

Wood-inhabiting Basidiomycetes in the Caucasus Region Systematics and Biogeography

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تقدیم به دو کوهربی همتای زندگی ام، پدر و مادرم
به همراه همیشگی‌م، همسر م

به تک تک اعضای خانواده ام برای محبت بیدریغشان

و به تمام کسانی که به سربلندی ایران می‌اندیشند

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List of Original Publications

Ghobad-Nejhad M (2011) Wood-inhabiting basidiomycetes in the Caucasus region, systematics and biogeography. – Publications in Botany from the University of Helsinki. No 40. 30 pp.

This thesis is based on the following papers, which are referred to in the text by their Roman numerals:

- I.** Ghobad-Nejhad M, Hallenberg N, Parmasto E, Kotiranta H (2009) A first annotated checklist of corticioid and polypore basidiomycetes of the Caucasus region. – *Mycologia Balcanica* 6: 123–168.
- II.** Ghobad-Nejhad M, Dai YC (2010) *Diplomitoporus rimosus* is found in Asia and belongs to the Hymenochaetales. – *Mycologia* 102: 1510–1517.
- III.** Ghobad-Nejhad M, Hallenberg N (2011) *Erythricium atropatanum* sp. nov. (Corticiales, Basidiomycota) from Iran, based on morphological and molecular data. – *Mycological Progress* 10: 61–66.
- IV.** Ghobad-Nejhad M, Nilsson RH, Hallenberg N (2010) Phylogeny and taxonomy of the genus *Vuilleminia* (Basidiomycota) based on molecular and morphological evidence, with new insights into Corticiales. – *Taxon* 59: 1519–1534.
- V.** Ghobad-Nejhad M, Hallenberg N (2011) Multiple evidence for recognition of *Phlebia tuberculata*, a more widespread segregate of *Phlebia livida* (Polyporales, Basidiomycota). – *Mycological Progress*. DOI: 10.1007/s11557-010-0722-1.
- VI.** Ghobad-Nejhad M, Hallenberg N, Hyvönen J, Yurchenko, E (2011) Insights into the biogeography of corticioid fungi (Basidiomycota) in the Caucasus region. – Submitted Manuscript.

Contributions

Paper	I	II	III	IV	V	VI
<i>Original idea</i>	MG	MG	MG	NH	NH	MG
<i>Field work</i>	MG, NH, EP, HK	MG, YCD	MG, NH	MG, NH	NH, MG	–
<i>Microscopy</i>	MG, NH, EP	MG	MG	MG, NH	MG	MG, EY
<i>Lab work</i>	–	MG	MG	MG, NH	NH, MG	MG, NH
<i>Analysis</i>	MG	MG	MG	HN, MG	MG	MG
<i>Manuscript preparation</i>	MG, EP	MG	MG, NH	MG, HN, NH	MG	MG, NH, JH

Initials refer to authors of the paper in question: YCD = Yu-Cheng Dai, MG = Masoomeh Ghobad-Nejhad, NH = Nils Hallenberg, JH = Jaakko Hyvönen, HK = Heikki Kotiranta, HN = Henrik Nilsson, EP = Erast Parmasto, EY = Eugene Yurchenko.

Abstract

Ghobad-Nejhad M (2011) Wood-inhabiting basidiomycetes in the Caucasus region, systematics and biogeography. – Publications in Botany from the University of Helsinki. No 40. 30 pp.

The Caucasus region is a hotspot of biodiversity and is one of the few areas in the Northern Hemisphere which harbor Pleistocene glacial refugia. The region encompasses Armenia, Azerbaijan, Georgia, the southernmost European Russia, NE Turkey, and northern Iran. The study on fungal composition of the Caucasus region and its connection and possible contribution to the present mycota of Europe has largely escaped empirical scrutiny. Using taxonomic surveys, phylogenetic reconstruction methods, haplotype analysis, and similarity tests, this study has aimed to, 1) summarize the knowledge on the occurrence of corticioids and polypores in the Caucasus region, 2) resolve the phylogenetic relationships of selected, resupinate wood-inhabiting basidiomycetes for which the Caucasus region is currently the mere, or one of the noteworthy areas of distribution, and, 3) assess the similarity of Caucasian corticioid fungi to those of Europe and important areas in the Northern Hemisphere, and to examine the significance of the Caucasus region as a glacial refugium for these fungi.

This study provides the first catalogue of corticioids and polypores (635 species) occurring in the Caucasus region. The phylogeny and systematics of the Caucasian resupinate taxa in focus has been resolved and the usefulness of some morphological characters has been re-evaluated. In this context, four new genera and two new species were described and five new combinations were proposed, two of which were supplemented with modern descriptions. The species composition of corticioids in the Caucasus region is found to be distinctly more similar to Europe and North America than to East Asia and India. The highest molecular diversity and within population pairwise distance for *Peniophorella praetermissa* has been detected in the Caucasus and East Asia, with the isolates of the latter area being highly divergent from the European ones. This, and the assignment of root haplotype to the Caucasian isolates in a haplotype network for *Phlebia tuberucalta* and *P. livida*, call attention to the role of the Caucasus region in shaping the current mycota of Europe.

Keywords: Basidiomycota, corticioids, *Cyanotrampa*, fungi, glacial refugia, haplotype, integrative taxonomy, Iran, MrBayes, mycology, new species, phylogeny, polypores, raxmlGUI, resupinate basidiocarp, *Vuilleminia*

INTRODUCTION

The Caucasus Region

The Caucasus region is traditionally regarded as the meeting point of Europe and Asia, situated between the Black Sea (west) and the Caspian Sea (east). It spans an area of about 500,000 km² (Zazanashvili et al. 1999), approximately one third of the size of Iran, and encompasses the total area of the three countries Armenia, Azerbaijan, Georgia, as well as the southernmost European Russia, NE Turkey, and northern part of Iran (Fig. 1; paper I). The delimitation of the Caucasus region varies in different publications, but it is widely acknowledged as a high-priority area for biodiversity conservation, particularly because of its high level of species richness among the temperate Northern Hemisphere regions (Mittermeier et al. 1999). The grey-colored region in Fig. 1 corresponds to a large extent to the area defined as *Caucasus biodiversity hotspot* (Zazanashvili et al. 1999: 269). The hotspot concept, originally developed by Myers (1990) and elaborated by Myers et al. (2000), has been adopted by the Conservation International which enumerates the Caucasus region among the 25 hotspots of biodiversity, areas with considerable species richness as well as a high number of endemic, rare and threatened species. Accordingly, the region is also categorized among the IUCN's recognized centers of plant diversity and endemism (Davis et al. 1995).

Physical Geography, Geology, and Glaciation

The Caucasus is a mountainous region, with about 65% of its area covered by mountains (Krever et al. 2001). There are three major mountain ranges in the Caucasus region: 1) the Greater Caucasus Mountain range with Mt. Elbrus (5,644 m) which is recorded as the highest European summit (Volodicheva 2002), 2) the lesser Caucasus Mountain range including Armenian highlands and Mt. Ararat (5,165 m), and, 3) Talysh-Alborz mountains (with Mt. Damavand, 5,610 m, the highest point in the Middle East) which stretch along south of the Caspian Sea from southern Azerbaijan to northern Iran. These ranges extend approximately in a WNW-ESE direction and belong to the Alpine-Himalayan mountain belt (Khain & Koronousky 1997). The development of the Caucasus dates back to the Mesozoic, when it first appeared in the form of several micro-continents, but its mountain uplifting took place late in the Miocene (*ca.* 23–5 million years ago [mya]) as a result of collision of Eurasian, Anatolian and Arabian plates, and enclosure of the Tethys Sea. Therefore, tectonically, it is among the youngest mountainous formations on the earth. Yet in its relatively short history it has experienced dramatic transformations, and active faulting and crust shortening is still evident there (Thorez 1990; Volodicheva 2002).

The Greater Caucasus Mountain range is at the boundary between the temperate and the subtropical zones. Its northern slopes extend into the vast north Caucasus steppes (Fig. 2) while the southern slopes face more diverse vegetation types. Due to the complex topography of the region, the climate is highly variable. The altitude ranges from more than 5,000 meters above- to 28 meters below sea level. The Black Sea plays an important role in sustaining the humidity in the region, while the effect of the Caspian Sea is limited to its southern coasts (Talysh and Hyrcan); this has resulted in an eastward increase of continentality and arid climate, with some 3,000–4,000 mm annual precipitation in the Colchis area in the eastern Black Sea to

about 200 mm in the western Caspian Sea shores (Kremer et al. 2001). In the south easternmost stretches of the Transcaucasus, in Talysh as well as Hyrcan, the humidity and precipitation prevail again.

