Publications in Botany from the University of Helsinki
No: 43

Taxonomy and phylogeny of the ‘manna lichens’ and allied species (Megasporaceae)

Mohammad Sohrabi

Helsinki 2011

Department of Biosciences
Faculty of Biological and Environmental Sciences
University of Helsinki
Finland

Botanical Museum
Finnish Museum of Natural History
University of Helsinki
Finland

ACADEMIC DISSERTATION

To be presented for public examination with the permission of the Faculty of Biological and Environmental Sciences of the University of Helsinki, in the lecture room (Nylander-sali) of the Botanical Museum, Unioninkatu 44, on January 27th 2012, at 12 noon.

Helsinki 2011

Author’s address
Botanical Museum, Finnish Museum of Natural History
P.O. Box 7, FI–00014 University of Helsinki, Finland.
Department of Plant Science, University of Tabriz, 51666 Tabriz, Iran.
Email: msohrabi@myco-lich.com, mohammad.sohrabi@helsinki.fi

Supervisors

Prof. Jaakko Hyvönen University of Helsinki, Finland	Prof. Soili Stenroos University of Helsinki, Finland

Pre-examiners

Prof. Thorsten Lumbsch Field Museum of Natural History, Chicago, Illinois, USA	Dr. Christian Printzen Senckenberg Research Institute and Natural History Museum, Frankfurt, Germany

Opponent
Prof. Helmut Mayrhofer
University of Graz, Austria

Custos
Prof. Heikki Hänninen
University of Helsinki, Finland

ISSN 1238-4577
ISBN 978-952-10-7399-1 (paperback)
ISBN 978-952-10-7400-4 (PDF)
http://ethesis.helsinki.fi

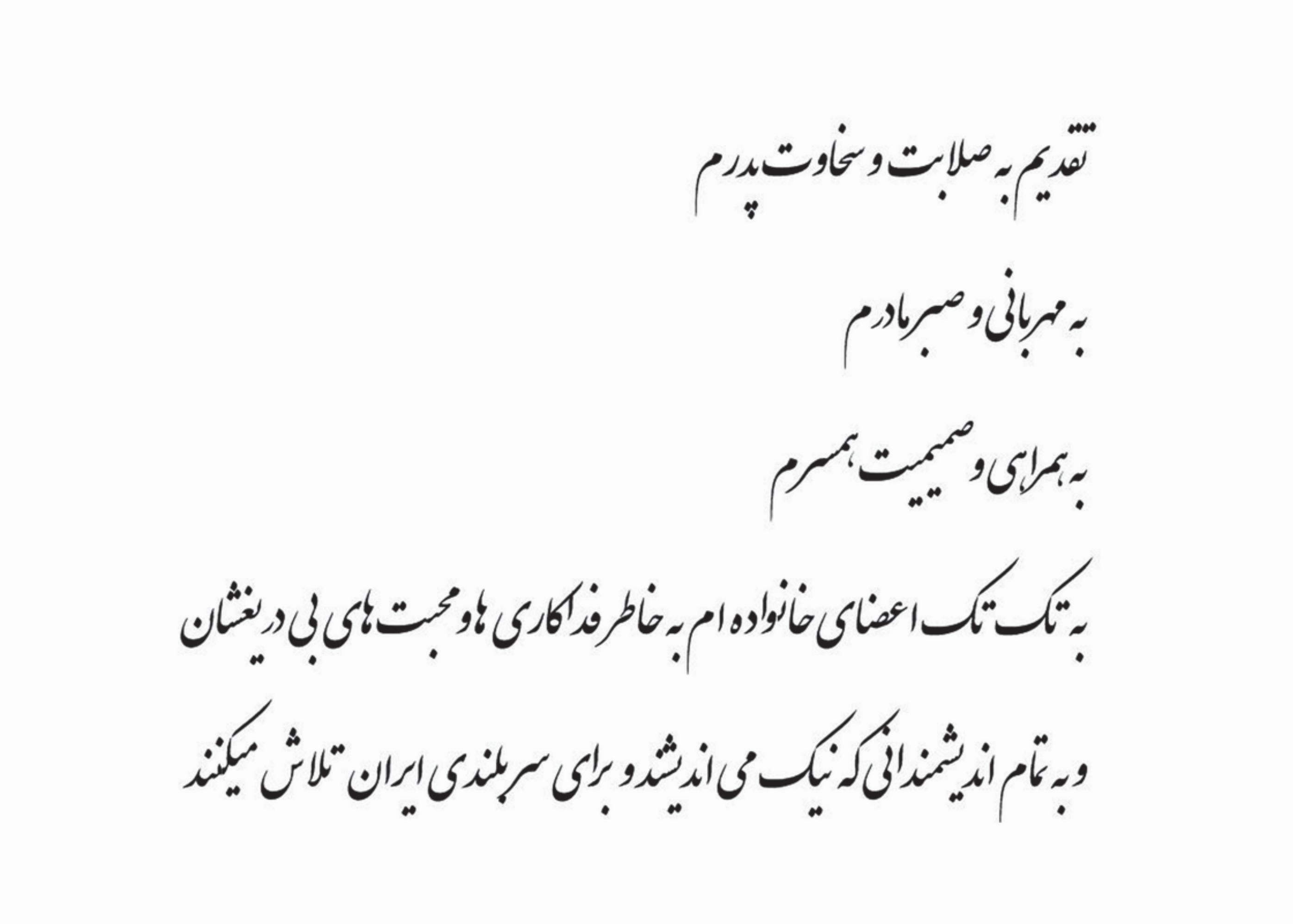
Layout: Mohammad Sohrabi

Cover photo: The three vagrant species, *Circinaria fruticulosa*, *C. gyrosa*, and *C. hispida*, growing at the same spot: Iran, East Azerbaijan province.

Yliopistopaino
Helsinki 2011

Copyrights

Note – In the study **VII**, the manuscript includes descriptions of two new species and 13 new combinations. This manuscript has been submitted for publication elsewhere and in order to make it clear that these new names are not validly published in this thesis, the Latin diagnoses and basionyms, which are necessary for valid publication according to the International Code of Botanical Nomenclature (Vienna Code), are not presented here.



تقدیم به صلابت و سخاوت پدرم

به مهربانی و صبر مادرم

به همراهی و صمیمیت همسرم

به تک تک اعضای خانواده ام به خاطر فداکاری ها و محبت های بی دریغشان

و به تمام اندیشمندانی که نیک می اندیشند و برای سربلندی ایران تلاش میکنند

List of Papers

The following publications are included in the thesis and indicated by their Latin numerals in the text.

I. **Sohrabi**, **M**. & T. Ahti (2010) Nomenclatural synopsis of the Old World's "manna" lichens of the genus *Aspicilia* (Megasporaceae). Taxon 59: 628–636.

II. **Sohrabi**, **M**., Owe-Larsson, B., Nordin A. & W. Obermayer (2010) *Aspicilia tibetica*, a new terricolous species of the Himalayas and adjacent regions. Mycological Progress 9: 491–499.

III. **Sohrabi**, **M**., Myllys, L. & S. Stenroos (2010) Successful DNA sequencing of a 75 year-old herbarium specimen *Aspicilia aschabadensis* (J. Steiner) Mereschk. The Lichenologist 42: 626–628

IV. **Sohrabi**, **M**., Ahti, T. & B. Litterski (2011) *Aspicilia digitata* sp. nov., a new vagrant lichen from Kyrgyzstan. The Lichenologist 43: 39–46.

V. **Sohrabi**, **M**., Stenroos, S., Högnabba, F., Owe-Larsson, B. & A. Nordin (2011) *Aspicilia rogeri* sp. nov., (Megasporaceae) and other allied vagrant species in North America. The Bryologist 114: 178–189.

VI. Owe-Larsson, B., Nordin, A., Tibell, L. & **M. Sohrabi** (2011) *Aspicilia arida* sp. nov. and the *A. desertorum* complex. Bibliotheca Lichenologica 106: 231–242.

VII. **Sohrabi**, **M**., Stenroos, S., Myllys, L., Søchting U. & J. Hyvönen (2011) Phylogeny and taxonomy of the 'manna lichens', a new insight into the relationships of vagrant and crustose morphotypes. Submitted Manuscript.

Contributions

The following table displays the main contributions of the author to the original articles and manuscripts.

	I	**II**	**III**	**IV**	**V**	**VI**	**VII**
Original idea	MS	MS	MS	MS	MS	BO	MS
Field /herbarium work	—/MS	WO/ MS	MS	BL/MS	—/MS	BO/MS	MS
Morphology/microscopy	MS	MS, BO, WO	MS	MS	MS	BO	MS
Laboratory work	—	MS	MS	MS	MS, FH	MS, LT	MS
Analyses	—	—	MS, LM	MS	MS, SS	AN, MS, LT	MS
Manuscript preparation and data collection	MS, TA	MS, BO, AN	MS, LM, SS	MS, TA, BL,	MS, AN, BO, SS	BO, AN, MS, LT	MS, SS, LM, JH, US

AN=Andres Nordin

BL= Birgit Litterski

BO= Björn Owe-Larsson

FH= Filip Högnabba

JH= Jaakko Hyvönen

LM= Leena Myllys

LT= Leif Tibell

MS= Mohammad Sohrabi

SS= Soili Stenroos

TA= Teuvo Ahti

US= Ulrik Søchting

WO= Walter Obermayer

Abstract

This dissertation is focused on the taxonomy, phylogeny, and ecology of the vagrant, erratic and allied terricolous and saxicolous species of the genera *Aspicilia* A. Massal. and *Circinaria* Link (Megasporaceae, Pertusariales, lichenized Ascomycota), particularly those traditionally referred to as 'manna lichens'. The group has previously been defined on the basis of relatively few morphological characters (mainly growth form), and the phylogeny of the group has not been previously studied.

