003; Atkinson et al. 2006; Randi 2006; Kotlík et al. 2008). The fungal composition of the Caucasus has, however, largely escaped empirical scrutiny. Our study seeks to address the connections between the corticioid fungi of the Caucasus region with that of Europe, compared with North America, East Asia, and India (see Suppl. Table 1). The corticioid fungi are a group of predominantly saprotrophic basidiomycetes with simple and mostly effused fruiting body configurations and colonizing dead wood. According to the recent studies by MG and colleagues on Caucasian wood fungi (Ghobad-Nejhad et al. 2009; Ghobad-Nejhad 2011), some 380 species of corticioids are known to occur in the region. In this study, we also investigate the possible contribution of the region to the present mycota of Europe, by analysing the genetic diversity within and between populations of the widespread corticioid species *Peniophorella praetermissa* (P. Karst.) K.H. Larss. (Hymenochaetales, Basidiomycota), based on samples from different parts of its range. Finally, putative species endemism and disjunction of corticioids in the Caucasus region are discussed.

Materials and methods

Checklist analysis We compared corticioid fungi of the Caucasus region with those of Europe (northern, eastern-central, and southern or Mediterranean), North America (western, eastern), East Asia, and India, based on the availability of updated and reliable species lists. Similarity between the corticioid species of the Caucasus and the areas listed above was addressed by employing a Tripartite similarity index (Tulloss 1997; Tulloss and Tulloss 2004). This index (T) takes into account not only the number of entries common between two lists, but also the number of entries in one list that are not present in the other list (see Tulloss 1997). To increase sensitivity to several aspects of

input data, T employs cost functions into its three elements U, S, and R which are calculated as the following:

$$U = \frac{\log\left(1 + \frac{\min(b,c)+a}{\max(b,c)+a}\right)}{\log 2}$$

$$S = \sqrt{\frac{\log 2}{\log\left(2 + \frac{\min(b,c)}{a+1}\right)}}$$

$$R = \frac{\log\left(1 + \frac{a}{a+b}\right) \cdot \log\left(1 + \frac{a}{a+c}\right)}{(\log 2)^2}$$

where a is the number of entries common to both lists, b is the number of entries in the first list that are not in the second, and c is the number of entries in the second list that are not in the first. U corrects for the difference in the size of the two lists being compared. S provides a penalty for the difference between the size of a and the smaller of the two lists being compared. R takes into account whether a covers a fraction (percentage) of one list that is different from that of the other list (see Tulloss 1997). The T is obtained by multiplying the three cost functions:

$$T = U \times S \times R$$

The value of T ranges from 0 to 1, where 0 indicates no elements in common while 1 indicates that the two lists are identical (Tulloss 2005).

We calculated the T index for the three largest corticioid genera in the Caucasus region, i.e. *Hyphodontia*, *Phlebia*, and *Peniophora* (see Ghobad-Nejhad et al. 2009). These genera represent different ecological guilds, inhabiting dry branches and twigs in exposed habitats, or decayed wood in humid habitats (Suppl. Table 2). The occurrence of these genera in the Caucasus region was compared with their presence in the areas as defined above. To check if T values would differ by checklist size, similarity between the total corticioids of the Caucasus and the total corticioids of the above mentioned areas was also calculated using the T index. The species data come from well-edited checklists surveyed or assembled from available publications (Suppl. Table 1) or received from specialists, and the specimens examined by us. Available publications include Akulov et al. (2003); Andreasen and Hallenberg (2009); Bemicchia and Gorjón (2010); Breitenbach and Kränzlin (1986); Dai (2010); Dai et al. (2004); Dämon (2001); Denchev and Assyov (2010); Ginns and Lefebvre (1993); Hansen and Knudsen (1997); Hjortstam and Ryvarde (1984); Hjortstam et al. (1998); Kotiranta et al. (2009); Langer (1994); Lee and Jung (2005, 2006); Lee et al. (2002); Legon et al. (2005); Lim et al. (2005); Maurer et al. (2009); Natarajan and Kolandavelu (1998); Parmasto (1986); Rattan (1977); Ryvarde (2010);

Ryvarden et al. (2003); Yurchenko (2010), and some other sources pointed out in Suppl. Table 1. The size of the checklist compiled for each area is shown in Suppl. Table 3 (lists available from the corresponding author).

An agglomerative hierarchical cluster analysis was performed for each genus and for total corticioids to further deduce the similarity of the Caucasus to the seven geographical locations mentioned above, using R v. 2.8.1 (R Development Core Team 2008) with the Euclidean metric and compact method. UPGMA dendrograms were computed with the Jaccard coefficient, and bootstrap branch supports were calculated using WinBoot (Yap and Nelson 1996) with 1,000 replicates. Bootstrap support values were superimposed on the tree obtained in R.

Genetic diversity Haplotype analysis was performed for the widespread corticioid species *Peniophorella praetermissa*. The nuclear ribosomal internal transcribed spacer (ITS1, 5.8S, ITS2) dataset by Hallenberg et al. (2007) was modified and supplemented with new sequences (Table 1), and the final dataset consisted of 66 sequences from 10 locations (populations): Caucasus (CAU, 10 samples), East Asia (EAS, 8 samples), eastern-central Europe (ECEU, 5 samples), northern Europe (NEU, 12 samples), Mediterranean Europe (MEU, 9 samples for ITS1, 8 samples for ITS2), Greenland (4 samples), North America (NAM, 8 samples), South America (SAM, 6 samples), Africa (AF, 1 sample), and New Zealand (NZ, 3 samples). This is one of the largest samplings of a species among corticioid fungi studied so far. Despite the potential problems with ITS (e.g., Nilsson et al. 2008), the region has been shown as a useful marker for phylogeographic studies and haplotype analyses not least in fungi (e.g., Kauserud et al. 2007b; Geml et al. 2008; Moncalvo and Buchanan 2008; Wirtz et al. 2008; Carlsen et al. 2011). Tajima's D neutrality test separately performed for both loci did not reject the neutral 'null' hypothesis, which eliminates the concerted evolution to be likely. Phylogenetic analysis by Hallenberg et al. (2007) has shown that the species complex is monophyletic and the extant cryptic species within this complex appear to have a similar ecology and substantial overlap in morphology. It is therefore reasonable to treat *P. praetermissa* as one species and the genetic divergence within this complex as a function of time. The procedure of DNA extraction, PCR and sequencing follow Ghobad-Nejhad et al. (2010). Sequences were assembled in SeqMan NGen (DNASTAR) or Sequencher[®] v. 4.1 (GeneCodes, Ann Arbor, USA) and aligned in MAFFT v. 6.624b (Katoh and Toh 2008). The ITS1 and ITS2 portions were extracted from the ITS dataset, and analysed separately.