As noted by Volodicheva (2002), the development of biota in the Caucasus region has been affected by three main factors: the connections with Eurasia and Gondwanaland, disparate topography, and variation of climate. In the early Tertiary (*ca.* 66 mya), the biota consisted of tropical vegetation, while boreal elements like *Abies*, *Picea* and *Betula* gradually migrated into the region in the Oligocene (*ca.* 36 mya). Following the tectonic events of the Miocene, routes were created for the spread of xerophytic species with Gondwanic origin, which prevailed in the region during the arid climate of the upper Miocene. Tropical and subtropical communities retreated into more humid locations, namely Colchis and Hyrcan (Tertiary refugia), and their remaining elements are called the relict Tertiary flora. Besides relict species which form mono- or polydominant forests communities in lower altitudes, there are also several other relict plant species in the high elevations, on the southern slopes of the Great Caucasus (Volodicheva 2002).

During the Pliocene forest cover advanced out of the refugia in the Caucasus, but it became fragmented or disappeared during cold periods of Pleistocene, and only the remnants were sheltered in the above mentioned refugia or in mid-altitudes. At the height of glaciations, coniferous forests were developed in the Great Caucasus, advancing into the Transcaucasus, and moving back after glacial depauperation (Volodicheva 2002). During the late Pleistocene, ice caps and some large glaciers (17–35 km length) were formed only on some peaks in the central parts of the area, in the Great Caucasus (mountain-valley glaciations), but did not merge with ice sheet of East European plain (Gobejishvili 2004). This is a reason why there are not many arctic species in the Caucasus region.

There are more than 2000 glaciers located in the Great Caucasus which cover about 0.3% of the total area of the Caucasus region. Their lower limit has been retreating upwards due to climate warming, with 29% decrease of glaciated area documented between the years 1880s–1970s, resulting in the emergence of numerous lakes (Volodicheva 2002).

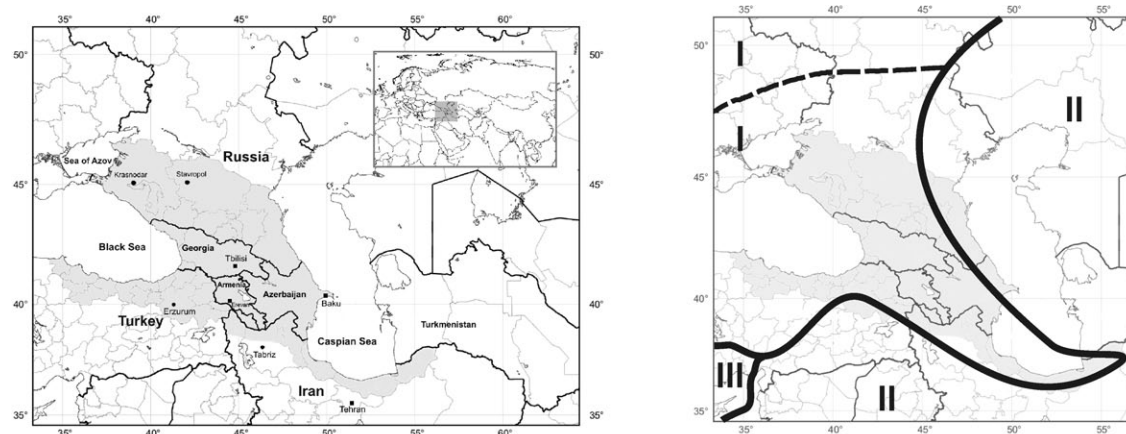


Fig. 1. The Caucasus region (left) as covered by the checklist in paper I, and its phytogeographical position (right). I: Euro-Siberian, II: Irano-Turanian, III: Mediterranean. Dashed line separates the Pontic Province to the south from the Medio-European Province to the north. After Zohary (1963).

Phytogeography

The phytogeographical assignment of the Caucasus region has been made differently in various botanical literature in global or regional scales. Among these, Zohary (1973) has provided a thorough account of phytogeography of the Middle East (in his definition) including the area in our focus, and I adopt his treatment here. Almost all of the study area is included in Zohary's Pontic province of the Euro-Siberian region (Fig. 1), except for a narrow belt along western Caspian Sea coasts, which belongs to the Medio-Asiatic province of the Irano-Turanian region. For the bulk of the area between the southern- to eastern coasts of the Black Sea down to the southern coasts of the Caspian Sea, Zohary (1973) used the term Euxino-Hyrcanian subprovince which fits well with the area highlighted in grey in Fig. 1. The region can be subdivided into Euxinian district (east) and Hyrcanian district (west), but as acknowledged by Zohary (and later by Browicz 1989) the border between these two is vague. Each of these two districts has a number of specific plant species, but more importantly, they share several Euxino-Hyrcanian endemic species among which are Tertiary relict woody plants like *Acer cappadocicum*, *Diospyros lotus*, *Mespilus germanica*, *Pterocarya fraxinifolia*, *Zelkova carpinifolia*, *Jasminum officinale*, *Laurocerasus officinalis*, and *Vaccinium arctostaphylos*, the latter three being evergreen species (Meusel et al. 1964–1992; Zohary 1973; Hedge & Wendelbo 1978; Browicz 1982–1997). The flora of the Caucasus region, while predominantly Euro-Siberian, is strongly influenced by the Mediterranean flora from the south-west, and the Irano-Turanian elements from the south (Fig. 1). This becomes apparent by the mixture of the vegetation types (Fig. 2) with Mediterranean shrubs and Irano-Turanian steppe elements especially in the southern Caucasus (Transcaucasus).

Vegetation

The zonation of vegetation in the Caucasus is complex due to the high altitudinal differences. Major vegetation types are forests, xerophytic woodlands, alpine-subalpine meadows, wetlands, steppes, deserts and semi-deserts (Fig. 2). Forests cover some 20% of the region (Krever et al. 2001) and their lower boundary lies at different altitudes, from sea level in Colchis and Hyrcan, to above 2,000 m in the eastern and south-eastern Caucasus, depending on the temperature and moisture (Volodicheva 2002). Most of the forests in the eastern Black Sea coasts are dominated by one or two species, while several polydominant forest types exist in Hyrcan (southern Caspian Sea coasts).

Subtropical forests with evergreen understory and lianas are found in lowlands of Colchis and Hyrcan (Serebryanny 2002). At higher altitudes in Colchis, these are replaced with *Abies nordmanniana* and *Picea orientalis* which form coniferous and mixed forests also in the western periphery of the Colchis forests (Fig. 2). Other coniferous forests are formed by *Pinus* stands, mostly along the western part of the Great Caucasus mountain range, and are partly mixed with *Betula* spp.

Fagus orientalis, *Carpinus betulus* and *Quercus* spp. are important elements in the Caucasus forests (Fig. 2). Out of 17 species of *Quercus* in the Caucasus, 14 are endemic (Volodicheva 2002). Depending on the altitude and latitude, xerophytic species like *Paliurus spina-christi*, *Rhamnus pallasii*, *Berberis* spp., *Cotoneaster* spp., *Lonicera* spp., *Jasminum fruticans*, and *Punica granatum* are common in dry shrublands, sometimes mixed with *Juniperus* or *Quercus*.

About 25% of plant species of the Caucasus are endemic to the region (Myers et al. 2000). Most of these can be found in the high mountains, and a great part of them are considered as autochthonous endemics, i.e. having originated in the same area as they occur now. Intensive habitat alteration and the long history of human settlement since around 32,000 years ago (Arslanov et al. 2007; hominid settlement since 1.77 mya, Mgeladze et al. 2010) has resulted in expansion of steppes and xerophytic plant communities, and many contemporary landscapes are actually secondary communities (Volodicheva 2002).