The phylogeny of the family Megasporaceae is inferred from the combined dataset of nuLSU and mtSSU sequences. Five genera i.e., *Aspicilia*, *Circinaria*, *Lobothallia* (Clauzade & Cl. Roux) Hafellner, *Megaspora* (Clauzade & Cl. Roux) Hafellner & V. Wirth, and *Sagedia* Ach. are recognized. *Lobothallia* is sister of the four other genera, while *Aspicilia* and *Sagedia* form the next clade. All these genera have small asci with eight spores. *Circinaria* is a sister genus of *Megaspora*, and these two have in common asci with (1–4) 6–8 large spores. In the resulting trees, *Circinaria* forms a monophyletic group and sphaerothallioid species form a monophyletic group within *Circinaria*. The presence of certain morphological characters such as pseudocyphellae, thickness of cortex and medulla layers, as well as ecological differences in sphaerothallioid species distinguish it from some other crustose species, especially those containing aspicilin and characterised by thin cortex and medulla layers, conidium length c. 6–12 μm and absence of pseudocyphellae. If sphaerothallioid species are accepted as a distinct genus, the rest of the *Circinaria* species would remain as a paraphyletic assemblage. The combined dataset of nrLSU and mtSSU did not fully resolve infrageneric relationships in Megasporaceae. Currently, the genus *Circinaria* includes all the sphaerothallioid species and its generic position is confirmed and accepted. Thus, it is proposed as a correct generic name also for the peculiar 'manna lichens' described originally in other genera.

Phylogeny at the species level has been studied using nrITS sequence data. Traditionally, certain morphological characters (e.g., growth form, anatomy of apothecium, pycnidia and cortex layer) have been used for the recognition of species in *Aspicilia* s.lat. In order to find more reliable characters they were re-evaluated in the light of molecular data. Since characters such as vagrant, erratic and crustose growth forms proved to be misleading for the recognition of some species, a combination of several characters (including molecular data) is recommended for species recognition.

Vagrant growth form seems to have evolved several times among the distantly related lineages and even within a single population, resulting in either crustose or erratic and vagrant growth forms. This pattern of crustose, erratic and vagrant growth forms distribution in the genus *Circinaria* may help us to interpret the morphological convergence and ecological adaptation through the evolutionary history. Despite these insights, the reasons behind the high plasticity in the external morphology of vagrant, erratic and crustose species in the sphaerothallioid *Circinaria* still remain unknown.

Of the 15 species placed in the 'manna lichens' (except *Circinaria tominii* nom. provis.), 14 are included in the molecular study along with some additional species from closely related groups. Four new species of 'manna lichens' are recognized: *Circinaria rogeri* nom. provis., (syn. *Aspicilia rogeri*) from the U.S.A.; *C. digitata* nom. provis. (syn. *Aspicilia digitata*) from Kyrgyzstan; *C. gyrosa* nom. provis. from Armenia, Azerbaijan, Iran, Turkey, Turkmenistan and Spain, and *C. rostamii* nom. provis. from Azerbaijan, Iran and Turkey. *Circinaria arida*, described from the USA, contains aspicilin and lacks pseudocyphellae. *Aspicilia tibetica*, a terricolous species with small spore size (8–14 × 5–9 μm) and a 8-spored ascus, is described from China. Based on an analysis of nrITS dataset, three new erratic, vagrant and crustose species were also recognized, but these require additional study. The results also reveal that *C. elmorei* and *C. hispida* are not monophyletic as currently understood. In addition, 13 new combinations in the genus *Circinaria* are proposed.

Keywords: *Aspicilia*, Central Asia, *Circinaria*, crustose, desert, 'manna lichens', Megasporaceae, morphological convergence, North America, phylogeny, *Sphaerothallia*, steppe, taxonomy, vagrant

Contents

Background

I became interested in lichens when I was accepted as an undergraduate in the Gorgan University of Agricultural Sciences and Natural Resources. My first lichen collection was made in 1999 from the surroundings of Daran village in Jolfa County (East Azerbaijan province) of Iran. The high steppes of the Kiamaki Mountain (c. 3,347 m), located to the south of Daran, is a suitable habitat for vagrant subfruticose *Aspicilia* or 'manna lichens'. The region is also rather close (c. 160 km) to Mount Ararat where the first report of 'manna lichens' in SW Asia (including Iran, Turkey and Armenia) was made by Göbel (1830). In the course of a literature survey of Iranian lichens and during the preparation of the first national lichen checklist in 2004 I became more interested to track the history of the first collections of 'manna lichens' made in 1820–1825. I was also interested to study the stories of lichen "falls" claimed to have taken place in some areas of NW Iran.

I was awarded a scholarship by the Iranian Ministry of Science and Technology and moved to Finland to continue my studies towards MSc and PhD degrees in the University of Helsinki. During the discussions with my PhD supervisors, I proposed the topic "The taxonomic studies of the genus *Aspicilia* s.lat.". My original idea was only to revise 'manna lichens' of the Eurasian steppes and deserts. In 2007 and 2008 I was able to conduct two excursions throughout the steppes and deserts of central and NW Iran, collecting different vagrant lichens and many terricolous and saxicolous species of *Aspicilia* s.lat.; additionally, in the course of herbarium study, I received many specimens on loan from different herbaria. Since I found a wide range of variation within the whole group, I found it necessary to expand my project to include some allied terricolous and saxicolous species, and to use molecular data in phylogenetic studies of vagrant and erratic species and their relationship with allied crustose species in *Aspicilia* s.lat.

Aims

The studies presented here primarily deal with the vagrant, erratic and allied terricolous and saxicolous species of the genera *Aspicilia* A. Massal. and *Circinaria* Link (Megasporaceae, Pertusariales, lichenized Ascomycota), particularly those traditionally referred to as 'manna lichens'. The aims were to address nomenclatural and taxonomic issues and the phylogeny of these lichen taxa. This thesis concentrates on the following topics:

- **Paper I**. The aim was to elucidate the nomenclatural problems of the 'manna lichens' in *Aspicilia* s.lat. In addition, the history of the 'manna lichens' and the protologues of species were evaluated. Most of names were typified and valid publications and the accepted names were presented in accordance to ICBN.

- **Paper II**. The aim was to list all terricolous *Aspicilia* s.lat. worldwide in order to better understand their growth forms and morphological characters. A further aim was to introduce a new species of *A. tibetica*, occurring in Tibet.

- **Paper III**. Extracting and amplifying certain areas of DNA from some of the old herbarium specimens of 'manna lichens' and other closely related species were attempted. The successfully obtained sequences from *Aspicilia aschabadensis* from 75 year-old specimen were compared with other reliable *Aspicilia* sequences available from the GenBank.

- **Paper IV**. Current knowledge of vagrant *Aspicilia* species in the large steppe areas of Central Asia was summarized. In this study, DNA sequences of *A. fruticulosa*, *A. hispida*, and a new vagrant *A. digitata*, were obtained. The monophyly of new species was confirmed and formally described.

- **Paper V**. Taxonomy and phylogenetic relationships of common North American and Eurasian vagrant *Aspicilia fruticulosa* and *A. hispida* species were revised. A new species *A. rogeri* was found and described as an additional member of manna lichens in U.S.A. *A. fruticulosa* was excluded from the North American checklist temporarily.

- **Paper VI**. The *Aspicilia* '*desertorum*' complex in the Sonoran Desert was revised and the generic name *Circinaria* adopted. The identity of the two saxicolous *C. arida* and *C. elmorei* were confirmed by using nrITS dataset. A preliminary assessment of the genetic relationships among a few extremely polymorphic vagrant and crustose species belonging to *Aspicilia* '*desertorum*' s. lat. was undertaken.

- **Paper VII.** The taxonomy and phylogeny of 'manna lichens' in Eurasia and North Africa were revised and the currently available knowledge on the phylogeny of Megasporaceae was reconsidered. A new phylogenetic analysis with extensive sampling from the erratic, vagrant and crustose sphaerothallioid species (including 'manna lichens') was presented. In this study, we attempted to present a better overview on generic and species level delimitation among the sphaerothallioid species in the genus *Circinaria* with respect to inconsistency of morphological (i.e. growth form, ascospores, conidia, cortex and pseudocyphellae) and chemical characters used for species identification. New insights into genetic similarities between vagrant and crustose morphotype of the erratic sphaerothallioid species were provided.

Introduction

Lichens

The biological term "lichen" refers to a symbiotic interaction, which relies upon intimate physical and nutritional relationships between the fungal heterotroph "mycobiont" and a photosynthetic autotroph "photobiont" (either eukaryotic green algae, prokaryotic blue-green algae or both). The photobiont is often restricted to the upper layers of fungal tissue, where sufficient light is available for photosynthesis. The photobiont (green algal/cyanobacterial cells) produces carbohydrates, which are consumed by the mycobiont (fungal cells), and the fungal partner provides photobiont with a habitat where it is able to survive in an otherwise uninhabitable or poor condition environments.

Lichens are diverse group of organisms found in almost all terrestrial environments, from the tropics to Polar Regions (see also Nash 2008). It has been hypothesized that one of the first steps in the colonization of land by eukaryotes may have been the formation of a lichen symbiosis (reviewed in Heckman *et al.* 2001). It is now generally accepted that lichen-forming fungi are ancient with a fossil record dating back 400 Ma to the Early Devonian in the Rhynie chert deposits in Scotland (Taylor *et al.* 1995, 1997, 2004). Yuan *et al.* (2005) reported a lichen-like symbiosis from South China in marine phosphorite of the Doushanto Formation at Weng'an with the age of c. 620 Ma.