Sequences were collapsed into haplotypes using FaBox (Villesen 2007) and analysed with Arlequin v. 3.5.1.2 (Excoffier and Lischer 2010). Within and between popula-

tion pairwise distances, population comparisons (*Fst*, 100 permutations), and molecular diversity (π , as a measure of nucleotide diversity, i.e. the probability that two randomly chosen homologous nucleotides are different) were computed with pairwise distance method at a 0.05 significance level. To infer population differentiation (*Fst*), the number of steps in the Markov chain was set to 100,000 and burn-in to 10,000. A high *Fst* implies a considerable degree of differentiation among populations. Genetic diversity of populations was compared using the obtained values of molecular diversity (π) in each of datasets and expected heterozygosity (*H*) over polymorphic nucleotides in each of ITS1 and ITS2 regions.

Results and discussion

Similarity tests A graphical display of all the obtained T indices as well as dendrograms from cluster analysis is presented in Fig. 1. In general, T indices from the checklists of the three genera and the checklists of total corticioids largely agree with each other (Fig. 1a), and some conclusions can be drawn: 1) Among the regions studied here, the highest similarity of the Caucasus is to eastern-central Europe (cf. *Phlebia*), and the least similarity to India (cf. *Hyphodontia*). 2) The Caucasus is more similar to Europe and North America than to East Asia and India (see also Suppl. Table 3). Moreover, the T values between the Caucasus and Europe are significantly greater than the values between the Caucasus and North America ($p=0.05$), with the exception of the genus *Phlebia*. High similarity between the Caucasus and Europe could indicate that there may have been an effective exchange of biota between them. The case with *Phlebia* contradicts all other analyses presented here, and therefore is difficult to explain. 3) The Caucasus is significantly more similar to East Asia than to India ($p=0.05$) (cf. *Hyphodontia*). A higher similarity to Southeast Asia than to the Himalayas has been documented for European mountain plant species, apparently via a former, northerly deciduous forest belt (Zhang et al. 2007). Dendrograms from cluster analysis (Fig. 1b) were largely congruent with T diagrams in Fig. 1a. [See Suppl. Table 3 for Tripartite similarity values obtained from comparisons of total corticioids of the Caucasus, Europe, eastern N America, western N America, East Asia, and India].

Mueller et al. (2001) used the Simpson similarity index to deduce the biogeographical relationships between North American and Chinese macrofungi, and Núñez and Stokland (2000) used the Dice index to infer the biogeographical affinities of East Asian polypores with those of other north temperate areas. It must be noted that these indices simply apply the number of entries common to two lists and do not consider the number of entries differing between the

Table 1 Haplotypes, isolates, and ITS GenBank accession numbers for *Peniophorella praetermissa*. Haplotypes of ITS1 are shown by numerical numbers (1, 2, 3, ...), haplotypes of ITS2 are shown by letters (a, b, c, ...). Accession numbers starting with HQ were generated in this study (accession numbers AY618668 and AY781256 downloaded from GenBank had no isolate name, so the accession number is used directly for isolate name in the list of haplotypes). Haplotype numbers in bold contain more than one sequence and their isolates are shown with different colours to mark different locations: Caucasus (light green), East Asia (orange), northern Europe (light blue), Mediterranean Europe (dark green), Greenland (dark blue), North America (light purple), South America (dark purple), and New Zealand (brown). Isolates from Africa and eastern-central Europe appeared in singletons, i.e. haplotypes consisting of one sequence only. Singletons are not colour-marked. Isolates from Iran and Turkey refer to the collections from Caucasian parts of these countries (see Ghobad-Nejhad et al. 2009)