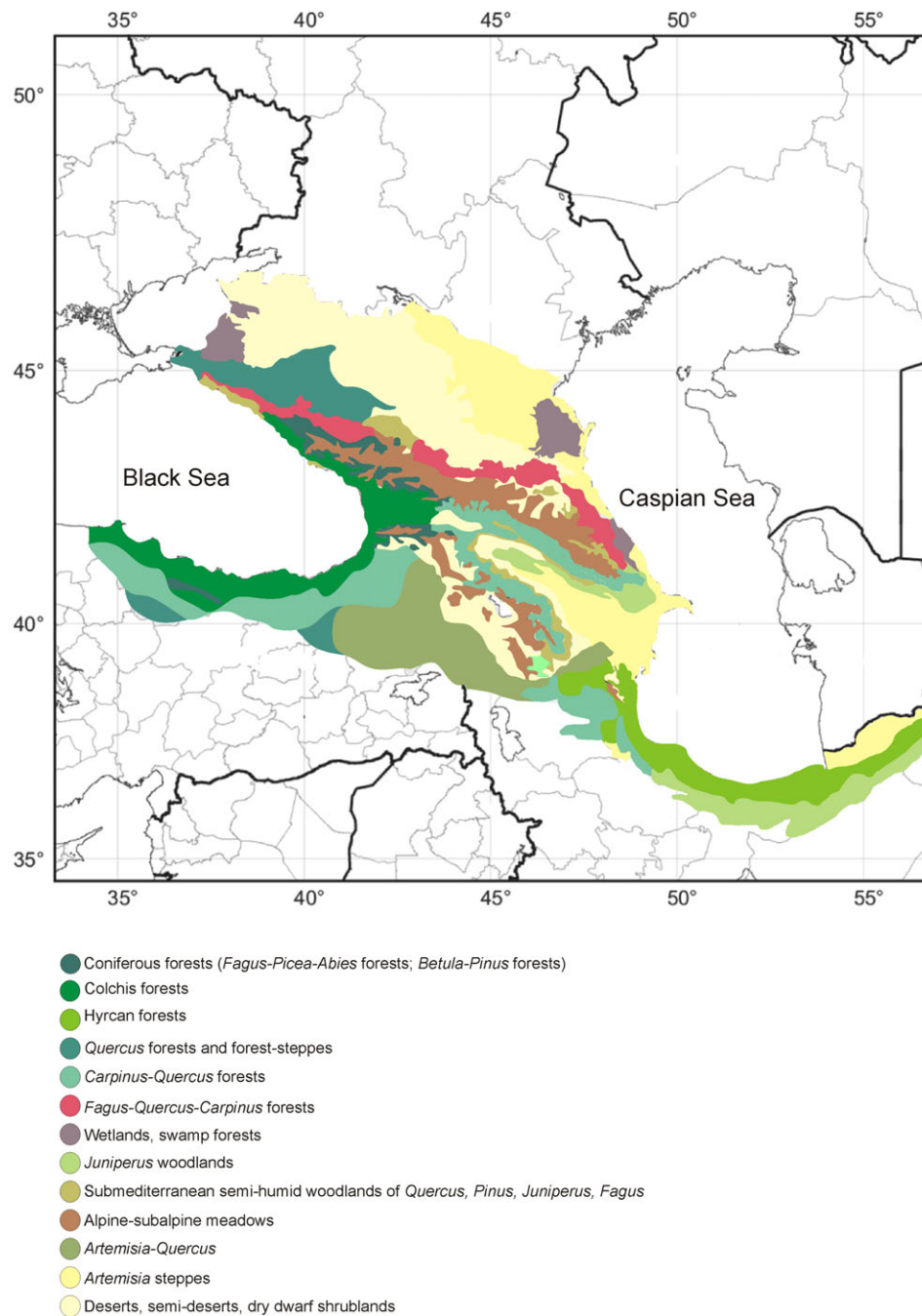


Fig. 2. Vegetation map of the Caucasus region. Mainly after Beruchashvili (1995) and Zohary (1963).

Glacial Refugia

Much of the biota of Europe was either wiped out or heavily changed during the Pleistocene glaciations. Many species in northern areas became extinct and the ranges of others were contracted into the refugia in more southerly areas (Fig. 3) which provided suitable habitats for persistence of organisms, and later became sources of re-colonization following glacial periods (Taberlet et al. 1998; Milne 2006). A considerable part of the present European biota is therefore a result of range expansions from such refugia. Three major routes have been proposed for post-glacial biotic re-colonization of Europe (Randi 2006): 1) southward expansion from cryptic northern refugia, 2) northward expansion of biota from Mediterranean refugia, and, 3) a westward path where refugial elements in the eastern Europe, the Caucasus region and western Asia, are thought to have dispersed into Europe. The existence of the refugia in northern Europe is still under debate, but the two latter routes are well-documented by numerous studies (e.g. Taberlet et al. 1998; Hewitt 1999, 2004). In comparison, still most of the phylogeography papers configure the northward path more frequently than the westward route, possibly because of more intensive sampling in southern Europe.

The Caucasus region harbors two western Palearctic glacial refugia, namely Colchis and Hyrcan (Tumajanov 1971; Volodicheva 2002). It seems that the recognition of this region as a source of, and contributor to the European biodiversity has been made already some decades ago. For instance, on their account of Flora of Azerbaijan, N Iran, Gilliat-Smith & Turrill (1930) mention their assumption about the migration of plants from and across Asia Minor into Europe, or as they state “Oriental contribution to the European flora” and enumerate a number of plant species which “extend from [Iranian] Azerbaijan into Europe”.

Modern evidence for the above assumptions can be found for instance in recent palynological and phylogeographical studies and a few examples are mentioned here. Atkinson et al. (2006) studied longitudinal pattern of genetic diversity of oaks and their associated gallwasps across Pleistocene refugia in Iberia, Italy, Balkans, and Asia Minor/Iran. They found that the highest species richness for oaks and the highest genetic diversity for oak gallwasps are found in eastern refugia in Turkey and Iran, while the Iberian lineages were assumed to have diverged from the eastern ones. Bănărescu (1991) and Kotlík et al. (2008) pointed out that refugia located in Ponto-Caspian region (the Black and the Caspian Sea basins) were one of the most important areas from which freshwater fishes colonized Europe after glacial periods. Based on pollen and plant macrofossil analyses of northern Eurasia, Tarasov et al. (2000) concluded that at Last Glacial Maximum, broad-leaved trees were confined to small refugia, including the eastern coast of the Black Sea from where they later spread into Europe.

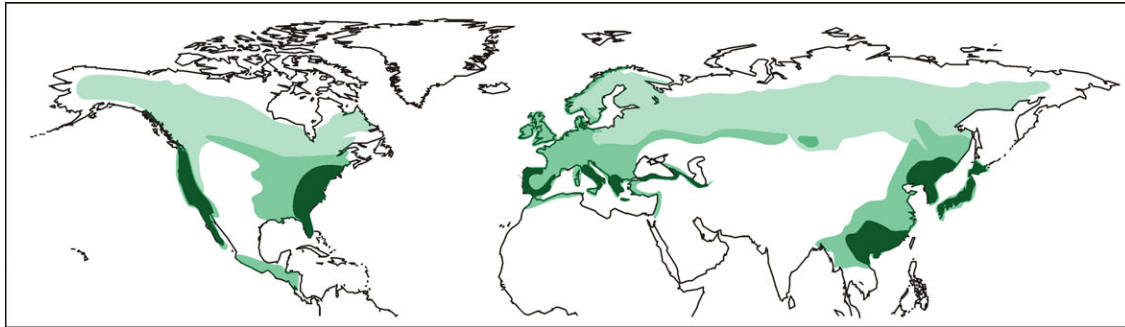


Fig. 3. Northern Hemisphere Pleistocene glacial refugia (black), and the present temperate (dark green) and boreal (light green) forests. Black areas (not to scale) mainly after Milne (2006), Taberlet et al. (1998), and Tarasov et al. (2000). Green areas after Lomolino et al. (2006).

Wood-inhabiting Basidiomycetes

Wood-inhabiting (lignicolous) fungi use the woody substrata as their nutrient supply, or, as physical support for their fruiting body (Rayner & Boddy 1988: 119), and they mostly belong to the basidiomycetes (Nakasone 1993).

Wood-inhabiting basidiomycetes play an integral role in forest ecosystem and its food webs by recycling wood, the most important reservoir of organic carbon in the living world (Watkinson et al. 2006). Several of them have been used as indicators of habitat quality and rich biodiversity (Parmasto & Parmasto 1997), some participate in mycorrhizal associations (Tedersoo et al. 2010), and some of them provide habitat (as well as food) for other organisms (e.g. Fritz & Heilmann-Clausen 2010). Several species are exploited in industry and biotechnology, used for instance in biopulping, medicine, production of ‘myco-wood’ and ‘myco-fodder’, and in food science (Schmit 2006; Gadd 2001; Rayner & Boddy 1988).

This study deals with the two conspicuous groups of wood-inhabiting basidiomycetes, i.e. corticioids and polypores, traditionally known among ‘aphyllophoroid’ fungi. These fungi have for long been treated under the collective family names Corticiaceae and Polyporaceae, but their taxonomy and classification has seen many changes during past four to five decades and is still far from settled. Many traditional taxa have not yet been closely examined in a phylogenetic context and their delimitation has remained largely subjective. Sound morphological characters to circumscribe taxa are few. The situation is most complicated in taxa with a resupinate basidiocarp. Their fruiting body is largely confined to two dimensions and hence macroscopical features, better developed e.g. in capitate/pileate taxa, are further reduced in these taxa. Cryptic species are frequently found in resupinate basidiomycetes (Hallenberg 1991). The difficulties in taxonomy of resupinate basidiomycetes may partly be linked to a slower rate of morphological change in fungi with less elaborate fruiting bodies (Taylor et al. 2006).