In modern classifications lichens are regarded as "lichen-forming fungi" (Hawksworth & Hill 1984, Gargas *et al.* 1995, Honegger 1996, Tehler & Wedin 2008). According to the ICBN (McNeill *et al.* 2006) the taxonomy and nomenclature of the lichen species is based on the mycobiont, which constitutes the major part of the lichen association and it reproduces and sustains speciation. All algal or cyanobacterial partners (photobiont) bear independent binomial names (Jørgensen 1996). Only about 100 algal or cyanobacterial species have been reported to be associated with more than 13,500 lichen-forming fungal species, so that various different fungi may share the same photobiont (Nash 2008).

Most lichens are ascomycetes, being found in more than 17 of the 45 orders currently documented (Hawksworth *et al.* 1995 and Lumbsch & Huhndorf 2007, Kirk at al. 2008). Only five of these orders, however, exclusively contain lichenized taxa. The other orders and many families, genera or even species involve both lichenized and non-lichenized, but often lichenicolous, fungi (Rambold & Triebel 1992). It seems that lichenization has occurred multiple times; therefore, in an evolutionary sense, lichens cannot be regarded as monophyletic but polyphyletic (Lutzoni & Miadlikowska 2009). From the 1950s until the end of the 1990s, based on the observation of mixed group of lichenized and non-lichenized species in many orders of the Ascomycota, it was widely assumed that the lichen symbiosis arose independently several times (see also Lutzoni & Miadlikowska 2009). During the last ten years, assembling and conducting large-scale multilocus phylogenetic studies of the Ascomycota (e.g., Lutzoni *et al.* 2001, 2004) have revealed that the tremendous diversity of lichen-forming ascomycetes might be the result of only three to five independent origins (Lutzoni & Miadlikowska 2009).

Feuerer & Hawksworth (2007) re-evaluated the number of known lichen species worldwide and estimated it to be somewhere between 13,500 (previously proposed by Hawksworth *et al.* 1995) and c. 20,000 (previously proposed by Sipman & Aptroot 2001), but the latter included “orphaned” species, i.e. “species which have not, or have only rarely, been recorded after their initial description and are not covered in modern revisions” (Feuerer & Hawksworth, 2007). In the most recent study by Lücking *et al.* (2009) it was estimated that the diversity of lichens is much higher and there are about 28,000 species worldwide.

It is estimated that more than 40% of Ascomycota species are lichenized. Furthermore, 98% of lichenized fungi are found in the Ascomycota, the largest fungal phylum (see also Lutzoni & Miadlikowska 2009), and the rest of lichenized species are found within the Basidiomycota.

Taxonomy of the lichenized fungi has developed independently from the taxonomy of other fungi for more than a century. This was mainly due to the prevalent interpretation that taxonomy of lichenized and non-lichenized fungi deal with separate groups of species (Aptroot 1998). Since the last decade of the 20th century it has been possible to connect the phylogenetic inconsistency of the artificial division of “lichens” and “fungi” (Nannfeldt 1932, Santesson 1952, Tehler & Wedin 2008). During recent years, through on-going contributions of large scale molecular data to fungal systematics, major changes to our understanding of the evolution of fungi and of their phylogenetic affinities has been possible (see Lutzoni *et al.* 2001, 2004, Hibbett *et al.* 2007, Schoch *et al.* 2009 and Printzen 2010 for a review).

The ‘Manna lichens’

An exciting phenomenon in most of temperate arid and semiarid regions of the world is the occurrence of erratic and vagrant lichens (see **I**, **V**, **VII**, Kappen 1988, Rosentreter 1993, Pérez 1997a, b). Vagrant lichens are known from windswept steppes and deserts in the C and SW Asia, N Africa, S Europe and NW North America. Because of their loose growth form that varies in size from a pea to a hazel-nut, and with no attachment to the substrate, they can easily be blown around in heavy winds. These lichens have been hypothesized to be the best candidate for the “Biblical manna” (cited in Exodus 16:31) that was eaten by the Israelites when they wandered the Sinai wilderness for 40 years (Perez-Llano 1944, Richardson 1974, Brodo *et al.* 2001). The word “Manna” was also used in Qur'an, but no lichen species has been suspected to be Qur'anic manna (**I**).

The “Biblical manna” is defined as the food “miraculously” provided for the Israelites in the wilderness during their escape from Egypt. In many textbooks and popular books (see Evans *et al.* 2002, Kiple & Coneè Ornelas 1999, Webster & Weber 2007) it has been quoted that the “Biblical manna” might have been a lichen. In *Aspicilia* s.lat. (currently *Circinaria*) species with vagrant form (subfruticose and even with amorphous thalli), and without proper attachment to the substrate are known as ‘manna lichens’. The most widely accepted view in textbooks is that the manna of the Bible might be the “manna lichen” (*Lichen esculentus* Pall. ≡ *Lecanora esculenta* (Pall.) Eversm. or ≡ *Aspicilia esculenta* (Pall.) Flagey ≡ *Circinaria esculenta* (Pall.) Sohrabi nom. provis.) which is moved around by the wind in the Eurasian steppes and deserts, sometimes accumulating in drifts so large that people consume it as food, or use it as additive to bread (see also Nelson 1951, Crum 1993, Brodo *et al.* 2001). It must be noted that the ‘manna lichen’ is considered more as a famine food rather than everyday food stuff. Most lichen carbohydrates are indigestible when raw and need to be specially prepared before they are eaten (Crawford 2007).

The informal term ‘manna lichen’ has been used in publications since the 18th century by several authors (e.g., Pallas 1776, Göbel 1830, Eversman 1831, Link 1848, 1849, Berkeley 1849, Pitra 1868, Reichardt 1864, Visiani 1865, Krempelhuber 1867, Errera 1893, Elenkin 1901a, b, c, d, e, 1907, Mereschkowsky 1911a, b, 1921, Perez-Llano 1944, Donkin 1980 and Crum 1993). Donkin (1981) undertook a large literature survey on the nature and source of 'manna' as a miraculous food of biblical times. He documented an extensive number of references to manna lichens and provided some historical information and observations by European naturalists and travellers in Asian deserts (e.g., Eversmann in1820-25, Aucher-Éloy in 1825-30, Thénard in 1828 and Parrot in 1824-25). According to Aucher-Éloy (1843) falls of the ’manna lichen’ do occur in the surrounding area of [‘Reżā'iyeh’] Urmia Lake (Daryacheh-e-Orumiyeh), and in some localities in the southern Caspian to central Asia Minor. However, based on my own knowledge of Iranian literature no document of such lichen fall has been made in recent years and I have never heard about it from the local nomads, or their traditional knowledge.

Up to now, the most commonly cited ‘manna lichen’ (*Lecanora esculenta* or *Aspicilia esculenta*) has not been reported from the Sinai Desert and Egypt. The most recent publications from the entire region were provided by Temina *et al.* (2005) and Seaward & Sipman (2006). In their publications, it was shown that *A. esculenta* (*Circinaria esculenta* nom. provis.) does not occur in the area (see also study **I)**. Recently, Thor & Nascimbene (2010) published the lichen checklist of Libya and the name *A. esculenta* was included. Based on my extensive herbarium study, I presume that the name *A. esculenta* in their study most probably refers to *C. jussuffii* nom. provis. The latter is one of the most widespread species known from Algeria (Link 1848, 1849), Libya and Morocco (see **VII**) and Iran (Rabenhorst 1871, see **VII**) recently also found from Iraq (see **VII**). Most of the old reports of manna lichen from Iran (Persia, western Caspian Sea region) are misidentifications and refer to saxicolous members of this group (see also Seaward *et al.* 2008, Sohrabi *et al.* 2010 and **VII**), or perhaps to the new species described as *Circinaria gyrosa* nom. provis. (**VII**).

According to Zohary (1982) the miraculous manna of the Sinai Desert is probably a product of a vascular plant (e.g., *Hammada salicornica*, *Anabasis setifera*, *Capparis cartilaginea* or *Asclepias sinaica* as *Gomphocarpus sinaicus*) rather than a lichen species. It was also hypothesized that manna is most probably sweet excretions, which in some dry areas can be produced by species of Aphididae (Al-Aswad *et al.* 1977).

Megasporaceae

The family *Megasporaceae* (Pertusariales, Lecanoromycetes, Ascomycota), (*sensu* Lumbsch *et al.* 1994; Nordin *et al.* 2010; **VII**), includes five genera (see below) and c. 300 species worldwide. Species of the family are lichenized with green algae. Most of them are crustose, but also several (sub)fruticose and a few subfoliose to umbilicate species are included. According to Cannon & Kirk (2007) ascomata in the family are often deeply immersed in the thallus. However, in some taxa apothecia are elevated and form large flat discs. Asci are thick-walled with a strongly thickened apical cap, without an ocular chamber, have the outer layer, faintly I+, and have (1–)4–6 (rarely 8) spores per ascus. The size of the ascospores is variable; they are hyaline, with a single cell and a two-layered wall. Pycnidia and conidia are common and known from many species. Species are known from maritime habitats, open forests and from semiarid steppes to very hot deserts; the majority grow on rocks, some on soil and few on bark and wood, crustose (obligatorily attached), some are vagrant (obligatorily unattached) and very few grow erratic (facultatively attached).