ITS1 (222 bp)		ITS2 (218 bp)		GenBank		
Haplotype	Isolate	Haplotype	Isolate	Isolate	Origin	Accession number
1	FP110337	a	FP110337	FP110337	USA (Mississippi)	GQ409533
2	FCUG 1358	b	FCUG 1358	FCUG 1358	Sweden	DQ647441
3	FCUG 1831, FCUG 1874, AY781256, FCUG 1708	c	FCUG 1831	FCUG 1831 FCUG 1874 FCUG 1708	Spain Spain Sweden Finland	DQ647446 DQ647445 AY781256 DQ647444
4	GEL 2182	d	FCUG 1874, AY781256	GEL 2182	Norway	DQ647442
5	FCUG 1828	e	GEL 2182	FCUG 1828	France	DQ647443
6	TMIC 34061	f	FCUG 1708	TMIC 34061	Japan	DQ647452
7	FCUG 461, FCUG 900	g	FCUG 1828	FCUG 461 FCUG 900	Norway Denmark	DQ647450 DQ647451
8	FCUG 465	h	TMIC 34061	FCUG 465	Canada (BC)	DQ647448
9	CanadaBC493	i	FCUG 461	FCUG 493	Canada (BC)	DQ647449
10	CanadaBC646	j	FCUG 900	FCUG 646	Canada (BC)	DQ647447
11	AY618668	k	FCUG 465	–	Canada (BC)	AY618668
12	HHB 9446	l	FCUG 493	HHB 9446	USA (Florida)	GQ409534
13	FCUG 3190	m	FCUG 646	FCUG 3190	Iran	HQ392620
14	FCUG 939	n	AY618668	FCUG 939	Scotland	DQ647464
15	FCUG 1052	o	HHB 9446	FCUG 1052	Romania	DQ647465
16	FCUG 2429	p	FCUG 3190	FCUG 2429	Russia (Krasnodar)	DQ647466
17	FCUG 1804	q	FCUG 939	FCUG 1804	Spain	DQ647467
18	FCUG 1799, FCUG 2375	r	FCUG 1052	FCUG 1799 FCUG 2375	Spain Greenland	DQ647454 DQ647459
19	FCUG 277, FCUG 3200, FCUG 3031, FCUG 2376, FCUG 962	s	FCUG 2429, FCUG 1804	FCUG 277 FCUG 3200 FCUG 3031	Denmark Iran Canada (Quebec)	DQ647453 HQ392618 DQ647463
20	FCUG 2232	t	FCUG 1799	FCUG 2376	Greenland	DQ647458
21	FCUG 2373	u	FCUG 1799	FCUG 962	Scotland	DQ647460
22	FCUG 2371	v	FCUG 277	FCUG 2232	Turkey	DQ647455
23	FCUG 2130	w	FCUG 2232	FCUG 2373	Greenland	DQ647457
24	FCUG 2147	x	FCUG 3031	FCUG 2371	Greenland	DQ647456
25	FCUG 3208	y	FCUG 2373	FCUG 2130	Tenerife	DQ647461
26	FCUG 2414	z	FCUG 2376	FCUG 2147	Tenerife	DQ647462
27	FCUG 2461	aa	FCUG 962	FCUG 3208	Iran	HQ392619
28	FCUG 758	bb	FCUG 2147	FCUG 2414	Russia (Krasnodar)	DQ647469
29	FCUG 1682	cc	FCUG 3208	FCUG 2461	Russia (Krasnodar)	DQ647470
30	FCUG 950	dd	FCUG 2375	FCUG 758	Canada (Ontario)	DQ647471
31	MG125	ee	FCUG 2414	FCUG 1682	Sweden	DQ647473
32	MG123	ff	FCUG 2461	FCUG 950	Sweden	DQ647472
33	MG124	gg	FCUG 758	MG125	Estonia	HQ392623
34	FCUG 2160	hh	FCUG 1682	MG123	Estonia	HQ392621
35	TMIC 33862	ii	FCUG 950	MG124	Germany	HQ392622
36	Wu 9506-27	jj	MG125	FCUG 2160	Gomera	DQ647474
37	FCUG 3094	kk	MG123	TMIC 33862	Japan	DQ647476
38	FCUG 2966	ll	MG124	Wu 9506-27	Taiwan	DQ647493
39	FCUG 2500, FCUG 2512, FCUG 2514, FCUG 2531	nn	FCUG 2160	FCUG 3094, FCUG 2966, FCUG 2967, FCUG 2500, FCUG 2512, FCUG 2514, FCUG 2531, FCUG 2247, FCUG 2490, FCUG 2218, TMIC 32107	Tasmania New Zealand	GQ409532 DQ647480
40	FCUG 2495	oo	TMIC 33862	FCUG 2500	Argentina	DQ647488
41	FCUG 824	pp	Wu 9506-27	FCUG 2512	Argentina	DQ647489
42	FCUG 2165, FCUG 2493	qq	FCUG 3094, FCUG 2966, FCUG 2967, FCUG 2500, FCUG 2512, FCUG 2514, FCUG 2531, FCUG 2247, FCUG 2490, FCUG 2218, TMIC 32107	FCUG 2514	Argentina	DQ647490
43	FCUG 2967	rr	FCUG 2495, FCUG 2165, FCUG 2493	FCUG 2531	Argentina	DQ647491
44	FCUG 2247, FCUG 2218	ss	FCUG 824	FCUG 2495	Argentina	DQ647492
45	FCUG 2430	tt	Wu 0104-3	FCUG 824	Denmark	DQ647479
46	TMIC 32107	uu	Wu 9610-10	FCUG 2165	Tenerife	DQ647485
47	Wu 0104-3, Wu 9610-10, TMIC 34389	vv	TMIC 34389	FCUG 2493	Argentina	DQ647486
48	Wu 0309-175	ww	Wu 0309-175	FCUG 2967	New Zealand	DQ647487
49	MUCL32673	xx	MUCL32673	FCUG 2247	Turkey	DQ647481
50	MG122	yy	MG122	FCUG 2218	Turkey	DQ647483
				FCUG 2430	Russia (Krasnodar)	DQ647482
				TMIC 32107	Japan	DQ647484
				Wu 0104-3	Taiwan	DQ647495
				Wu 9610-10	Taiwan	DQ647494
				TMIC 34389	Japan	DQ647496
				Wu 0309-175	China (Jilin)	DQ647497
				MUCL32673	Cameroon	DQ647498
				MG122	Estonia	HQ392624

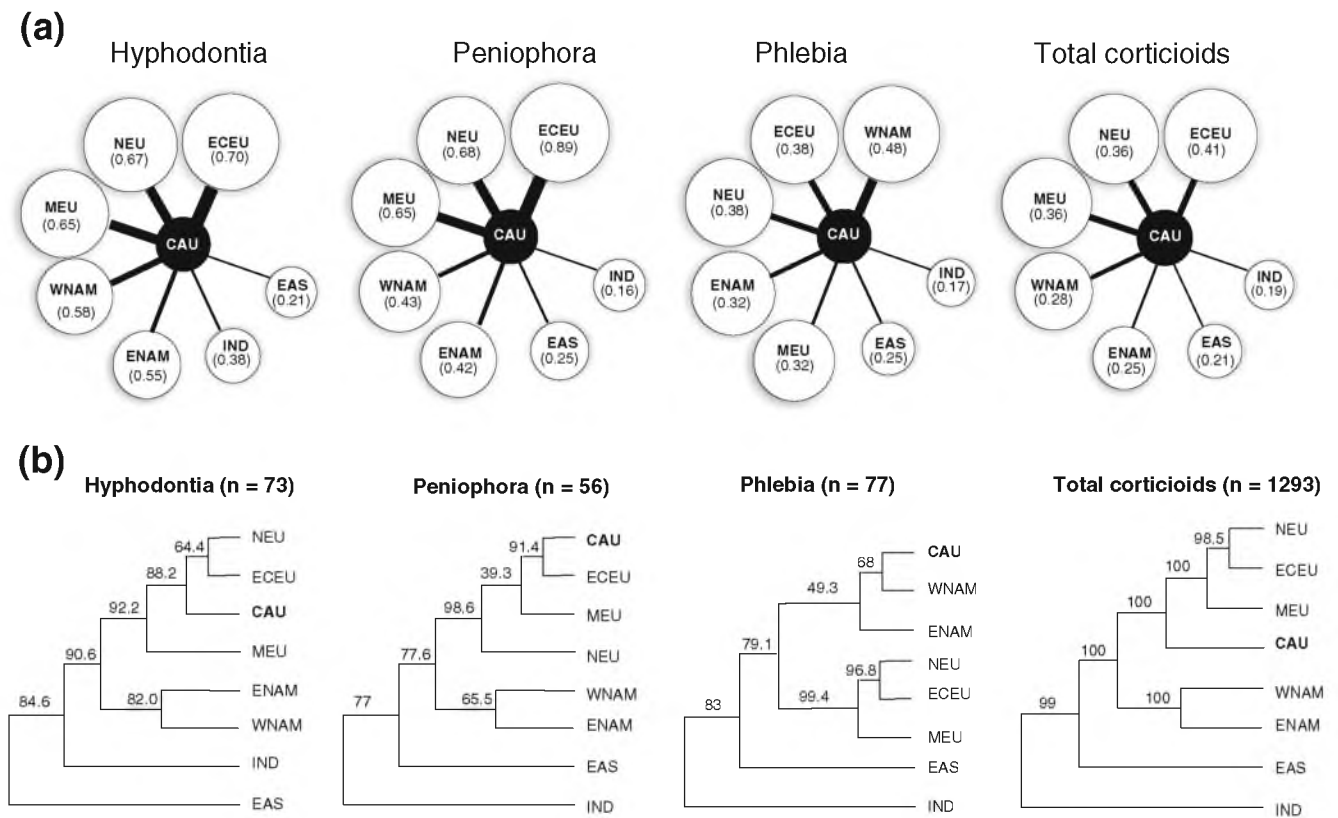


Fig. 1 a Diagrams representing the Tripartite similarity values for *Hyphodontia*, *Peniophora*, *Phlebia*, and for total corticioids. The size of the circles and the thickness of radii are relative to the T values (numbers in brackets). **b** Dendrograms from cluster analysis. Numbers above branches are bootstrap support values. n=the total number of