Corticioids (non-poroid resupinate) and polypores comprise phylogenetically heterogeneous groups of basidiomycetes (Fig. 4). Corticioid lineages are present in all clades of Agaricomycetes (sensu Hibbett et al. 2007, but Auriculariales not included), while polypores are absent from Atheliales, Cantharellales, Corticiales, and Jaapiales (Fig. 4). It has been speculated that corticioid type of basidiocarp may represent the ancestral form of basidiomycete fruiting bodies (Binder et al. 2005, 2010).

The concept of corticioids in this study generally follows *Corticiaceae of Northern Europe* (ed. John Eriksson et al.), and that of polypores mostly follows

European Polypores (ed. Leif Ryvarden and Robert Gilbertson) and *Polypores of Finland and Estonia* (ed. Erast Parmasto) (see more detailed explanation and full citations in Paper I), and their accepted names generally agree with the public databases *Cortbase* and *Mycobank*.

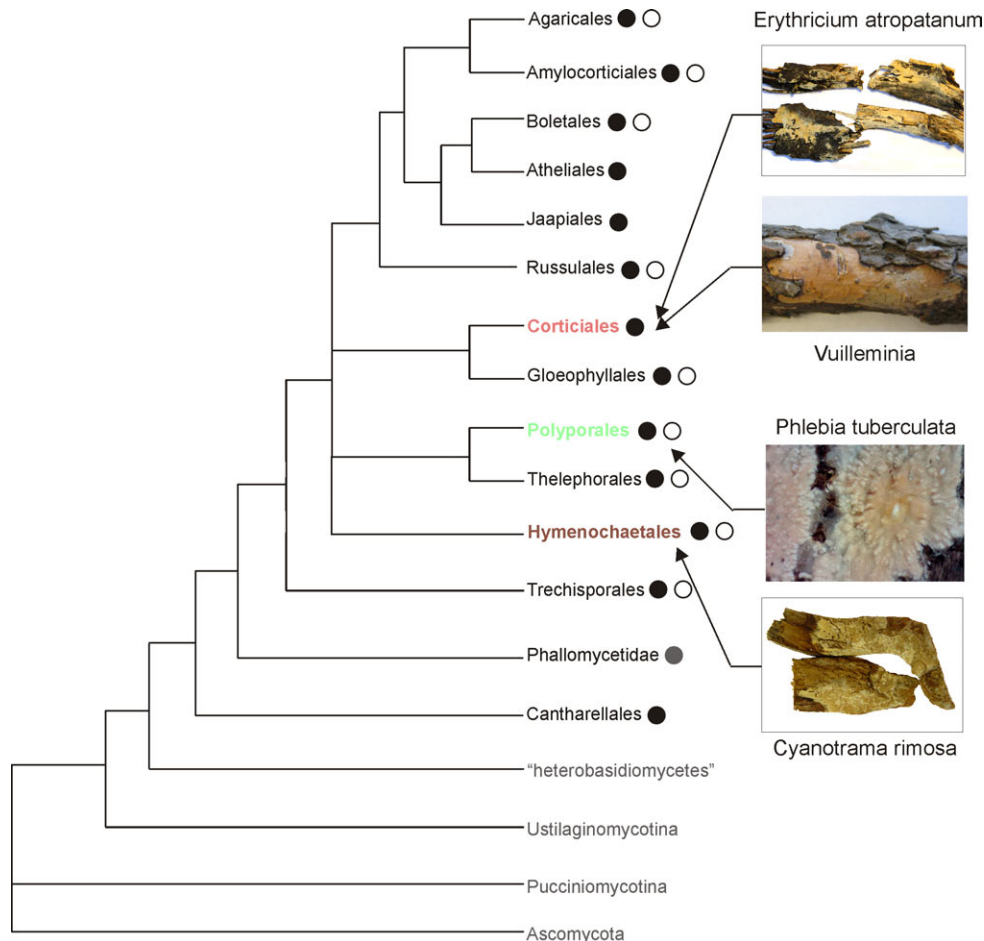


Fig. 4. Distribution of corticioids (●) and polypores (○) in the basidiomycete phylogeny (left), and the resupinate taxa studied in papers II–V (right). Phylogenetic tree after Hibbett (2006), Hibbett et al. (2007), and Binder et al. (2010). Clades other than Agaricomycetes are named in grey font (Auriculariales excluded). Corticioids are present in all clades of Agaricomycetes (*ca.* homobasidiomycetes), while polypores are absent from Atheliales, Cantharellales, Corticiales, and Jaapiales. Currently, the only taxon in Agaricales which is studied among polypores is *Fistulina*. Phallomycetidae, mostly composed of clavarioid taxa, contains *Kavinia* which is usually studied among corticioids. Photos by MG.

Aims

Unlike vascular plants of the Caucasus region which are well studied, wood-inhabiting basidiomycetes have received little attention. The knowledge on corticioids and polypores needed to be compiled and standardized for further detailed and applied studies such as taxonomic and mycogeographical treatments. On the other hand, regarding the difficulties in delimitation of resupinate basidiomycetes discussed

above, they would merit attempts towards clarification of their systematics, and hence they were prioritized in this thesis.

Therefore, this study has three focal aims:

- To summarize and update the knowledge of corticioids and polypores in the Caucasus region (papers **I–III**)
- To resolve the systematics and phylogeny of selected, resupinate wood-inhabiting basidiomycetes for which the Caucasus region is currently the mere, or one of the noteworthy/common areas of their distribution (papers **II–V**)
- To assess the similarity of Caucasian corticioid fungi to those of the well-known areas in the Northern Hemisphere, and to examine the importance of the Caucasus region as a glacial refugium for species of wood-inhabiting basidiomycetes (papers **V–VI**)

MATERIALS AND METHODS

Taxon Sampling

I examined specimens from the collections I made in 2005–2008 in northern Iran (dupl. mostly at H and/or IRAN) and from material deposited in B, BPI, CFMR, CWU, DAOM, FH, GB, H, HUBO, IFP, IRAN, K, LY, MA, MEL, NY, O, PC, PDD, S, SVER, TAA, TFM, and TNS (for herbaria acronyms see Thiers 2010). For molecular studies, the specimens were selected from dried material and from authenticated fungal cultures in the Fungal Culture collection of the University of Gothenburg (FCUG) kept in Liquid Nitrogen, which is the standard and optimal condition for long-term preservation of cultured basidiomycetes (Homolka et al. 2010). Before proposing taxonomic novelties (Appendix 1), I tried to examine types as well as additional material of critical taxa. In phylogenetic analyses (papers **II–V**), attention was paid to sample the generic types, to include more than one specimen per taxa in question, and in large phylogenetic analyses, to avoid sampling bias toward any clade or subclade (paper **II**). Moreover, taxon sampling was enhanced using sequences deposited in GenBank. In papers **IV** and **V**, environmental sequences (GenBank) were added to the dataset, following recommendations by Nilsson et al. (2010).

Morphology

Macro- and micromorphological characters of the specimens were studied under a binocular and a light microscope, using bright field or phase contrast optics, and these characters were carefully denoted when compiling species descriptions. Squash mounts were prepared in 5% potassium hydroxide (KOH), Melzer's reagent (IKI) and Cotton Blue in lactic acid (CB) (see e.g. Largent et al. 1977). Sulfovanillin (SV) reagent (vanillin crystals in 80% sulphuric acid) was used to examine the aldehyde reaction of (gloeo-)cystidia (paper **IV**). Most of the measurements and drawings were made in CB. If the size or shape of the structures changed in KOH mounts, this was denoted. Conventions used in spore measurements are explained in papers **II–V**. In some cases the original annotation on the type of wood (conifer, hardwood) for

published records was revised (esp. papers **I**, **IV**, and **V**) and some misidentifications were reported when relevant (paper **IV**).

While advantages (e.g., Wahlberg et al. 2005; Lopardo et al. 2010) and disadvantages (e.g. Gaubert et al. 2005; Klingenberg & Gidaszewski 2010) of incorporating morphological characters into phylogenetic analyses have been much disputed, I hesitated to use these characters directly in the analyses mainly because of time constraint, and also because the results in the few studies implementing them for wood-fungi do not seem to be satisfactory (e.g., Hallenberg & Parmasto 1998; Parmasto & Hallenberg 2000). Compared to e.g. vascular plants, fungi have far fewer taxonomically useful morphological characters (Feuerer & Hawksworth 2007), and there is high polymorphism in many fungal morphological traits (Slepecky & Starmer 2009). Instead, selected characters were mapped on the phylogenetic trees obtained from DNA sequence data (paper **IV**), and this usually helps re-interpretation of the characters and examining their usefulness in delimiting taxa.