Some higher-level phylogenetic analyses have included data of the family Megasporaceae (Stenroos & DePriest 1998, Wedin *et al.* 2005, Miadlikowska *et al.* 2006, Schmitt *et al.* 2006, Lumbsch *et al.* 2007). The position of *Aspicilia* was found to be more closely related to Pertusariales than to Hymeneliaceae in Wedin *et al.* (2005) and Miadlikowska *et al.* (2006). Miadlikowska *et al.* (2006) used combined datasets including three ribosomal RNA: nuSSU, nuLSU and mtSSU and two protein-coding genes: RPB1 and RPB2, and their results strongly supported the pylogenetic placement of *Aspicilia* and its sister relation with *Ochrolechia* A. Massal., and both genera were included in the family Pertusariaceae. Schmitt *et al.* (2006), using a combined nrLSU and mtSSU rDNA dataset, placed *Aspicilia* in the family Megasporaceae, as confirmed by Lumbsch *et al.* (2007) with *Aspicilia* and *Megaspora* nested in the family Megasporaceae. The most recent phylogenetic analysis has shown Megasporaceae to be monophyletic (Nordin *et al.* 2010 and **VII**), supporting the results obtained by Schmitt *et al.* (2006) and Lumbsch *et al.* (2007). Some studies have focused on the Megasporaceae at the infrageneric level (Ivanova & Hafellner 2002, Nordin *et al.* 2007, 2008, **IV**, **V**, and **VI**).

The following genera are now accepted in the family Megasporaceae:

Aspicilia A. Massal., Ric. Auton. Lich. Crost.: 36. 1852, nom. cons.
– Type specimen: "*Urceolaria cinerea* β *alba*", Schaerer, Lich. Helv. Exs., ed. 2, 6: No. 127 (VER) (typ. cons.) [= *A. cinerea* (L.) Körb.].

Circinaria Link, in Neues J. Bot. 3: 5. 1809.
– Type species: *Urceolaria hoffmannii* (Ach.) Ach., nom. illeg. [≡ *Circinaria contorta* (Hoffm.) A. Nordin, S. Savić & Tibell].

= *Sphaerothallia* Nees in Nova Acta Phys.-Med. Acad. Caes. Leop.-Carol. Nat. Cur. 15: 360. 1831 – Type species (see study **I**): *Sphaerothallia esculenta* (Pall.) Reichardt [≡ *Circinaria esculenta* (Pall.) Sohrabi nom. provis.].

= *Chlorangium* [Link in Bot. Zeitung (Berlin) 7: 731, Taf. X, figs. 1–4. 1849, nom. provis.] Link ex Rabenh., Lich. Eur. Exs. 7: No. 199. 1857 – Type species (see study **I**): *Chlorangium jussuffii* (Link) Rabenh. [≡ *Circinaria jussuffii* (Link) Sohrabi nom. provis.].

= *Agrestia* J.W. Thomson in Bryologist 63: 246. 1960 – Type species (see study **I**): *Agrestia cyphellata* J.W. Thomson [=*Circinaria hispida* (Mereschk.) A. Nordin, S. Savić & Tibell].

[– "*Jussufia* Link ex Wiegmann" in Arch. Naturgesch. (Berlin) 13: 248. 1847, nom. nud. – Based on *Jussufia edulis* Link ex Wiegmann, nom. nud. [=*Circinaria jussuffii* (Link) Sohrabi nom. provis.]].

Lobothallia (Clauzade & Cl. Roux) Hafellner in Acta Bot. Malac. 16: 139. 1991.
– Type species: *Lobothallia alphoplaca* (Wahlenb.) Hafellner
Megaspora (Clauzade & Cl. Roux) Hafellner & V. Wirth in Wirth, Die Flechten Baden-Württembergs: 511. 1987.
– Type species: *Megaspora verrucosa* (Ach.) Hafellner & V. Wirth
Sagedia Ach., Kongl. Vetensk. Akad. Nya Handl. 30: 164.1809.
– Type species Laundon & Hawksworth (1988). *Sagedia zonata* Ach.

The most recent phylogenetic study on Megasporaceae is provided in this thesis (**VII**). It is based on a combined dataset of nrLSU and mtSSU, and representatives of the five genera are included. The current morphology-based classification was compared with the phylogenetic hypothesis obtained. It seems that thallus morphology, presence/absence of pseudocyphellae, number of ascospores per ascus and the size of ascospores, conidia length, and presence/absence of some compounds such as aspicilin are all useful characters for recognizing different genera. Pseudocyphellae are only present in the sphaerothallioid species and absent from others, and in the phylogenetic analysis (**VII**) sphaerothallioid species form a monophyletic group. Moreover, vagrant, subfruticose thallus seems to have evolved from a crustose thallus several times independently (**VII**).

Character/ genus	***Aspicilia***	***Circinaria***	***Lobothallia***	***Megaspora***	***Sagedia***
Thallus	crustose, areolate sometimes, radiating	crustose, subfoliose, subfruticose, amorphous	lobate, crustose	crustose, areolate	crustose, areolate
Ascopore /ascus	8 per ascus	1–4–6 (–8) per ascus	8 per ascus	8 per ascus	8 per ascus
Ascopore shape	ellipsoid, rarely globose	broadly ellipsoid to globose	ellipsoid	ellipsoid	ellipsoid
Ascopore size	10–27 × 8–19 μm	18–36 × 12–26 μm	8–18 × 5–12 μm	50–65 × 32–50	14–25 × 7–14 μm
Pseudocyphellae	absent	present in some	absent	absent	absent
Algal layer	continuous layer	continuous layer or scattered, clustered cells in some	continuous layer	continuous layer	continuous layer
Medulla	thin, c. 1–2 mm	thin to thick c. 1–20 mm	thin, c. 1–2 mm	thin, c. 1–2 mm	thin, c. 1–2 mm
Cortex	thin, one layer	thin, one or two distinct layers in some	thin, one layer	thin, one layer	thin, one layer
Conidium length	11–40 μm	8–35 μm	3–8 μm	8–12 μm	8–12 μm
Aspicilin	absent	present in some species	absent	absent	absent
Stictic acid	present in some species	present in some species	absent	absent	absent
Substictic acid	present in some species	absent	absent	absent	absent

Table 1 — A comparison of morphological and chemical characters between accepted genera in Megasporaceae, based on Nordin *et al.* (2010) and study **VII**

The genus *Circinaria*

Circinaria is distinguished from *Aspicilia* by the characters indicated in **Table 1.** The new taxonomic circumscription for the genus is presented here.

Thallus crustose, subfruticose, subfoliose, or umbilicate. Subfruticose thallus forming globular masses, lump shaped, with dumpy erect branches or condensed squamulose, round or occasionally irregular, slightly concave to flat or ±convex to verrucose to verruculose. Umbilicate thallus attached with central strands to the substrate. Subfoliose thallus free (vagrant), more or less rolled up by the lobes. Crustose thallus weakly cracked to distinctly areolate, rimose, more or less scattered, sometimes radiating, contiguous, margin indistinct to distinct; some species with radiating marginal lobes. **Prothallus** occasionally develops when thallus in crustose form, rare, often indistinct, sometimes ± well developed, fimbriate or forming a zone or a thin rime at the margin, grey to dark olive or brown-black to dark black. **Surface** white to grey, brown or brownish-black, often muddy or earthy color, sometimes ochre or olive, sometimes ± reddish-orange (when ferriferous oxides present in soil), dull to ± shiny. Sufficient data on **isidia** or **soredia** lacking. **Cephalodia** absent. **Pseudocyphellae** present in some species. **Cortex** one or two layers, with even to uneven thickness, mainly paraplectenchymatous, in some subfruticose species forming two layers, outer part paraplectenchymatous and inner part prosoplectenchymatous, upper one usually covered with an epinecral layer or crystals. **Medulla** white, I–. **Photobiont** *Trebouxia* or other chlorococcoid genera; cells ± globose. **Ascomata** apothecial, urceolate, aspicilioid, sometimes ± sessile forming crypto-lecanorine, round to angular, sometimes elongated or irregular. **Disc** flat to concave, rarely convex, black to brown-black or bluish-black, sometimes white-pruinose. **Thalline margin** formed by the margin of the areole, flat and indistinct to ± elevated, sometimes prominent; concolorous with thallus, or sometimes darker, or in some species with a conspicuous white rim in inner part or entirely white. **True exciple** often thin but rather distinct in some species, sometimes visible as a dark ring or wall around the disc section, cells in the uppermost part rounded and brown to olive-brown, ± I+, partly entirely blue. **Epihymenium** green to olive, olive-brown or brown, rarely blue-green, N ± green to light-green ("*Aspicilia*-green"), K ± brown, sometimes contains crystals dissolving in N. **Hymenium** hyaline, rather variable in thickness in several species, often more than 90 µm thick, usually I+ blue, persistent or ± rapidly turning yellow-green, yellow-brown or rusty-red. **Paraphysoids** (paraphyses) moniliform, with (3–)4–7(–8) uppermost cells ± globose (3–6 µm in diam.), to submoniliform with 1–2(–3) uppermost cells ±globose to subglobose, or largely ellipsoid, very rarely non-moniliform with simply septate paraphysoids without globose apical cells. Paraphysoids often rather variable even in the same apothecium (best examined in KOH), in lower part narrow, (1–)1.5–2(–2.5) µm wide, simple to ± branched and ± anastomosing. **Subhymenium and hypothecium** hyaline, usually I+ blue or turning yellow-green to copper-red, sometimes muddy colour and indistinct. **Asci** clavate, *Aspicilia* type, wall and apical dome I–, outer coat I+ blue, with 1–4–(6–8) spores. **Ascospores** hyaline, simple, globose to ellipsoid, I– , usually 10–35 µm long. **Conidiomata** pycnidial, immersed, single or sometimes aggregated; wall colorless but in upper part brown or sometimes olive to green; ostiole dark, punctiform to elongated; conidiogenous cells sessile or on short conidiophores (might be particular to *Circinaria* and more or less of *Arthonia galactites* (DC.) Dufour type *sensu* Vobis 1980). **Conidia** hyaline, simple, bacilliform to filiform, straight or curved, in some species quite variable in length. **Spot tests:** cortex and medulla I–, K–, C–, P– or P+ orange. **Secondary metabolites**: aspicilin in some species, hypostictic and stictic acid in *C. jussuffii*, but in many species no substances found. **Geography:** mostly Holarctic, frequently found in temperate regions, some vagrant groups restricted to arid regions. **Substrate**: mainly on rocks, on pebbles and small rocks, often on calciferous or calcareous rocks, or on soil, or without substrate (vagrant). **Habitat**: often in open and sun exposed sites, few species in steppe-forest area.