species analysed. Area abbreviations: *CAU* Caucasus, *ECEU* eastern-central Europe, *NEU* northern Europe, *MEU* Mediterranean Europe, *ENAM* eastern North America, *WNAM* western North America, *EAS* East Asia, *IND* India

two sets being compared. They could also give misleading values when the size of the two lists differ greatly (Tulloss 1997). The percentage of corticioid species shared between the Caucasus region and other areas considered above (Simpson index, see Tulloss 1997; Tulloss and Tulloss 2004) is shown in Fig. 2. For instance, the percentage of *Hyphodontia* species in common between the Caucasus and northern Europe is 100%. It appears that similarity can be more accurately shown by T values than by simply the percentage of species in common. The Tripartite similarity index has been used in several studies (e.g., Robba et al. 2005; Schils and Wilson 2006; Winemiller et al. 2008), and it has been recently modified to infer the distribution pattern of a group of taxa in a given region (Schils 2006).

We also believe that there are limitations to the use of similarity indices for assessing ‘biogeographical relationships’ (see above). Indices can represent the overall similarity of biota, but not their intricate biogeographical history (Lomolino et al. 2006). Moreover, these indices do not take into account the similarities in distribution patterns (Schils 2006), nor do they take into account the importance of shared history and phylogeny of the taxa.

Establishing similarity assumptions based on checklists could have some potential limitations, such as compromised reliability of input data and inconsistencies in taxonomic treatments (see Feuerer and Hawks-

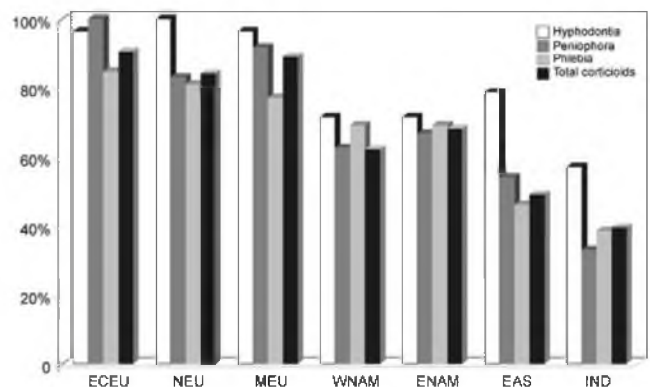


Fig. 2 The percentage of species common between the Caucasus region and other areas (Simpson index) as calculated for *Hyphodontia*, *Peniophora*, *Phlebia*, and for total corticioids. Area abbreviations as in Fig. 1

worth 2007). Such concerns can, however, be satisfied to a considerable degree by avoiding poor quality data and by availability of recently revised information. For the present study, we used updated, well-edited or expert-made lists, while unreliable data were excluded. The problem with competing species interpretations as well as conflicting nomenclature and synonymy in corticioid fungi has been tackled via the open-source nomenclatural database *Cortbase* (Parmasto et al. 2004). It is clear that such databases not only serve taxonomy, but can also be relevant for biodiversity and biogeographical studies. All input data in our study were controlled, coordinated and adjusted prior to the analyses so that different species interpretations were avoided (see Suppl. Table 2)

Genetic diversity Sixty six sequences of ITS1 (222 bp) belonging to *Peniophorella praetermissa* were collapsed into 50 haplotypes (Table 1) of which 42 haplotypes were singleton while eight haplotypes contained more than one sequence. Among the shared haplotypes, one Caucasus sequence collapsed with another one from the same region in haplotype **44**, and one Caucasus sequence appeared in haplotype **19** consisting of sequences from northern Europe, Greenland and North America (Quebec). The highest value of within population pairwise distance (Fig. 3a), molecular diversity, and mean expected heterozygosity (Table 2) of ITS1 was found in the Caucasus, slightly higher than East Asia, but considerably higher than other populations. Molecular diversity in the Americas, Greenland, New Zealand and Africa was significantly lower than the Caucasus/East Asia/Europe (Fig. 3a, Table 2). According to *Fst* calculations (Table 3, Fig. 3a), the Caucasus is significantly differentiated only from East Asia and South America, while the smallest calculated differentiation was found with northern Europe. East Asia is significantly differentiated from almost all other populations.

The ITS2 dataset consisted of 65 sequences with 218 bp, rendering 50 haplotypes (Table 1), of which five haplotypes were shared and sequences from the Caucasus incorporated into three of these: 1) haplotype **s** consisting of sequences from the Caucasus and Spain, 2) haplotype **w** including Caucasus and Greenland isolates, and 3) haplotype **qq** consisting of sequences from the Caucasus, Japan, New Zealand/Tasmania, and Argentina. The highest within population pairwise distance (Fig. 3b), molecular diversity, and mean expected heterozygosity for ITS2 (Table 2) was found in East Asia and, after this, in the Caucasus, the values for both being considerably higher than for other populations. As was the case with ITS1, molecular diversity of ITS2 in the Americas, Greenland,

New Zealand and Africa was significantly lower than in the Caucasus/East Asia/Europe. Sequences from East Asia showed significant *Fst* p-values for almost all other populations (Table 3), which means that they are highly differentiated and divergent (see also Fig. 3b). Caucasus sequences were significantly different only from those of East Asia, eastern-central Europe and South America, but were least differentiated from (most similar to) northern- and Mediterranean Europe (Fig. 3b, Table 3).

According to the results obtained for *Peniophorella praetermissa*, genetic diversity and within population pairwise distances in the Caucasus region were shown to be higher than in Europe; the values are not only higher than those of northern Europe which was unforested during LGM (cf. cryptic northern refugia speculated by some studies; see e.g., Randi 2006), but also exceed those of the Mediterranean area. Since the molecular diversity of East Asian samples is also high, a Caucasian and/or an East Asian route could be postulated for the species to reach Europe (an East Asian route could be justified by the past existence of a continuous temperate forest cover in the Northern Hemisphere; see Donoghue and Smith 2004). However, both ITS regions of the East Asian samples are significantly differentiated from all other North Hemispheric populations studied here, an indication of their isolation and different history from Europe as well as from the Caucasus region. These results might indicate a possible colonization of Europe by the species from the Caucasus.