DNA Markers

Internal transcribed spacer (ITS) region of nuclear ribosomal DNA (including ITS1, 5.8S, and ITS2) was used for phylogenetic inference at species level, and phylogenetic relationships above species level were inferred using analyses of partial nuclear large subunit ribosomal gene (LSU). While the use of nLSU has been shown disadvantageous for inferring phylogeny in Ascomycota (Schoch et al. 2009), it is widely used in studies of basidiomycete phylogeny (Hibbett 2006; Binder et al. 2010).

Procedure of DNA extraction, amplification, and sequencing was described in papers **II–IV**. For basidiocarp-guided extractions, specimens were checked microscopically, and clean, spore-rich samples were selected. Using basidiomycete-specific primers, I did not face serious problem with minor wood or microfungus contamination of dried samples. In many cases where DNA was extracted from cultured isolates, I tried to supplement it with DNA extracted from fruiting body of the same taxon. As stated by Paterson et al. (2008), cultured hyphae may have detrimental effect on fungal DNA structure, which would in turn affect the phylogenetic signal. Moreover, extraction and sequencing DNA from authentic and well-preserved herbarium material is highly advantageous for the currently expanding molecular identification endeavour (Hibbett et al. 2009) and has been looked upon as a priority for building reference sequence databases (Brock et al. 2009; Hyde et al. 2010). Especially in fungi, the percentage of sequences based on misidentified specimens is high (Vilgalys 2003).

All obtained sequences were submitted to GenBank and accession numbers were reported in the pertinent papers. In this study, the oldest herbarium material from which I was able to successfully extract DNA was collected in 1958 (paper **II**). Sequences were individually subjected to BLAST search (Altschul et al. 1990) to examine the possibility of contamination, or to roughly estimate their allied taxa before the actual analyses. Prior to final alignments, I checked alignment scores for datasets using open-source ClustalW2 at EBI platform (see Larkin et al. 2007). Sequences corresponding to low scores (usually below 50) were excluded from the dataset. Alignments were performed using the program MAFFT (Katoh & Toh 2008), and adjusted with PhyDE (Müller et al. 2005).

Analyses

Phylogeny

DNA datasets were analyzed individually and combined (papers **II–IV**). In all analyses, phylogenetic relationships were inferred using static homology (*vs.* dynamic) and optimality criteria- (*vs.* pure algorithmic) based approaches. Model-based approaches (Bayesian, papers **II–V**; Maximum Likelihood, paper **V**) as well as those based on parsimony (papers **IV, V**) were used. Outgroups were chosen as inferred from earlier published phylogenies. The best-fit model of nucleotide substitution was estimated using MrModeltest (Nylander 2004) with the Akaike information criterion (Posada & Buckley 2004). Bayesian phylogenetic inference was made using MrBayes (Ronquist & Huelsenbeck 2003), with search settings as explained in the respective papers. Most of the Bayesian analyses were performed using computing resources of the Finnish IT center for science, CSC (Espoo, Finland).

For parsimony analyses, performed using TNT, or Nona within Winclada shell (see papers **IV, V**), branch supports were calculated using Jackknife resampling. As argued by Freudenstein & Davis (2010), jackknifing is preferred over bootstrapping because it is closer to the original data. It is clear, however, that no support measure would serve more appropriate than expanding the dataset to examine the robustness of branches, and to see how the inferred phylogeny would be sensitive to repeating the analyses, by inserting new terminals or more characters (e.g., Grant & Kluge 2003).

In paper **V**, Maximum Likelihood analysis was performed using RAxML implemented in raxmlGUI (Stamatakis 2006; Silvestro & Michalak 2010), with search strategy as mentioned therein.

Similarity Tests

In paper **VI**, the similarity between corticioids of the Caucasus region and seven areas in the Northern Hemisphere (northern Europe, eastern-central Europe, southern Europe, eastern North America, western North America, East Asia, and India) was studied by employing Tripartite similarity index ([T], Tulloss 1997) at two different levels: either at genus level by comparing species lists of three corticioid genera (*Hyphodontia*, *Phlebia*, and *Peniophora*), or by applying T to the checklists of all corticioids of the areas given above. Well-edited checklists were surveyed and assembled from available publications, or received from regional specialists, and occasionally supplemented by specimens examined. To further deduce the similarity of the Caucasus to the seven geographical locations mentioned above, UPGMA dendrograms with bootstrap support values were computed (see paper **VI**).

Haplotype Analysis

Haplotype networks were drawn in papers **IV** and **V** using TCS (Clement et al. 2000), to examine the distinctiveness of *Vuilleminia alni* from *V. comedens* (paper **IV**), and *Phlebia tuberculata* from *P. livida* (paper **V**), as well as inferring the root for the haplotype network of *P. tuberculata* and *P. livida*.

In paper **VI**, haplotypes were obtained using FaBox (Villesen 2007) and analyzed with Arlequin (Excoffier & Lischer 2010) to compute population comparisons (*Fst*), molecular diversity (π), and mean expected heterozygosity (*H*) for ITS1 and ITS2 sequences belonging to the isolates of the widespread corticioid species *Peniophorella praetermissa* sampled from different parts of its range. Attention was also paid to the contribution of the Caucasus isolates to the obtained shared haplotypes (see paper **VI**).

DELIVERABLES FROM THIS STUDY

Knowledge on the Occurrence of Polypores and Corticioids

Papers **I–III** provide updated and new data about the corticioids and polypores of the Caucasus region. Paper **I** summarized the knowledge of corticioids and polypores for the Caucasus region, to serve as a baseline for more detailed studies. In this paper, the first combined checklist of corticioid and polypore species for the Caucasus region was provided (389 corticioid and 246 polypore species). Checklists expedite the taxonomic treatments and facilitate later compilation of lists of endangered and threatened organisms, a crucial practice for conservation. Furthermore, before concluding how mycota of one area would be connected with other areas, basic knowledge on the occurrence of species and a compiled checklist are essential.

In paper **II** a resupinate polypore was recognized as disjunctly occurring in the Caucasus region, western North America, and Africa, while in paper **III** a corticioid species from the region was described as new to science. As well-exemplified by papers **II** and **III**, it is clear that checklists need to be made up-to-date when new information is obtained. Therefore, and due to the importance of online resources for taxonomists as well as taxonomy-users, the checklist is planned to appear online and become updated at the MYCO-LICH website (www.myco-lich.com; Sohrabi & Ghobad-Nejhad 2010).

Systematics and Phylogenetic Relationships

Systematics and phylogenetic relationships of selected resupinate wood-inhabiting basidiomycetes were studied in papers **II–V**. These taxa were selected because the Caucasus region is the mere (*Erythricium atropatanum*) or one of the noteworthy areas of their distribution (*Cyanotrampa*, *Vuilleminia*) or because they are common in the region (*Phlebia tuberculata*, *Vuilleminia*).

In paper **II**, the relatedness of the Iranian and North American material of the resupinate polypore *Diplomitoporus rimosus* was tested, and its phylogenetic placement was reconstructed. The species occurs disjunctly in the Iranian part of the Caucasus region, western North America and Ethiopia, growing on dead decorticated wood of *Juniperus* (rarely *Cupressus*). A preliminary hypothesis on the affinity of *D. rimosus* to *Megasporoporia* through sharing narrow and strongly cyanophilous skeletal hyphae was rejected via phylogenetic analysis. Moreover, unlike the generic type of *Diplomitoporus* (*D. flavescens*) which was shown to belong to the Polyporales, *D. rimosus* was positioned in the Hymenochaetales, and *Cyanotrampa* gen. nov. was introduced to accommodate it. The genus is characterized by a set of characters which is absent in its sister taxa namely *Trichaptum* and *Fibricium* (paper

II). This study also showed that the cyanophily of skeletal hyphae appears to be a result of morphological convergence, having developed in several distantly related taxa (paper II).

It seems that *Cyanotrampa rimosa* could be awaiting discovery in Europe, due to its connection to *Juniperus* and the juniper-associated polypores, namely *Antrodia juniperina* and *Pyrofomes demidoffii* (Hjortstam & Ryvarden 1996). Distribution of *Cyanotrampa rimosa* is fairly similar to that of *Pyrofomes demidoffii* and these species may belong to the same ecological guild. However, the reason for their disjunct distribution pattern remains to be explained. Even though many parts of Europe have been well-inventoried mycologically, open and dry *Juniperus* woodlands may not seem too attractive for finding polypores, and *C. rimosa* might have been overlooked (cf. Bernicchia 2000). But certainly more inventories are needed to judge its occurrence in *Juniperus* or similar woodlands in central Asia.