Sphaerothallia, *Agrestia* and *Chlorangium* were proposed to delimit some vagrant or erratic species (see also **I**). Originally two vagrant species i.e. *Lecanora esculenta* (Pall.) Eversm. and *L. fruticulosa* Eversm. were transferred to *Aspicilia* s.lat. by Flagey (1896) and the names were accepted for over a century, but in the light of DNA studies the three generic names were synonymized under the newly resurrected genus *Circinaria*. Some attention was paid to the known terricolous *Aspicilia* in the study **II**. A basic grouping for substrate preference of *Aspicilia* species at the soil surface level (including obligatory unattached, facultatively attached and obligatory attached) species was proposed (see **II** & **VII**).

Due to correspondence of vagrant, erratic and some saxicolous species to the concept of *Sphaerothallia* Follmann & Crespo (1974), the term '*sphaerothallioid*' is accepted here as an additional term to outline both subfruticose and subfoliose vagrant or erratic species (='manna lichens') plus some crustose species with well-developed cortex and medulla layers, owning pseudocyphellae and lacking of aspicilin within the traditionally recognized genus *Aspicilia* s.lat. or within the new genus *Circinaria*. The majority of sphaerothallioid species have a vagrant-subfruticose growth form, but a few are erratic or crustose. Fifteen vagrant species of *Circinaria* are documented worldwide (**VII)**, and a revision of the saxicolous species with three potentially undescribed erratic and crustose species is under preparation. Some new combinations are proposed based on the results obtained in **VII.**

The following taxonomic novelties discussed in this thesis are presented here as provisionally unpublished names (nomen provisorium) and will be validly published elsewhere in accordance with the current code (McNeill *et al.* 2006).

Circinaria alpicola (Elenkin) Sohrabi **comb. nov. provis.**
Circinaria aschabadensis (J. Steiner) Sohrabi **comb. nov. provis.**
Circinaria aspera (Mereschk.) Sohrabi & Şenkard. **comb. nov. provis.**
Circinaria cerebroides (Mereschk.) Sohrabi **comb. nov. provis.**
Circinaria digitata (Sohrabi & Litterski) Sohrabi **comb. nov. provis.**
Circinaria esculenta (Pall.) Sohrabi **comb. nov. provis.**
Circinaria fruticulosa (Eversm.) Sohrabi **comb. nov. provis.**
Circinaria gyrosa Sohrabi, Sipman, V. John & V.J. Rico, **sp. nov. provis.**
Circinaria jussuffii (Link) Sohrabi **comb. nov. provis.**
Circinaria lacunosa (Mereschk.) Sohrabi **comb. nov. provis.**
Circinaria rogeri (Sohrabi) Sohrabi **comb. nov. provis.**
Circinaria rostamii Sohrabi **sp. nov. provis.**
Circinaria sphaerothallina (J.Steiner) Sohrabi **comb. nov. provis.**
Circinaria tominii (Oxner) Sohrabi **comb. nov. provis.**
Circinaria vagans (Oxner) Sohrabi **comb. nov. provis.**

Materials and Methods

Terminology and abbreviations

In this thesis the mycological terminology generally follows Kirk *et al.* (2008). In the description of species, delimitation of some characters (e.g., ascus type, phycobiont, hymenium, hypothecium and subhymenium) follows Hafellner (1991), Clauzade & Roux (1984), Janex-Favre (1985), Lumbsch (1997), Owe-Larsson *et al.* (2007) and Roux *et al.* (2011). Terms describing conidiospore and conidiophore cell structures follow Vobis (1980) and Vobis & Hawksworth (1981). The abbreviations of the authors of lichen names follow Index Fungorum (http://www.indexfungorum.org). The plant names mainly follow IPNI (http://www.ipni.org/). Herbarium abbreviations in all publications (**I–VII**) follow Index Herbariorum (Thiers 2011, continuously updated website at http://sweetgum.nybg.org/ih/). The geographical names in some cases follow Room (2009) and in few cases Brummitt (2001) and Merriam-Webster's Geographical Dictionary, 3rd rev. ed. 2001. Reference abbreviations mainly follow IPNI, TL2 (Stafleu & Cowan 1981) and BPH-2 (Bridson *et al.* 2004), otherwise they are in accordance with the particular journal instructions and requirements.

Some of the selected terms used in this study are briefly described below.

Terms	**Description**	**References**
Manna lichens	An informal term used only for vagrant morphotypes of sphaerothallioid species in the genus *Aspicilia* s.lat. or *Circinaria*, with subfoliose, subfruticose, amorphous thalli. Any attached forms or saxicolous-crustose species are excluded.	Berkeley 1849; Elenkin 1901d; Donkin 1980, 1981; Rosentreter 1993; Hafellner *et al.* 2004; and study **I, IV-VII**
Sphaerothallioid species	Including vagrant (obligatorily unattached), erratic (facultatively attached) and crustose (obligatorily attached) species in the genus *Circinaria* or traditional *Aspicilia* s.lat., particularly species with well developed medulla and cortex layers, possessing pseudocyphellae, conidium length (c. 8–35 µm) and lacking aspicilin.	study **VII**
Crustose	One of the main types of growth form in lichens. Used for species that are obligatorily attached to the substrate, e.g., rocks, soil, bark or wood.	Büdel & Scheidegger 2008; and study **II & VI**.
Erratic	Facultatively attached to the substrate, found occasionally attached on rocks or soil (crustose morphotype) or unattached (vagrant morphotype). Some species which can persist either in crustose or vagrant morphotypes within a single species population. Sometimes the term *semivagrant* or *crustose-vagrant* are used for these species	Büdel & Wessels 1986; Pérez 1997a, b; and study **II**, **V** &**VII**
Vagrant	Obligatorily unattached to the substrate. A peculiar morphotype of some lichen species that persist without proper attachment to the substrate. Thalli subfoliose, subfruticose or even amorphous.	Büdel & Wessels 1986; Rosentreter 1993; Pérez 1994, 1997a, b; Litterski 2002; Hafellner *et al.* 2004; study **I-VII**

Field and herbarium studies

Study **VII** is based on material collected during field trips in Iran in 2007–2008. Fieldwork was undertaken in the Iranian provinces of East Azerbaijan, Semnan and Golestan in October and November 2007 and a few localities were visited in Golestan province in May 2008. All studies (**I–VII**) were mainly based on herbarium specimens loaned from ANES, ASU, B, C, CANL, CANB, CBFS, E, F, FH, FR, G, GFW, GZU, H, H-NYL, HAL, HMAS, IRAN, LE, M, MAF, MIN, MSK, O, POLL, PRA, S, SRP, TNS, TSB, TU, TUR, TUR-V, UPS, US and the private herbarium of M.R.D. Seaward (hb. MRDS). The first set of my own collections from Iran are deposited in my personal reference herbarium (hb. M. Sohrabi) with some duplicates in IRAN and H.

Preparation of examined specimens and mapping

Fresh material collected by the author, as well as herbarium material, was used in this study. As a rule more than one specimen for each locality has been cited, except in study **V** for which only a single collection is cited for each state/province of USA and Canada (Note: dot map in the study **V** was based on the complete set of examind specimens, however only selected specimens was listed therein following the journal recommendation). The last updated online map is presented at www.myco-lich.com). Records of specimens were mapped and presented as dot-maps in **IV**, **V** and **VII** and as distribution maps in the online catalogue of the lichen family Megasporaceae by Sohrabi *et al.* (2010). The label data and given localities of examined specimens were first recognized in an approximate area size (~10–30 km) using Google maps and Earth programmes (http://maps.google.com). For each species a KML file was provided, after which each species was exported into free software GPSbabel (http://www.gpsbabel.org/) and transformed into the text file. Lastly, the distribution maps (dot maps) were drawn using the freeware PanMap (M. Diepenbroek, H. Grobe & R. Sieger – PanMap 2000; http://www.pangaea.de/Software/PanMap). An improved map from the MSN Maps was used for the distribution map of *Aspicilia tibetica* and marked spots were approximate locations as well. But based on GPS information of label data an online distribution map for *Aspicilia tibetica* is also presented at the MYCO-LICH website.

Microscopy and measurements

For characterizing and comparing species, a set of characters was used in papers **II**, **IV**, **V**, **VI** and **VII**. General observations of external morphology (e.g., thallus shape, branches, subsquamules apothecia, pycnidia, pseudocyphellae, and presence or absence of black tips) were carried out under the dissecting microscope. Hand-cut sections of thalli and apothecia were mounted in water and slightly squashed. The preparations were examined using Leica DM 2500 compact light microscope and interference contrast in few cases for *Aspicilia tibetica*, *Circinaria rogeri* and *C. gyrosa*. For preparations of anatomical sections, a crystal freezing microtome Leica Cryocut was used and sections 10–20 µm thick were prepared. All slices were mounted in lactophenol cotton blue (LCB) and examined with a light microscope. For most species, specimens from several different geographical regions were studied excluding species such as *C. aschabadensis* and *C. tominii* that have been collected from a very restricted geographical area. The size measurements of external morphology were made with digital caliper micrometers. The estimated values were based on 10–15 samples. Except for the thickness of the cortex, hymenium, subhymenium, exciple, epihymenium, ascus and cell size of the photobiont, measurements of ascospores and conidia were made under a dissecting microscope and the estimated sizes of the ascospores and conidia are given in the study **II**.