Greenland samples appear in three shared haplotypes (Table 1), i.e. with Spain (haplotype **18**, ITS1), with the Caucasus/northern Europe/Quebec (haplotype **19**, ITS1), and with the Caucasus (haplotype **w**, ITS2). Genetic diversity in Greenland isolates is lower than in Europe and North America. They are significantly different from several populations (incl. North America) but not from the Caucasus, northern Europe, and Mediterranean Europe. This may indicate that Greenland colonization has taken place at several times from different parts of Europe and the distribution has possibly extended from northern Europe to NE North America (Fig. 3; Tables 2 and 3). Molecular diversity in New Zealand and South America is very low, which can be explained by insufficient sampling in these areas or perhaps more recent colonization from the Northern Hemisphere.

The idea of a region being designated as the 'source' or 'origin of re-colonization' has most commonly been evaluated by the 'genetic diversity gradient' model, applied in numerous studies (see e.g., Taberlet et al. 1998; Hewitt 1999 and 2004; Weiss and Ferrand 2006, and several references they cite). Accordingly, the source areas are supposed to have a higher genetic diversity than the

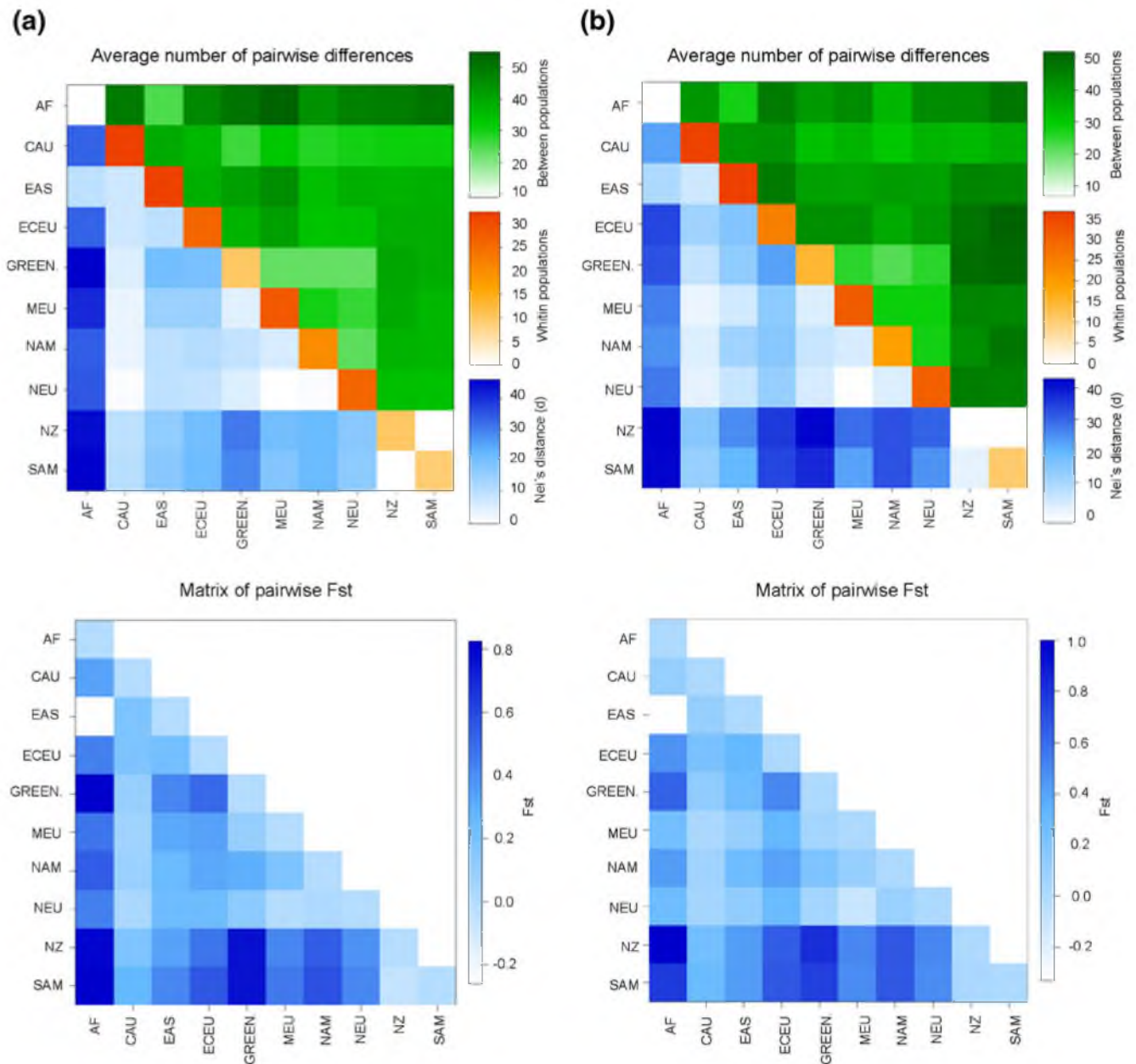


Fig. 3 Genetic diversity calculations for ITS1 (a) and ITS2 (b) in *Peniophorella praetermissa* from 10 locations. First row diagrams plot average number of population pairwise differences (i.e. the mean number of base-pair differences between all pairs of sequences in a samples); above diagonal shows average number of pairwise differences between populations, diagonal element indicates average

number of pairwise differences within population, and below diagonal is corrected average pairwise difference (Nei's distance). Second row diagrams plot matrices of population pairwise *Fsts*. A high *Fst* implies a considerable degree of differentiation among populations. Distance method: pairwise difference. Abbreviations as in Table 2, but also GREEN. = Greenland

areas where the organism(s) has dispersed. Additional models are also being developed to propose much more complex scenarios having operated in nature, however. In some cases, the area with the highest diversity has been shown to have acted as a ‘container’, retaining a high diversity (and divergence) due to its isolation and poor biota exchange with

the adjacent areas (e.g. Atkinson et al. 2006; Pokryszko et al. 2011). This can be tested, for instance, by examining the level of divergence and differentiation of the areas under study, as we did by performing *Fst* calculation (Fig. 3; Table 3). A high *Fst* implies a considerable degree of differentiation among populations.