In paper III, a new corticioid species *Erythricium atropatanum* was described from East Azerbaijan Province, NW Iran. *Erythricium atropatanum* was found on plant debris in an orchard, a place which at first glance does not look promising for finding a novelty. The species belongs to an understudied group of corticioids with a resupinate pinkish fruiting body, overlapping morphology, and blurred generic boundaries. They are all grouped in the Corticiales, awaiting detailed study. Phylogenetic relationships of *E. atropatanum* with other members of Corticiaceae (sensu paper IV) is not unequivocal, as shown by conflicting ITS and LSU phylogenies. But the tree from combined dataset was in accordance with that of ITS. The ITS and combined ITS-LSU phylogenetic trees place the new species well within the *Erythricium* clade, and based on morphology as well as nutritional mode, *E. atropatanum* fits *Erythricium*. Moreover, *Erythricium* is the oldest name in this clade. The other genera (generic types) found in the *Erythricium* clade are strikingly different in their nutritional strategies and morphology. This decision is supported by the fact that like *E. laetum* (generic type), *E. atropatanum* is saprotrophic, has pinkish resupinate basidiocarp, large ellipsoid-fusoid spores with firm cyanophilous walls, and lacks an anamorph. A more rigorous generic assignment can not be made before the genera in this clade are well-delimited. Interestingly, in the relatively small sampling of 'pinkish' corticioids in paper III, diverse nutritional modes can be found, and studying its role in delimiting the genera in the *Erythricium* clade and other 'pinkish' members in the Corticiales may well be warranted.

In paper IV phylogeny of the genus *Vuilleminia* was studied for the first time. *Vuilleminia* is a small corticioid genus, and its species grow on decaying and dead attached wood of angiosperms. Several species are decorticating, and rupture the bark upon growth. While fresh, they mostly appear as a hyaline gelatinous layer on decorticated wood (see cover photo). The genus is best represented in Europe and western Asia (paper IV), and all European species are also found in the Caucasus region (except one species recently described from France, not closely evaluated yet). The application of the genus name was aimed to be safeguarded through a recent proposal for conserving the generic type *Thelephora comedens* (Ghobad-Nejhad & Hallenberg 2010; see Appendix 3). As indicated in the recent Report of the Nomenclature Committee for Fungi (Norvell 2011), the proposal was accepted.

In paper IV, the circumscription of the genus *Vuilleminia* and the phylogenetic relationships among its species were examined. The 10 species accepted by *Cortbase*, as well as *V. oyensis* and *V. quercina* (= *Corticium quercicola*) were evaluated. Of these, two species were reduced to synonymy, while four species were shown to

belong to other genera. *Vuilleminia* species described from South America and Africa, and *V. comedens* reported from New Zealand were demonstrated to be distinct from those of the north temperate region, and were accommodated in the newly established genera *Punctulariopsis* and *Australovuilleminia*, respectively (paper IV). Moreover, *V. quercina* was shown to be nested in a completely different clade from the rest of *Vuilleminia* species, close to the lichenicolous anamorph *Marchandiomyces corallinus*, and due to its unique set of characters, a new genus (*Marchandiopsis*) was erected for this taxon. Out of the six species remaining in *Vuilleminia*, four species comprise a well-supported clade as the ‘core *Vuilleminia*’. They are decorticating, produce gelatinous fruiting body and have a unique 13 bp long insertion at the 5' end of the ITS2 region. To further elucidate the relationships between *Vuilleminia* and allied genera in the Corticiales, we examined a family assignment within the order, based on phylogenetically and morphologically well-supported clades and available family names. *Vuilleminia* together with the closely related genera *Cytdia* and *Australovuilleminia* were assigned to Vuilleminiaceae, *Punctulariopsis* and two other genera are in Punctulariaceae, while the ‘pinkish’ members of corticiales are all in Corticiaceae (sensu paper IV).

In paper IV, we re-examined the taxonomic value of decorticating ability, host specificity, and spore size, commonly considered as important characters for distinguishing species of *Vuilleminia*. It turned out that decorticating ability characterizes the ‘core *Vuilleminia*’ at most, while it does not warrant a generic delimitation of *Vuilleminia*, and can even vary within one and the same species in *V. macrospora* (also in *Peniophora laeta*; see Hallenberg et al. 2010). Host range of several species was found to be wider than earlier assumed, and no species seems to be restricted to a certain plant, on the contrary to the statements in previous studies. But species may show some degree of host preference. Spore size was shown to be variable and not a good character to separate *V. comedens* from *V. coryli* and *V. alni* (the latter being synonymized with *V. comedens*). The results in paper IV also cast doubt on the unequivocal applicability of ITS in discriminating fungal species. The ITS region is the most commonly used genetic marker for fungal species discriminations and molecular identification (Nilsson et al. 2009; Seifert 2009). However, as shown in paper IV, despite having strikingly different spore shape, *V. megalospora* cannot be separated from *V. comedens* in the ITS phylogeny, nor by the ITS genetic distance measurements and ITS haplotype network. This, further highlights the role of taxonomists’ surveillance in the growing field of molecular identification, or ‘barcoding’ (Begerow et al. 2010; Nilsson et al. 2008).

As pointed out in paper IV, a great part of the present diversifications in *Vuilleminia* is shown to be concentrated to temperate Europe and to the Caucasus region, where the most prominent hosts for *Vuilleminia*, namely Fagaceae, Betulaceae and Rosaceae, are abundant. Especially for species of *Quercus*, Asia Minor/Caucasus region is considered to be the major area of diversity (Atkinson et al. 2006). The most commonly collected *Vuilleminia* species in the Caucasus are *V. comedens* and *V. coryli*. *Vuilleminia cystidiata* is also not rare there, but other species are rare almost everywhere in their distribution range, including the Caucasus region.

Paper V is a study of the *Phlebia livida* complex. Earlier studies recognized two subspecies, namely *P. livida* ssp. *livida* and *P. livida* ssp. *tuberculata*, based on incompatibility tests and isoelectric protein banding patterns. A wider sampling of the species led us to identify several characters that warrant recognition of two species. The two species can be distinguished based on morphology, phylogenetic analyses of

nuclear ITS sequences, genetic distance, haplotype network, and by substrate preference. Therefore, *ssp. tuberculata* is distinguished as a species of its own. *Phlebia livida* has reddish brown fruiting bodies and is mostly associated with conifer wood, while in *P. tuberculata* fruiting body is lighter in color and is mostly associated with hardwood, and unlike the former species, develops pointed ornamentations on its hymenium surface. The two species are well-separated from each other in two highly supported clades in the ITS phylogenetic tree, and also appear in two distinct clusters in the haplotype network (paper V). Moreover, their ITS sequences are different from each other by 6.1–10.8% pairwise distance. *Phlebia livida* is yet verified from Sweden, Finland, Estonia, Russian Karelia, and Georgia. Most of the specimens labeled as *P. livida* studied from across Europe turned out to be *P. tuberculata*. Its range includes eastern Europe, Mediterranean Europe, southern Scandinavia, UK, the Caucasus region, and New Zealand. The two species seem to co-occur in Scandinavia and in the Caucasus region.

Biogeography of the Caucasus Corticioids

In paper V, using a TCS haplotype network was drawn for *Phlebia tuberculata* - *Phlebia livida*. According to the TCS approach, the root haplotype is the oldest haplotype in a given TCS network, representing the oldest population within a species or species complex (Crandall & Templeton 1993; Posada & Crandall 2001). In this paper, the highest root probability was assigned to the haplotype consisting of isolates from different parts of the Caucasus region, which may be an indication of the region having served as a reservoir for old populations of this species during the last glaciation (see paper V).

In paper VI we assessed the similarity of Caucasian corticioid fungi to those of well known areas in the Northern Hemisphere for the first time, and examined the significance of the Caucasus region as a possible refugium for postglacial colonization of corticioids in Europe. Corticioid species endemism was also noted. The level of similarity was inferred using the Tripartite similarity index and cluster analysis of updated checklists for the three large genera *Hyphodontia*, *Peniophora*, and *Phlebia* (Appendix 2B), and for all corticioids of the Caucasus region. The refugium status was inferred by measuring genetic diversity within, and differentiation between the Caucasian and other isolates of ITS1 and ITS2 belonging to the corticioid fungus *Peniophorella praetermissa*.