Chemical analyses

The detection of secondary metabolites in lichens is necessary for accurate identification in numerous groups, and the presence of substances is often mentioned in taxonomic keys (Lumbsch 2002). Diversification of chemical compounds among the vagrant *Circinaria* is very poor and many of the vagrant sphaerothallioid species (except *C. jussuffii*) do not produce any characteristic secondary metabolites. In order to collect more informative characters, nearly 200 selected specimens were examined using thin layer chromatography (TLC), the methods in **II, IV, V, VI,** and **VII** following Orange *et al.* (2001). Solvents A, B and C were used. For detection of lichen substances in trace amounts High Pressure Liquid Chromatography (HPLC) was used. Among the examined selected material specimens were analysed. HPLC analysis was performed using methods standardized for lichen products (Søchting 1997). The pigments occuring as a black tip on top of the branches of the thallus (mainly in *C. hispida*) were examined independently by TLC and no lichen substances were detected. Many of the specimens were tested under UV light, but none of specimens reacted positively to UV-A and UV-B. For spot tests following reagents were used: K, C, P, KC, and N. Calcium oxalate was detected using 10% H_2SO_2.

DNA markers (DNA extractions, PCR ampification and sequencing)

Although it is easier to obtain high-quality DNA from fresh specimens, DNA extractions from rather old material (up to 75 years) proved to be successful. In study **III** the list of voucher specimens with their age is provided. The details and techniques of DNA extraction, PCR amplifications and sequencing were explained in the studies **III-VII.**

The phylogenetic analyses presented in this thesis are based exclusively on DNA sequence data. In studies **III–VII** genetic diversity and phylogenetic relationships of the taxa were studied using ribosomal nrDNA. A combination of ribosomal nrDNA and mitochondrial SSU was used in **VII.**

The ribosomal DNA consists of the small subunit (SSU/18S), the 5.8S, and the large subunit (LSU/28S). These genes are interrupted by two internal transcribed spacers (ITS1 and ITS2; **Fig. 1**). Nuclear ribosomal DNA cluster is the most widely used gene region in fungal phylogenetic analyses (see Lutzoni *et al.* 2004, Hibbett *et al.* 2007, Schoch *et al.* 2009). It is also the most commonly studied in lichen phylogenetics, including studies on the family Megasporaceae (Ivanova & Hafellner 2002, Miadlikowska *et al.* 2006, and Nordin *et al.* 2007, 2008, and 2010). A large number of primers are available for the different loci which are relatively easy to amplify; consequently there is a large number of sequences available in the GenBank (http://www.ncbi.nlm.nih.gov/genbank/). The ITS regions are recognised as the most variable regions within the entire cluster and therefore they are appropriate for phylogenetic analyses at infrageneric and even infraspecific levels (see also Högnabba 2007, and Kelly *et al.* 2011). The small and large subunits (nrSSU and nrLSU) are less variable and provide useful phylogenetic information at higher taxonomic levels (orders, families, genera).

To amplify the ITS1–5.8S–ITS2 region, the primers_ITS1–F (Gardes & Bruns 1993) combined with ITS4 (White *et al.* 1990), or ITS1–LM (Myllys *et al.* 1999) combined with ITS2–KL (Lohtander *et al.* 1998) were used. For nrLSU we used LR0R, LR7 and LR5 (Vilgalys and Hester 1990).

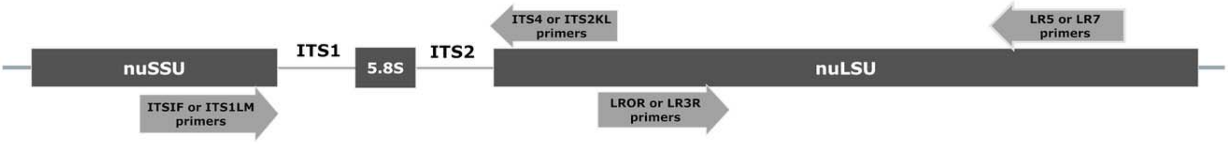


Fig. 1 — The diagram of the nuclear ribosomal DNA repeat. Boxes indicate genes and narrow lines (ITS1 and ITS2) are internal spacers. Primer names and directions are marked with arrows.

There are a huge number of mitochondria per cell, and each contains several mitochondrial genomes (Turker 2009). The genes for the small (mtSSU) and the large subunit (mtLSU) do not form a cluster as in the nuclear ribosomal DNA, and they exist in few copies only. In paper **VII** a small subunit of the mitochondrial ribosomes (mtSSU; see **Fig. 2**) was studied in combination with the ribosomal nuclear DNA (nrLSU). This region has also been used in Lumbsch *et al.* (2007) and Nordin *et al.* (2010). Several sequences of these are available in GenBank. For amplification of the mtSSU region, primers mtSSU1 and mtSSU3R (Zoller *et al.* 1999) were used.

Fig. 2 — Mitochondrial ribosomal small subunit. Directions of primers are marked with arrows.

Phylogenetic Analyses

The alignment of sequences is a fundamental part of phylogenetic analyses (for a review, see Rosenberg 2009), and necessary in studies that compare two or more biological sequences. Algorithms produce a hypothesis by which we attempt to infer which positions (sites) within sequences are homologous, that is, which sites share a common evolutionary history. A phylogenetic tree is a hypothesis of evolutionary history (Rosenberg 2009).

In many lichen groups ITS1 and ITS2 are found to be very variable in their length and this might result in ambiguous alignments (see also Lücking *et al.* 2011). In contrast to ITS1 and ITS2, the 5.8S, nrLSU and mtSSU are more conservative and appeared to be almost identical in length. In the studies **III**, **IV**, **VI**, and **VII** sequence alignments were performed. All sequences used in studies **III**, **IV** and **VII** were aligned using Muscle v4. web server (Edgar 2004) and then adjusted manually in PhyDE® (Phylogenetic Data Editor). In study **VI** sequences were aligned using ClustalW (Larkin *et al.* 2007) and then adjusted manually in Bioedit software (http://www.mbio.ncsu.edu/bioedit/bioedit.html). In study **VII** the web program Gblocks v. 0.91b (Castresana 2000) was used for removing ambiguously aligned positions from the aligned ITS datasets and allowing for smaller final blocks, gap positions within the final blocks and less strict flanking positions. According to Talavera & Castresana (2007), Gblocks facilitates and provides an objective and repeatable alignment method to exclude poorly aligned regions within a multiple sequence alignment, a method and procedure that have been shown to improve accuracy of phylogenetic results in some cases. Manual alignment was performed only in the study **V**. However, manual alignments are not repeatable exept in trivial cases (see also Giribet *et al.* 2002). Commonly, ambiguously aligned regions are removed from the aligned matrix; however, theoretically valuable data is then lost and the exact delimitation of "unalignable" regions is arbitrary. In order to avoid these problems we used direct optimization (optimization alignment; Wheeler 1996) as an alternative approach in study **V.**

Nowadays, most phylogenetic analyses are conducted using approaches based on parsimony, maximum likelihood or Bayesian inference, all of which try to elucidate detected variation by minimizing the number of character transformations (Frost *et al.* 2006). There are several different approaches for inferring phylogenetic relationships and these are discussed in several publications i.e., Felsenstein (2004) and Lemey *et al.* (2010). For this thesis two approaches were used; parsimony analyses in **III**, **V**, **VI** and **VII,** and Bayesian inference in **IV** and **VII**.

In parsimony analysis, equally weighting of characters is routinely applied to all types of transformations with the aim to minimize the overall number of hypothesized transformations, and these results in the most parsimonious solution(s) (Frost *et al.* 2006; Grant & Kluge 2003). In this thesis the following three programs were used for parsimony analyses: PAUP* (v. 4.0b10; Swofford, 2002; mainly in the studies **III**, **IV** and **VI**), POY (Wheeler *et al.* 1996; in the study **V),** and TNT (Goloboff *et al.* 2008a, b; in the study **VII)**.

Numerous alternative methods and techniques for studying the "support" of different monophyletic groups included in the phylogeny trees have been proposed. To discuss pros and cons of these methods is beyond the scope of this study, for detailed discussion see, for example Müller (2005). In studies **III**, **VI** and **VII** support values were calculated using one of the most widely utilized method, bootstrapping (Felsenstein 1985).