Table 2 Mean expected heterozygosity (H) and molecular diversity (pi) for ITS1 and ITS2 in *Pentiphorella praetermissa* for 10 geographic regions

	AF	CAU	EAS	ECEU	GREENLAND	MEU	NAM	NEU	NZ	SAM	
ITS1	H	0.00000± 0.00000	0.14665± 0.22175	0.14334± 0.22861	0.12117± 0.20237	0.04354± 0.15325	0.12788± 0.20074	0.09025± 0.16747	0.11835± 0.19027	0.04505± 0.16771	0.04054± 0.13843
	pi	0.000	32.556	31.821	26.000	9.667	28.389	20.036	26.273	10.000	9.000
ITS2	H	0.00000± 0.00000	0.16585± 0.22663	0.16907± 0.24075	0.11881± 0.19783	0.06728± 0.18119	0.14384± 0.20754	0.08814± 0.15479	0.14039± 0.19785	0.00000± 0.00000	0.04893± 0.15431
	pi	0.000	36.156	36.857	25.200	14.667	31.357	19.214	30.606	0.000	10.667

Area abbreviations: *AF* Africa, *CAU* Caucasus, *EAS* East Asia, *ECEU* eastern-central Europe, *MEU* Mediterranean Europe, *NAM* North America, *NEU* northern Europe, *NZ* New Zealand, *SAM* South America

Species endemism and disjunction

A high level of plant and animal species endemism is well-documented for the Caucasus region (Myers et al. 2000; Krever et al. 2001). Some 25% of its plant species (1,600 out of 6,300 spp.) are restricted to the region (Myers et al. 2000), and about 10% of these are woody plants. The situation for fungi has remained less evaluated. Parmasto (1968) briefly pointed out the poverty of aphylloroid fungi in the Transcaucasus compared with that of Europe, and considered *Oidium curtisii* (Berk.) Linder (*Botryobasidium curtisii* Hallenb.) its only species not present in Europe. The species is, however, now also known from Ukraine. Based on the checklists compiled by us, 12 corticioid species occurring in the Caucasus region are absent in Europe, and 96 species are absent from North America (details available from the corresponding author). Until the year 1981, 23 species were described from the Caucasus region (7% of the total spp., see Suppl. Fig. 2), many of which were later found outside the region, and only two species are currently restricted to the Caucasus (Table 4). Still, these may only be ‘endemic by ignorance’, i.e., a result of our poor knowledge about their distribution.

For fungi, it seems that factors like host specificity, diversity of substrata and habitats, fungal life form, geographic features and perhaps climate have an effect on the level of endemism (see e.g., Dai and Penttilä 2006; Arnolds 2007; Mueller et al. 2007). In a recent study on global diversity of macrofungi, Mueller et al. (2007) confirmed a general concordance between endemism levels in macrofungi and vascular plants. In wood-inhabiting basidiomycetes the situation seems to be different. Here, the level of host specificity is generally low, compared, e.g., with rust fungi (Berndt 2008). The disparity of endemism between plants and corticioid fungi in the Caucasus could also partly be explained by the same fact (see also Arnolds 2007 for comparisons of endemism in fungi and plants). In a study on polypore fungi, Dai and Penttilä (2006) noted low host specificity in NE China, but a high number of endemic polypore species. They linked the high endemism in the NE China with a high diversity of tree species and habitats and lack of Pleistocene glaciations. Such conditions are also present in the Caucasus region, even though forests now cover only about 20% of the region (Krever et al. 2001). According to Donoghue and Smith (2004), “The generation and retention of particularly great diversity in E(east) A(sia), compared with the other major Holarctic areas of endemism, has been attributed to topographic and climatic circumstances, and to the greater refuge area available there” (see also references cited therein). A more likely reason for the disparity of plant and corticioid fungal species endemism is, however, the effective spore dispersal in wood-inhabiting corticioid fungi,

Table 3 Population pairwise *F_{st}* p-values for ITS1 and ITS2 sequences of *Pentophorella praetermissa*, respectively (separated by a slash)

	AF	CAU	EAS	ECEU	GREENLAND	MEU	NAM	NEU	NZ	SAM
AF		0.081±0.02/ 0.50±0.03	0.47±0.05/ 0.77±0.04	0.16±0.03/ 0.16±0.03	0.22±0.039/ 0.19±0.05	0.04±0.02*/ 0.31±0.03	0.05±0.03/ 0.28±0.03	0.09±0.02/ 0.25±0.04	0.21±0.04/ 0.28±0.05	0.13±0.02/ 0.13±0.03
CAU			0.00±0.00*/ 0.04±0.01*	0.05±0.02/ 0.00±0.00*	0.18±0.03/ 0.11±0.03	0.07±0.03/ 0.30±0.04	0.08±0.03/ 0.14±0.04	0.27±0.04/ 0.23±0.03	0.16±0.03/ 0.13±0.04	0.02±0.01*/ 0.01±0.01*
EAS				0.037±0.01*/ 0.01±0.01*	0.02±0.01*/ 0.01±0.01*	0.00±0.00*/ 0.02±0.02*	0.00±0.00*/ 0.00±0.00*	0.00±0.00*/ 0.00±0.00*	0.04±0.01*/ 0.01±0.01*	0.00±0.00*/ 0.00±0.00*
ECEU					0.03±0.02*/ 0.01±0.01*	0.03±0.01*/ 0.01±0.01*	0.00±0.00*/ 0.00±0.00*	0.00±0.00*/ 0.00±0.00*	0.02±0.01*/ 0.03±0.01*	0.00±0.00*/ 0.00±0.00*
GREENLAND						0.16±0.03/ 0.25±0.04	0.02±0.01*/ 0.01±0.01*	0.09±0.02/ 0.22±0.04	0.02±0.01*/ 0.03±0.02*	0.02±0.01*/ 0.01±0.01*
MEU							0.01±0.01*/ 0.11±0.04	0.38±0.03/ 0.99±0.00	0.01±0.01*/ 0.00±0.00*	0.00±0.00*/ 0.01±0.01*
NAM								0.27±0.04/ 0.05±0.02	0.00±0.00*/ 0.00±0.00*	0.00±0.00*/ 0.00±0.00*
NEU									0.01±0.01*/ 0.00±0.00*	0.00±0.00*/ 0.00±0.00*
NZ										0.00±0.00*/ 0.00±0.00*
SAM										0.51±0.06/ 0.48±0.04

Significant values are marked with an asterisk at 0.05 level. Abbreviations as in Table 2

and the fact that the life cycles of basidiomycetes promote the survival of even low density populations (Hallenberg 1995). Accordingly, Mueller et al. (2007) noted low global endemism level for polypores and corticioids, in contrast to sequestrate fungi and Xylariaceae.