The composition of corticioids in the Caucasus region was distinctly more similar to Europe and North America than to East Asia and India. The Caucasus was found to be more similar to Europe than to North America. The highest similarity to Europe may indicate that there has been an effective flow of biota between them. Moreover, the Caucasus is more similar to East Asia than to India. A higher similarity to East Asia than to the Himalayas has also been documented for the European mountain plant species, apparently via a former, northerly deciduous forest belt (Zhang et al. 2007).

Despite the high level of plant endemism in the Caucasus (Myers et al. 2000; Krever et al. 2001), the level of species endemism for corticioids was shown to be very low, which may be a common feature for wood-inhabiting saprotrophic fungi (Mueller et al. 2007).

The highest molecular diversity in *Peniophorella praetermissa* for both ITS1 and ITS2 was in the Caucasus and East Asia, while these two areas were found to be

significantly differentiated from each other. Unlike Caucasian samples, East Asian sequences were highly divergent from the European ones, suggesting that the Caucasus could have been a source of colonization in Europe. Genetic diversity in Greenland isolates was lower than in Europe and North America. Greenland isolates showed significant differentiation from all populations (incl. North America) except from Caucasus, northern Europe, and Mediterranean Europe. This, and the composition of the shared haplotypes containing Greenlandic isolates (see table 1, paper **VI**) 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 (paper **VI**).

FINAL REMARKS

Species identification and recognition in fungi has been primarily based on morphology, and still formal species descriptions need to be formulated by phenotypic characters (*ICBN*). Some authors believe that “There is no indication that this tradition will change” (Hallenberg 1998), but some are already encouraging the taxonomic community to support the sequence-based descriptions (Hawksworth 2009; Hibbett et al. 2011). There is no doubt that molecular techniques provide valuable identification tools for fungal taxonomists. Especially for end-users of taxonomy it is highly beneficial to develop fast and easily applicable methods of identification. But this does not necessarily need to mean that non-DNA characters (if available) should be overlooked when a new species is described (Hyde et al. 2010). A taxonomic name would better be looked upon as an important repository for storing information about an organism, and therefore needs to be well-substantiated.

To minimize redundancy, particularly for species complexes, it has been frequently suggested that newly described species be preferably recognized by several lines of evidence rather than only one (e.g. see paper **V** and references therein). At least for resupinate basidiomycetes (papers **II–V**), the use of multiple lines of evidence is beneficial when establishing new taxa or decrypting species complexes (see also Crespo & Lumbsch 2010; such “integrative” approach is implied in many studies though not specifically named). Perhaps taxonomists should endeavor to tailor the ways of documenting *inheritable character discontinuities* (see Crespo & Lumbsch 2010) rather than developing more and more “species concepts”. Accordingly, the approach has the potential to encourage communication between scientists dealing with various tools of identification, and to alleviate the battle arising from conflicting species recognitions because of various species concepts (DeSalle et al. 2005).

This thesis, through paper **VI**, provides the first broad scale treatment of corticioids in a biogeographic context, and shows the level of connections of the Caucasus to the north hemispheric areas. In general, fungal biogeography is a less attended field when compared to plants and animals. The situation becomes more tangible when considering that we know only 7% out of about 1.5 million fungal species estimated to occur in the biosphere (Kirk et al. 2008; Hawksworth & Mueller 2008). Yet, our knowledge on detailed fungal distribution history and geographic structure is restricted. The elaborate comparisons of checklists and the use of molecular data for a well-sampled species complex (*Peniophorella praetermissa*) in paper **VI**, point out that the temperate forests that persisted in the Caucasus region

during the last glaciation harbored a wood mycota which later constituted at least part of the fungal diversity of the European forests.

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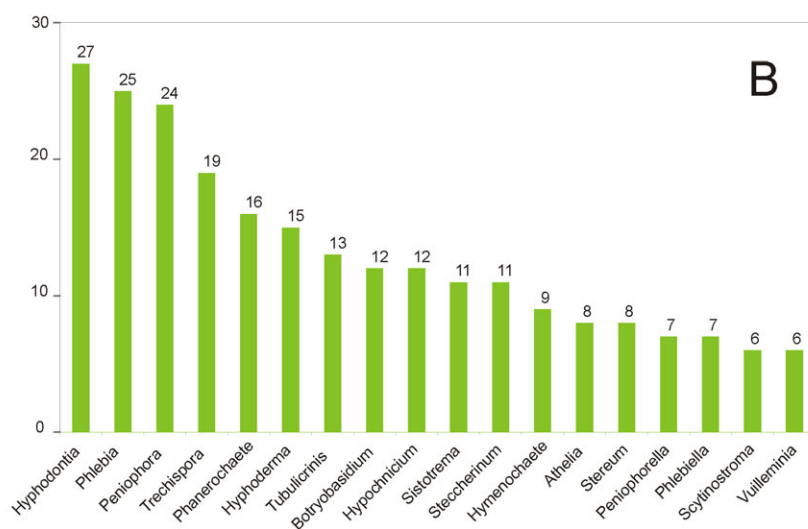
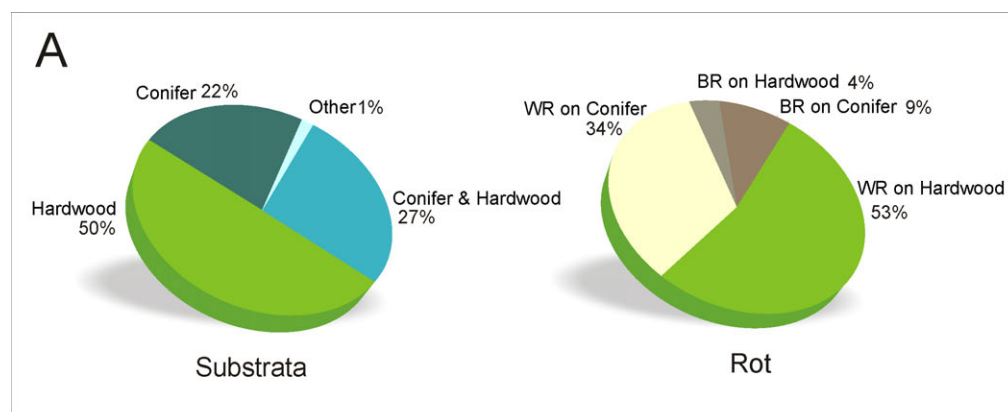
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Appendix 1. Taxonomic novelties in this study.

New genera	
<i>Australovuilleminia</i> Ghobad-Nejhad & Hallenb.	Paper IV
<i>Cyanotrama</i> Ghobad-Nejhad & Y.C. Dai	Paper II
<i>Marchandiopsis</i> Ghobad-Nejhad & Hallenb.	Paper IV
<i>Punctulariopsis</i> Ghobad-Nejhad	Paper IV
New species	
<i>Australovuilleminia coccinea</i> Ghobad-Nejhad & Hallenb.....	Paper IV
<i>Erythricium atropatanum</i> Ghobad-Nejhad & Hallenb.	Paper III
New combinations	
<i>Cyanotrama rimosa</i> (Murrill) Ghobad-Nejhad	Paper II
<i>Marchandiopsis quercina</i> (J. Erikss. & Ryvardeen) Ghobad-Nejhad.....	Paper IV
<i>Phlebia tuberculata</i> (Hallenb. & E. Larss.) Ghobad-Nejhad.....	Paper V
<i>Punctulariopsis obducens</i> (Hjortstam & Ryvardeen) Ghobad-Nejhad.....	Paper IV
<i>Punctulariopsis subglobispora</i> (Hallenb. & Hjortstam) Ghobad-Nejhad	Paper IV

Appendix 2. A. Pie charts representing the percentages of types of substrata (left) and types of rot (right) for corticioids of the Caucasus region. For instance, 22% of corticioids of the region grow on coniferous wood; 9% of corticioids species in the region cause brown rot and grow on conifers. BR = brown rot, WR = white rot. **B.** Corticioid genera in the Caucasus region with \geq six species (after an updated paper I).



South Chinese species. Consequently he has used the oldest valid described name. He has been in Vietnam recently and knew that the name is commonly used. I fully agree with Xia. As you might know, in the *Flora of China* a list is given with the names as used in Western countries before the treatment with all the genera recognised by Xia.

H.P. Nooteboom, Leiden, Netherlands

Committee recommendation. — Bearing in mind Art. 32.3 and the emphasis on the size and quality of the wood obtainable from the species, the committee concluded that the descriptive material does not constitute a description or diagnosis and voted 15–2, 1 abstention, to recommend that this not be considered a validly published name.