Bayesian inference (Rannala & Yang 1996, Huelsenbeck *et al.* 2001, Huelsenbeck & Ronquist 2001) is a mathematical and statistical formalization for inferring phylogenies based on an explicit choice of a model for evolutionary change. Bayesian inference was applied in studies **IV** and **VII**. The settings for the tree and other parameters of the model were executed using the program MrBayes version 3.0beta 4 (Huelsenbeck & Ronquist, 2001; Ronquist & Huelsenbeck 2003). The models for nucleotide substitutions were selected prior to the Markov Chain Monte Carlo (MCMC). The model of evolution was selected using MrModeltest Version 1.1b (Nylander 2002) in combination with PAUP* (Swofford 2002). MrBayes (Huelsenbeck & Ronquist, 2003) uses Markov chain Monte Carlo to approximate the posterior probabilities, and details of the technique to calculate posterior probabilities are explained in their publication. Detailed information of the analyses and settings of the parameters are presented in studies **VI** and **VII.**

Morphological Characters

Sphaerothallioid species are mainly included in the studies **I**, **III–VII,** and comparatively in **II**. In general, for a description of each species 16–20 morphological characters were evaluated from each specimen and studied in detail. The character sets were incorporated into small Access-based (Microsoft Corporation) databases, which made their conventional comparison, and construction of identification keys simple. In the following only morphological features of the sphaerothallioid species are discussed. According to Lumbsch & Kothe (1988) the subfoliose vagrant species can be divided into two groups: non-obligatory unattached species, normally attached to their substratum, and obligatory unattached species which are exclusively terricolous. According to Büdel & Wessels (1986), the facultatively unattached lichen species should be termed 'erratic', while the word for the obligatory unattached lichens should be 'vagrant'. In studies **V**, **VI** and **VII** the 'erratic' term is used for *Circinaria alpicola*, *C. aschabadensis* and *C. hispida* s.lat., that appeared either in crustose or vagrant morphotype. The vagrant (obligatory unattached) growth form is known in several species, e.g., *C, cerebroides*, *C. fruticulosa*, *C. gyrosa*, *C. lacunosa* and *C. rostamii*. Some specimens of *C. emiliae*, *C. esculenta*, *C. jussuffii* and *C. vagans* are nested in the erratic-vagrant group in study **VII**. In order to understand thallus placticity of certain species more data are clearly needed. Some of the vagrant species mentioned above are also found on pebbles, but the vagrant habit does not really change due to the movement of pebbles. This is because the thallus covers the whole pebble, forming a subglobose lumpy sphere with the hard and invisible substrate inside. Therefore, they can still move from place to place by wind and maintain their mobility in the habitat. In study **VII** saxicolous species were not the main target, therefore descriptions and other information on them are not provided. These species will be treated in another study and published elsewhere. However some of the saxicolous sphaerothallioid species (e.g., *C. aspera, C. elmorei* (E.D. Rudolph) Owe-Larss., A. Nordin & Sohrabi and *C. sphaerothallina*) have been included in the phylogenetic analyses and all of them are nested within a large sphaerothallioid group in the genus *Circinaria*.

Only few identification keys based on thallus morphology have been published for sphaerothallioid species, including 'manna lichens'(Poelt 1969, Oxner 1971, Esnault 1985, Andreeva 1987). In study **VII** the first worldwide identification key for 'manna lichens' is provided. This key is mainly based on morphological and anatomical characters as described below.

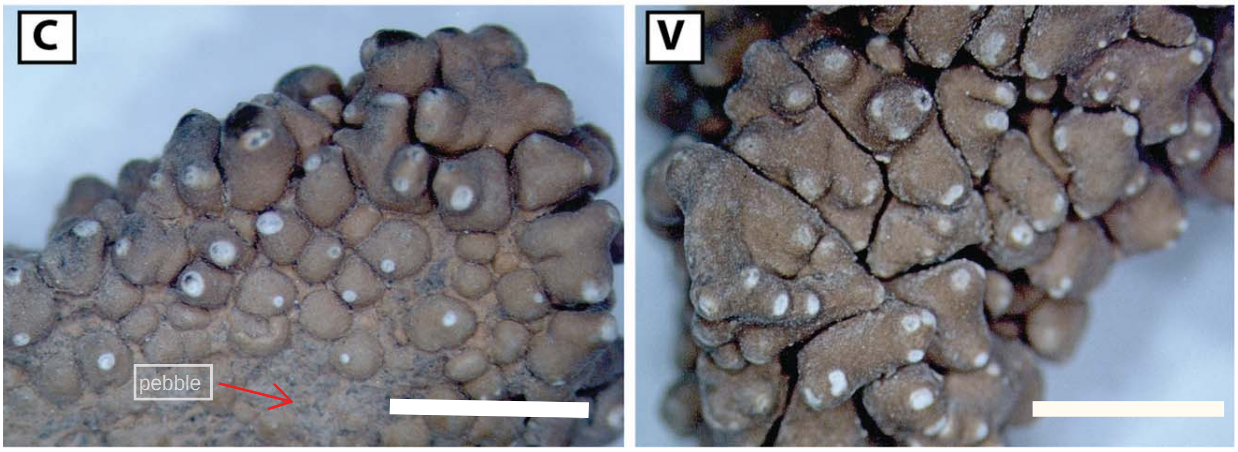


Fig. 3 — Erratic thalli of *Circinaria alpicola* (*Ringel & Jaschhof 5183*, H); scale= 3 mm. **C.** crustose morphotype (DNA MS175, growing on a pebble) and **V**. vagrant morphotype (DNA US2123).

Thallus growth form, thickness and surface type (Fig. 4)

Sometimes the formation of thalli in vagrant sphaerothallioid species results in peculiar phenotypes, which are rather difficult to categorize within the commonly recognized thallus types described in Grube and Hawksworth (2007). In Büdel & Scheidegger (2008) the vagrant growth form has been classified under foliose lichens. In studies **I-VII** they are treated as subfruticose lichens.

The surface of vagrant sphaerothallioid species (with subfoliose and subfruticose thalli) is formed by variously shaped, uneven and irregular projections. A digital vernier calliper to measure the size and describe the surface projections has been used and the following types distinguished: 1) smooth, with no projections (e.g., *Circinaria emiliae*), 2) wrinkled subsquamulose (e.g., *C. esculenta*), 3) gyroid warted, tuberculate, verrucose to verruculose (e.g., *C. gyrosa* and *C. vagans*), 4) long to narrow cylindrical branches, dichotomous (e.g., *C. fruticulosa, C. hispida* s. str.). Based on the external appearance of the thallus, an artificial grouping of species can be made (**Fig. 4**). Four different thallus forms were observed among the vagrant species, as follows:

***C. esculenta* thallus form** (**Fig. 4 G-H**)**.** These species are vagrant, free, with prominent to sessile subsquamules, large to medium size, compact, subsquamules or lobes entirely overlapping, forming spherical to subspherical, and sometimes irregular shapes. There are many intermediate forms. *C. esculenta*, *C. jussuffii* and *C. tominii* have intermediate forms and they are variable in size and sometimes resembling each other. *C. jussuffii* sometimes colonizes pebbles and then the substrate is completely covered by the thallus.

***C. fruticulosa* thallus form** (**Fig. 4 C-D**). Thalli of this group are unlike the previous form since they are extremely ramified, producing many short or long branches; branching is dichotomous or irregular, with radiation from the central axial body. Thalli are free or attached to soil. Species having this kind of a thallus are *C. digitata*, *C. fruticulosa*, *C. hispida* s. str. and *C. rogeri*.

***C. lacunosa* thallus form** (**Fig. 4 E-F**). This is the most distinctive form and species having this kind of a thallus are easily distinguished. The thalli are entirely free, subspherical to irregular, amorphous, without any clear shape. Lobes vary in size, and the external appearance is very variable, truffle-like (tuber-like) and their surface is cracked and often deeply fissured, with pits occurring in some parts. *C. cerebroides*, *C. lacunosa*, *C. rostamii*, and some specimens of subfoliate *C. emiliae* represent this kind of morphology.

***C. vagans* thallus form** (**Fig. 4 A-B**). This type is somewhat intermediate between the *C. esculenta* and *C. fruticulosa* forms. It is characterized by vagrant to crustose growth forms (saxicolous specimens are rare, then mainly on pebbles totally covered by thalli), with short, dumpy branches, tuberculate, verrucose to verruculose and even with more or less areolate thalli, pseudocyphellae common, conspicuous. Species with this kind of a thallus are *C. alpicola*, *C. aschabadensis*, *C. gyrosa* and *C. vagans*. This thallus form is morphologically very similar to saxicolous *C. elmorei* s.lat. (see paper **VI**) and to *Circinaria* sp. 1 and sp. 2, that are two undescribed species (see paper **VII)**.

Isidia, soredia and prothallus

All species of *Aspicilia* and *Circinaria* treated in this thesis lack an isidia and soredia. The prothallus is rarely present in some saxicolous species, for example *C. arida* Owe.-Larss., A. Nordin & Tibell (see the study **VI**). This character will be discussed in detail in the forthcoming study of saxicolous sphaerothallioid species by Sohrabi *et al.*

Pseudocyphellae (Fig. 5 A-C).

All sphaerothallioid species in the genus *Circinaria* have pseudocyphellae and their size varies between species. This character is lacking in some crustose species of the genus, such as *C. arida, C. caesiocinerea, C. calcarea*, *C. contorta*, *C. gibbosa* and *C. leprosescens*.

Apothecial size, position and abundance (Fig. 5 D-F).

The great majority of vagrant species have a sterile thallus. In some species apothecia appear in older parts, but they are often poorly developed. In some species, such as *Circinaria esculenta*, *C. tominii* and *C. vagans*, apothecia are immersed, urceolate or aspicilioid. In a few species they are elevated at the surface and fairly large, up to 2 mm in diameter, often appearing (crypto)lecanorine with a conspicuous thalline margin; for example, *C. fruticulosa*, *C. hispida* s.str. and *C. rogeri* have apothecia with a distinct thalline margin (**Fig. 5 E-F**). In some vagrant species (e.g., *C. cerebroides, C. digitata, C. emiliae* and *C. lacunosa*) only a single apothecium or no apothecia were found. All Eurasian *C. hispida* s.str., examined in study **VII**, were sterile. However, a few N American specimens were found fertile (see also study **V**).