In the Caucasus region, 23 putative disjunctive species, i.e. species with broken distribution ranges at a large scale, can be recognized (Table 4). We use the term putative because, as mentioned for the endemics, they may appear to be more widely (and continuously) distributed when more intensive inventories are done. As shown in Table 4, most of these disjunctions are of Caucasus–Mediterranean or Caucasus–northern Europe types, which might be an indication of a connection between the Caucasus and Europe (as shown by similarity tests and genetic diversity results mentioned above). However, such data must be used with caution, because the conspecificity has been inferred based on morphological criteria only (but for *V. megalospora* see Ghobad-Nejhad et al. 2010). A question arises as to whether fungi under a single binomial on different continents represent the same species when examined genetically. The answer is not straightforward because there are examples which either support their divergence or their conspecificity. Moreover, different authors treat the divergent lineages in different ways, either as distinct species, or as belonging within one species continuum. In wood-inhabiting fungi, some examples of genetic divergence leading to cryptic speciation are provided by Nilsson et al. (2003), Kausserud et al. (2006, 2007a), and Moncalvo and Buchanan (2008). They have shown that several cryptic species each show a huge range expansion which must have taken place during the Holocene. On the other hand, Thell and Miao (1999) and Thell et al. (1998 and 2002) provided examples in lichenized fungi, and Ghobad-Nejhad and Dai (2010) for a polypore fungus, where the specimens collected from different continents were shown to belong to the same species. In the Caucasus region, representatives of corticioid species of all continents are found (Suppl. Fig. 2) and at least 15% of its species can be characterized as ‘cosmopolitan’ (data not shown).

Several of the tabulated species have scattered point-like distribution, or are ‘rare everywhere’, and are known only from a few localities. This could perhaps be due to insufficient information on their occurrence, but there are also other disjuncts which do not seem to be due to lack of data. This is shown when a species appears to be common in one continent but rare in another, both being more or less similarly inventoried. *Boreostereum radiatum* is predominantly distributed in North America, and is known from only a few localities in Eurasia (Table 4). *Dendrothele incrustans* is mainly known from North America, but is also found in Argentina and the Russian Caucasus (Table 4). The polypore species *Cyanotrampa rimoso* (Murill) Ghobad-

Nejhad is common in western North America and found in a few localities in northern Iran and one locality in Ethiopia, yet is absent from Europe (Ghobad-Nejhad and Dai 2010).

Final remarks

Fungal biogeography (mycogeography) is still an underdeveloped discipline (Arnolds 2007; Lumbsch et al. 2008). Only a minor portion of the total estimated number of fungal species has been described (ca. 7% out of 1.5 million spp.; Hawksworth and Mueller 2008; Kirk et al. 2008) and currently our knowledge of distribution history and geographic structure in fungi is very limited. Compared to plants and animals, for which the fossil record is relatively rich and there is reasonable agreement over the age of major lineages, fossil records are scarce or lacking in saprotrophic fungi. To estimate past events in fungal biogeography, we are therefore confined to the use of indirect methods, and to calibrate our estimates with known events in the general vegetation history. In this study, we have presented the first large-scale comparison of corticioid fungi in the Northern Hemisphere. Such comparisons are still lacking for most groups of fungi.

The Caucasian Pleistocene refugia (Tumajanov 1971) are among the few forested regions in the Northern Hemisphere that remained unglaciated during the Pleistocene (Milne 2006). According to Volodicheva (2002), the Caucasus had favourable Pleistocene habitats compared with much of Europe. There are several examples showing that the Caucasus region has served as an origin of post-glacial dispersal and colonization in Europe for some plants (e.g., oak: Atkinson et al. 2006), animals (e.g., chamois: Randi 2006; root vole: Brunhoff et al. 2003; freshwater fishes: Kotlík et al. 2008) and ascomycetous fungi (*Letharia*: Arnerup et al. 2004). Our results (high similarity between species checklists from the Caucasus and Europe, comparatively high genetic diversity in the Caucasus for an exemplar species, and ITS similarity between the Caucasus and Europe) indicate that this could also be the case in wood-inhabiting basidiomycetes. It is clear that much more sampling is needed in future to explore the fine genetic structure and the actual route of dispersal in the wood mycota inhabiting these refugia. Investigating the history and agents of dispersal, and assessing the human impact on distribution vs. natural distribution of individual species was far beyond the scope of our study.

It must be noted that the scenario of the Caucasus having contributed to the European mycota does not necessarily exclude the role of other areas especially in Russia having served so, but these areas could not be included in this

Table 4 Putative endemic and putative disjunctive corticioid species in the Caucasus region

	Species	Known distribution	Category
Putative endemic ^a	<i>Botryobasidium grandinioides</i> Hallenb.	Iran	
	<i>Trechispora granulifera</i> Hallenb.	Iran	
Putative disjunct	<i>Boreostereum radiatum</i> (Peck) Parmasto	USA, Canada , China, Czech Republic, Poland, Georgia, Russian Caucasus	□
	<i>Corticium erikssonii</i> Jülich	N Europe , Russian Caucasus	●
	<i>Cylindrobasidium eucalypti</i> (M. Dueñas & Tellería) Tellería & Melo	France, Iran, Spain	●
	<i>Dendrothele incrustans</i> (P.A. Lemke) P.A. Lemke	Argentina, Canada , Russian Caucasus	■
	<i>Galzinia longibasidia</i> Hallenb.	Iran, France	●
	<i>Gloeocystidiellum permixtum</i> (Boidin, Lanq. & Gilles) E. Larss. & K.H. Larss.	France, UK, Turkey	●
	<i>Hyphoderma malenconii</i> (Manjón & G. Moreno) Manjón, G. Moreno & Hjortstam	Armenia, France, Spain, Morocco, Taiwan	◆
	<i>Hymenochaete minuscula</i> G. Cunn.	Georgia, Réunion, S America , New Zealand	*
	<i>Hyphodontia borealis</i> Kotir. & Saaren.	Italy, N Europe, Russian Caucasus	●
	<i>Hyphodontia halonata</i> J. Erikss. & Hjortstam	N Europe, Russian Caucasus	●
	<i>Intextomyces cystidiatus</i> Hjortstam	Italy, Russian Caucasus	●
	<i>Melzericium bourdotii</i> Jülich	France, Sweden, Iran	●
	<i>Phanerochaete xerophila</i> Burds.	USA, S America, Korea, Russian Caucasus	?
	<i>Phlebia badia</i> (Pat.) Nakasone	Cameroon, Costa Rica, Iran, USA, Vietnam	?
	<i>Phlebia caspica</i> Hallenb.	Iran, France	●
	<i>Phlebia pulcherrima</i> Parmasto	Altay, Russian Caucasus	○
	<i>Sistotrema athelioides</i> Hallenb.	Argentina, China, Japan, N America, Switzerland, Turkey	?
	<i>Sistotrema camshadalicum</i> Parmasto	Iran, Kamchatka	○
	<i>Sistotrema eximum</i> (H.S. Jacks.) Ryvarden & Solheim	Russian Caucasus, USA	■
	<i>Steccherinum gilvum</i> Maas Geest.	Iran, Japan	○
	<i>Trechispora subhelvetica</i> (Parmasto) Libertá	Armenia, Norway	●
	<i>Tubulicrinis incrassatus</i> Hallenb.	Iran , Italy, Spain	●
	<i>Vuilleminia megalospora</i> Bres.	Iran, Italy, France	●