(1945) Proposal to conserve the name *Thelephora comedens* (*Vuilleminia comedens*) with a conserved type (*Basidiomycota*)

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(1945) *Thelephora comedens* Nees, Syst. Pilze: 239. 1816–1817: Fr., Syst. Mycol. 1: 447. 1821, nom. cons. prop.
 Typus: [Czech Republic, Vidnava] “Weidenau in Ö. Schlesiens”, on *Quercus robur*, Jan 1913, Hruba, in Petrak, Fl. Bohem. Morav. Exs., Ser. 2, Abt. 1, Fungi, No. 638 (FH), typ. cons. prop.

The epithet *comedens*, first introduced by Nees (l.c.) in 1816–1817 as *Thelephora comedens*, and sanctioned as such by Fries (l.c.), has been consistently applied to the basidiomycetous corticioid fungus presently known as *Vuilleminia comedens* (Nees: Fr.) Maire (in Bull. Soc. Mycol. Fr. 18: 81. 1902), which provides the type of *Vuilleminia* Maire (l.c.). Examination of the specimen in herb. UPS that must be considered the type of *T. comedens* (see below) ascertained that the specimen does not accord with the current concept of the species in use. Consequently, to safeguard the application of the epithet *comedens*, and of the generic name *Vuilleminia*, it is necessary to conserve *T. comedens* with a conserved type, as proposed here.

Vuilleminia comedens is an easily recognized corticioid basidiomycete, colonizing weak and dead attached branches and twigs of deciduous trees, more commonly oaks and beeches (Hjortstam & al., Corticiaceae N. Eur. 8: 1591. 1988; Rayner & Boddy, Fungal decomposition of wood: 68, 421. 1988). The mycelia have an effective decorticating activity and cause white rot in the substrate. The species is widespread in Europe (e.g., Hjortstam & al., l.c.; Bernicchia & al. in Micol. Veg. Medit. 23: 3–20. 2008; Kotiranta & al. in Norrlinia 19: 190. 2009) and western Asia (e.g., Hallenberg in Mycotaxon 12: 490. 1981; Ghobad-Nejhad & al. in Mycol. Balcan. 6: 142. 2009) and its occurrence in Central and eastern Asia and North Africa has been verified by Ghobad-Nejhad & al. (in Taxon: in press). The name *Vuilleminia comedens* appears in 169 hits by Scirus database (www.scirus.com) and 196 references by Google Scholar (<http://scholar.google.com>), both retrieved in June 2010. It has been widely used in numerous regional floras (e.g., Bourdot & Galzin, Hym. Fr.: 338. 1928; Christiansen, Danish Resup. Fungi: 130. 1960; Jülich & Stalpers, Resup. Non-poroid Aphyllorphorales Temp. N. Hemisph.: 272. 1980; Breitenbach & Kränzlin, Fungi Switzerland: 194. 1986; Hjortstam & al., l.c.; Telleria in Bibl. Mycol. 135: 120. 1990; Ginns & Lefebvre in Mycol. Memo. 19: 180. 1993; Maekawa in Rep. Tottori Mycol. Inst. 32: 20. 1994; Hansen & Knudsen, Nordic Macromycetes 3: 180. 1997;

Dämon in Bibl. Mycol. 189: 205. 2001), checklists (e.g., Yurchenko in Mycotaxon 86: 61. 2003; May & al., Fungi Australia vol. 2B: 311. 2003; Gorjón & al. in Mycotaxon 109: e27. 2009), text- and handbooks (e.g., Boddy & al., Ecol. Saprotroph. Basidiomyc.: 215. 2008; Krieglsteiner, Grosspilze Baden-Württembergs: 354. 2000; Gerhardt, BLV Handbuch Pilze: 413. 2006), and gross phylogenetic treatments (e.g., Binder & al. in Syst. Biodivers. 3: 113–157. 2005; Lawrey & al. in Amer. J. Bot. 95: 816–823. 2008). Since the original description of the genus in 1902 (Maire, l.c.), a number of species have been added to or combined under *Vuilleminia* and the genus is shown to be monophyletic (Ghobad-Nejhad & al. in Taxon: in press).

In the original description of *Thelephora comedens* (Nees, l.c.) an illustration is referred to as *f.* 255 (Fig. 1a), and is provided in plate 34. This illustration is a color drawing of a specimen, apparently never examined since Nees’s publication of the name, and recently located by us in UPS herbarium, among the Fries collection (Fig. 1b–c). The specimen bears a label with Nees’s name on it and “*Thelephora comedens mihi*” in his handwriting (Fig. 1b); its appearance matches perfectly the drawing labelled *f.* 255 in Nees (l.c.) (see Fig. 1a–c). To the label of this specimen, Nees has added “*Bitte das größere Stück abzubilden*” (Fig. 1b), so no doubt this specimen is the one upon which figure 255 was based. Considering date of dispersal of Nees’s herbarium (after 1851, cf. Stafleu & Cowan in Regnum Veg. 105: 705–706. 1981), this material was unlikely to be seen by Fries before the publication of *Systema Mycologicum* (Fries, l.c.). Also no annotation exists on this specimen to show that Fries ever saw it. Collection or dispersal date of the only (four) other specimens assigned to *T. comedens* in the Fries collection in UPS postdate Fries’s sanctioning of *Thelephora comedens* (l.c.) and so are not associated with the account of the species in the sanctioning work. Moreover, none of these samples bear any annotations by Fries. We are not aware of any other Fries or Nees specimens under this name, so we consider this specimen at UPS and the illustration prepared from it as the only original material of *T. comedens* Nees.

However, especially in microscopic features, Nees’s sample in UPS deviates from the current concept of *Vuilleminia comedens*. It rather represents a *Hyphoderma* Wallr. with both gloeo- and metuloid cystidia, but the species could not be identified with certainty as the specimen seems contaminated. The illustration is widely associated

with the epithet in numerous reference works, but it was only Persoon (Mycol. Eur. 1: 137. 1822) who commented “*icon non adaequant*”. Before the detailed microscopic characterization of the species that now bears the name by Maire (l.c.), Masee (in J. Linn. Soc., Bot. 27: 155. 1891) provided spore size and an illustration (plate 6, fig. 5) for *T. comedens* (here under *Corticium comedens* (Nees:Fr.) Fr., Epicr. Syst. Mycol.: 565. 1838), but the specimen in UPS herbarium seems to have escaped mycologists’ attention.

As to the selection of a conserved type for the name, some old exsiccates made to exemplify the species were examined. The protologue by Nees (l.c.) describes the species on “*Eichenzweigen*”. Fries (l.c.) mentions “*Coryli*” but we do not consider *Corylus* as a common host for *V. comedens* in its strict current sense. Maire (l.c.) in his description of the genus and the species *V. comedens*, mentions [only] *Quercus* as the host. Therefore, a conserved type would preferably be selected from specimens on *Quercus*. The exsiccate made by Petrak in Petrak, Fl. Bohem. Morav. Exs., Ser. 2, Abt. 1, Lief. 13, No. 638 (1913) is a good representative of *T. comedens*, macroscopically and microscopically, and could well serve as a conserved type for the

epithet name and the genus *Vuilleminia*. The specimen was collected in what is now the Czech Republic on *Q. robur*, and we examined the material deposited in the Farlow Herbarium (Fig. 1d–e).

If *T. comedens* is not conserved, the application of the widely used epithet *comedens* as well as the generic name *Vuilleminia* and consequently those of included species would be threatened and impose a number of disadvantageous nomenclatural changes. Conservation of *T. comedens* as proposed here would therefore ensure the current usage of the generic name *Vuilleminia*, and would also retain the application of the epithet *comedens* in the sense it has been used for more than 180 years.

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Fig. 1. *Thelephora comedens*. **a**, Illustration *f.* 255 in Nees (l.c.); **b–c**, the illustrated specimen with Nees’s handwritten label, located by us in Fries collection at UPS; **d–e**, the specimen proposed here to serve as the conserved type for *T. comedens*. Scale bars = 1 cm.

Appendix 4. Corrections.

		Change
Paper I	Page 124	“Krever <i>et al.</i> (2002)” to “Krever <i>et al.</i> (2001)”
	Page 124, second column	“Browicz (1984–1988)” to “Browicz (1984–1989)”; “Amsaya” to “Amasya”
	Pages 131, 142	Alphabetic arrangement of entries corrected
	Page 163	“Browicz, K. 1988” to “Browicz, K. 1989”
Paper II	Page 1511, Latin diagnose	“laeves, CB+” to “laeves, CB–”
Paper III	Page 62	“24 LSU and 17 ITS” to “25 LSU and 18 ITS”
Paper IV	Page 1523	“ <i>V. pseudocystidia</i> ” to “ <i>V. pseudocystidiata</i> ”
	Page 1528	“thin, CB+” to “thin, CB(+)”
	Page 1529, first column	“CB–, IKI–” to “CB(+), IKI–”