Geographic names in bold are places where the species is more commonly found. Categories: Caucasus–Mediterranean/N Europe (●), Americas–Caucasus (■), Northern Hemisphere (□), Caucasus–East Asia (○), Caucasus–Southern Hemisphere (*), Eurasia (◆), undefined (?). Iran and Turkey refer to the Caucasian parts of these countries (see Ghobad-Nejhad et al. 2009)

^a Species recently described from the Caucasus region (after 1981) are not taken into account

study due to the lack of information. Accordingly, due to the lack of updated and satisfactory corticioid species lists from several parts of Asia, the similarity patterns presented here remain inconclusive. While we tried to use the most updated information about the occurrence of corticioids in the areas analysed here, it would be ideal to reiterate the analyses with information gained from future biodiversity inventories. Our inference about the ‘source area’ using the commonly applied measures (genetic diversity and the level of differentiation) needs to be supplemented in future by taking additional and more sophisticated models as well as other genetic markers into consideration, to further explore the hypotheses presented here. Moreover, the history of diversity reclamation in Europe and contrasting the magnitude to which this was derived from the Caucasus, relative to other areas, is still an open question.

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Supplementary Table 1 Published documents and sources used in assembling checklists of corticioids and the genera *Hyphodontia*, *Peniophora*, and *Phlebia*, as well as calculated T values. Numbers in square brackets are a, b, and c, respectively (a = the number of entries common to both lists, b = the number of entries in the first list that are not in the second, and c = the number of entries in the second list that are not in the first). Area abbreviations as in Fig. 1

Area	Source	T index			
		<i>Hyphodontia</i>	<i>Peniophora</i>	<i>Phlebia</i>	Total corticioids
CAU	10	–	–	–	–
CAU-ECEU	1, 2, 3, 7, 8, 22, 29	0.70 [27, 1, 7]	0.89 [24, 0, 2]	0.38 [22, 4, 18]	0.41 [344, 34, 258]
CAU-NEU	2, 12, 15, 19, 26	0.67 [28, 0, 9]	0.68 [20, 4, 5]	0.38 [21, 5, 17]	0.36 [318, 60, 282]
CAU-MEU	2	0.65 [27, 1, 9]	0.65 [22, 2, 7]	0.32 [20, 6, 20]	0.36 [339, 39, 310]
CAU-EAS	5, 6, 13, 16, 17, 18, 20, 21, 24, 28	0.21 [22, 6, 35]	0.25 [13, 11, 15]	0.25 [12, 14, 11]	0.21 [187, 193, 251]
CAU-WNAM	11, 27, 30	0.58 [20, 8, 3]	0.43 [15, 9, 7]	0.48 [18, 8, 9]	0.28 [236, 144, 247]
CAU-ENAM	11, 27, 30	0.55 [20, 8, 7]	0.42 [16, 8, 10]	0.32 [18, 8, 17]	0.25 [258, 122, 329]
CAU-IND	4, 9, 14, 23, 25	0.38 [16, 12, 7]	0.16 [8, 16, 3]	0.17 [10, 16, 14]	0.19 [150, 230, 126]

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- Several papers on corticioids of North America published after 1993

Supplementary Table 2 Groups selected for comparisons of Tripartite similarity index and for drawing dendrograms. n = number of species

Taxon	As treated in	Ecological guild
<i>Hyphodontia</i> (n = 73)	3	–
<i>Peniophora</i> (n = 56)	1, 5, <i>Cortbase</i> v. 2.1	On dying wood, in exposed habitats
<i>Phlebia</i> (n = 77)	4, <i>Cortbase</i> v. 2.1	On decayed wood, in moist habitats
Total corticioids (n = 1293)	2	Diverse

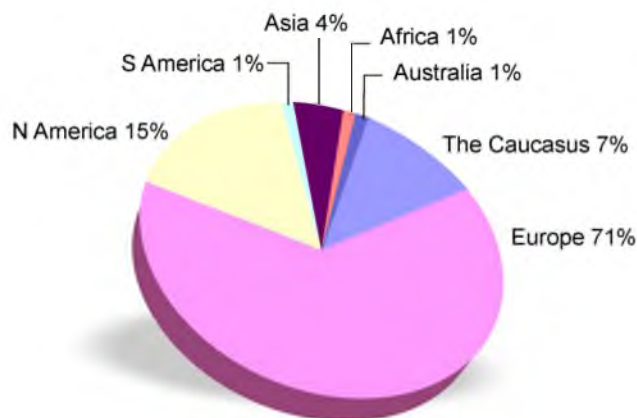
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Supplementary Table 3 Tripartite similarity values obtained from comparisons of total corticioids of the Caucasus, Europe, eastern N America, western N America, East Asia, and India. Numbers in square brackets are a, b, and c, respectively (a = the number of entries common to both lists, b = the number of entries in the first list that are not in the second, and c = the number of entries in the second list that are not in the first). Area abbreviations are as in Fig. 1. For EAS in this Table, only China could be included. The number of species from each area for calculations on total corticioids is as the following: CAU = 380, ECEU = 602, NEU = 600, MEU = 649, WNAM = 473, ENAM = 587, EAS = 438, IND = 276, Europe = 781

	T index
CAU-ENAM	0.25 [258, 122, 329]
CAU-Europe	0.31 [367, 12, 416]
CAU-IND	0.19 [150, 230, 126]
CAU-WNAM	0.28 [236, 144, 247]
EAS-CAU	0.21 [187, 193, 251]
EAS-ENAM	0.21 [240, 345, 195]
EAS- Europe	0.14 [253, 528, 182]
EAS-IND	0.15 [147, 288, 130]
EAS-WNAM	0.22 [209, 270, 226]
ENAM- Europe	0.28 [374, 407, 211]
ENAM-IND	0.11 [164, 421, 113]
Europe-IND	0.08 [184, 597, 93]
WNAM-ENAM	0.41 [346, 133, 239]
WNAM- Europe	0.24 [334, 447, 145]
WNAM-IND	0.13 [148, 331, 129]



Supplementary Fig. 1 Northern Hemisphere Pleistocene glacial refugia (black), and the present temperate (dark grey) and boreal (light grey) forests. Black areas mainly after Milne (2006), Taberlet et al. (1998), and Tarasov et al. (2000). Grey areas after Lomolino et al. (2006). See also Svenning et al. (2008) who propose larger refugia areas in Europe esp. for a number of boreal plant species



Supplementary Fig. 2 Pie chart representing the percentage of the corticioids occurring in the Caucasus region but originally described from places other than this region. Only seven percent of the corticioids of the Caucasus were originally described from this region, while the majority of the species (71%) have been described from Europe.