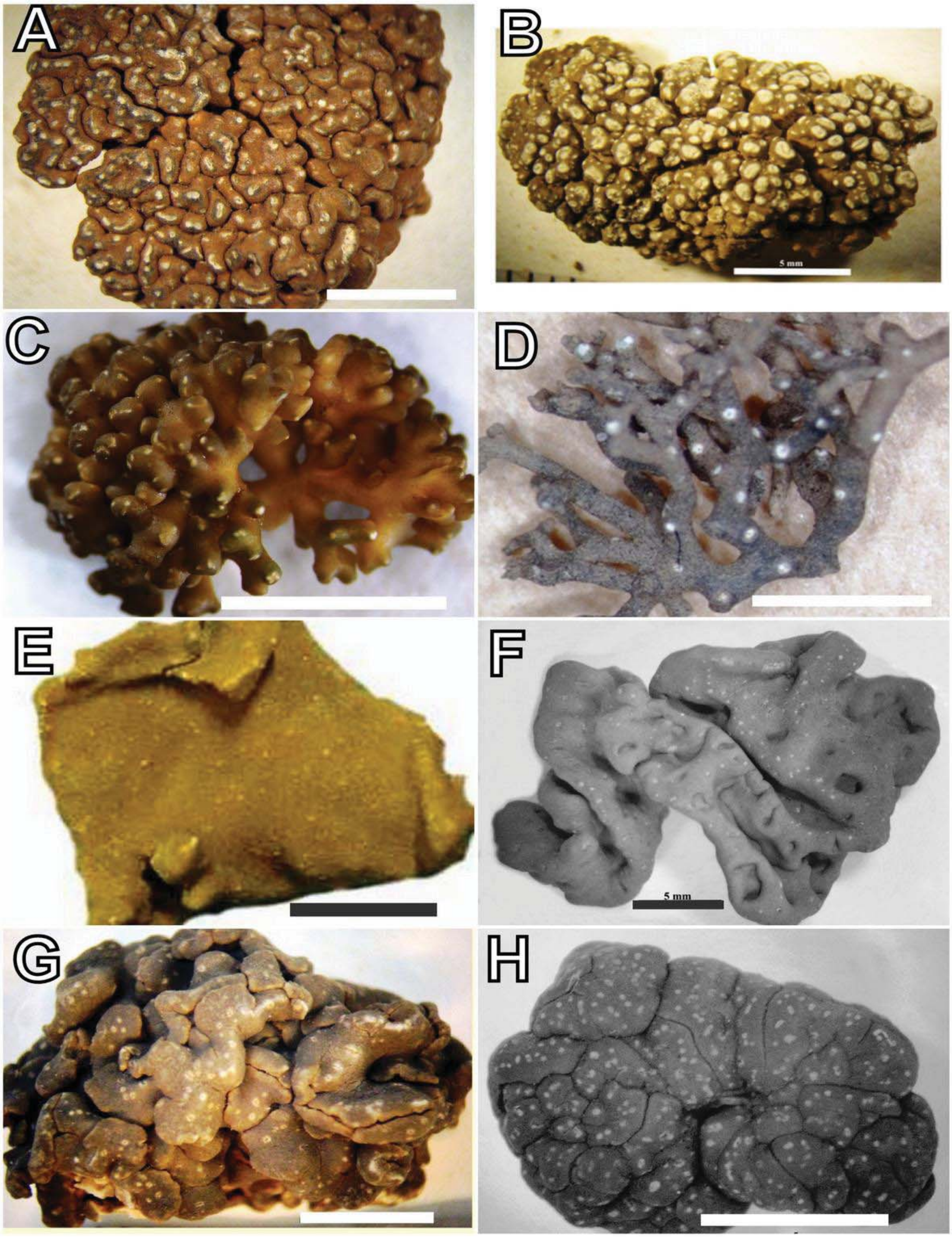


Fig. 4 — **A–H.** Variation of thallus morphology among the vagrant *Circinaria*, 'manna lichens.' **A:** *C. gyrosa* (*Radde s.n.*, LE); **B:** *C. vagans* **(***Kulakov s.n.*, LE); **C:** *C. fruticulosa* (*Mereschkowsky s.n.*, H); **D:** *C. hispida* s.str. (*Ochirova s.n.*, LE); **E:** *C. emiliae* (*Savicz*, Lichenoth. Ross. No. 115, H); **F:** *C. lacunosa* (*Piregoudov s.n.*, LE); **G:** *C. esculenta* (*Tomin s.n.*, H**)**; **H:** *C. jussuffii* (*Reboud s.n.*, H). Scale = 5 mm.

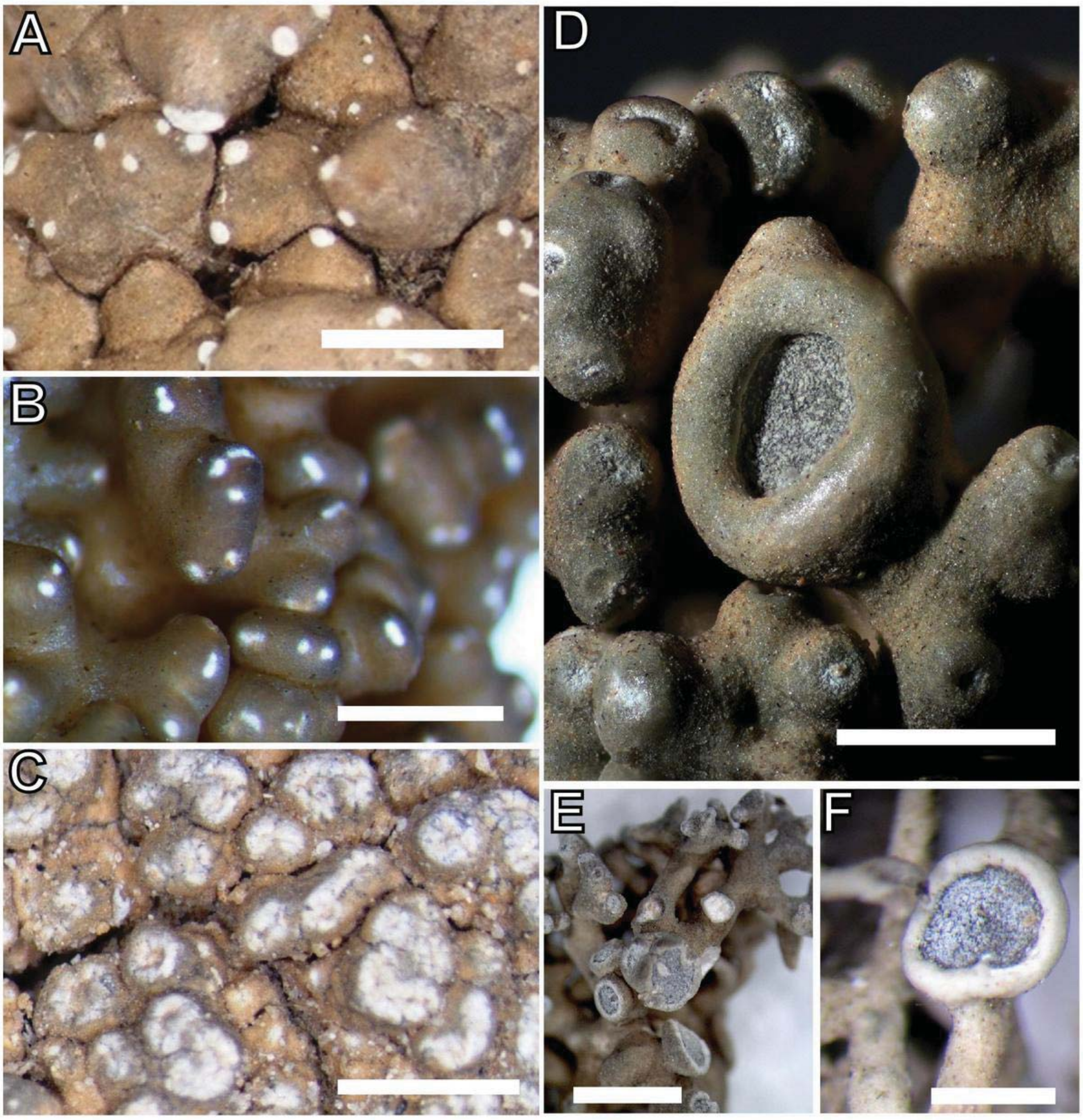


Fig. 5 — A–C. Pseudocyphellae. **A:** *Circinaria alpicola* (*Litterski 4848*, H); **B:** *C. fruticulosa* (*Mereschkowsky s.n.*, H); **C**: *C. vagans* (*Choy 5224*, LE); **D–F**. Apothecia. **D:** *C. fruticulosa* (*Wagner L-0070*, GZU, Photo by: *W. Obermeyer*), scale = 1.5 mm; **E:** *C. rogeri* (*Rosentreter 4874*, SRP; see study **V**); **F:** *C. hispida* s.str. (*Spribille & Wagner 25348*, GZU, see study **V**). **A-C & E-F**, scale = 1 mm.

Apothecial disc, margin and thalline exciple (Fig. 6)

Disc colour of the mature apothecia is often brownish-black, and frequently becomes white pruinose. Apothecial discs are sometimes not visible, especially when the apothecia are immersed within the thallus. White rim appears in the thalline exciple (thalline margin) of some species (e.g., *Circinaria alpicola, C. esculenta*, *C. rogeri*, *C. tominii* and *C. vagans*). In *C. fruticulosa*, *C. rogeri* and *C. hispida* s.str. apothecia are usually found in older parts of the thallus, and are more or less elevated from the surface of branches. Thalline exciples in *C. fruticulosa*, *C. rogeri* and *C. hispida* s.str. are well developed and distinctive as compared to other species of the group.

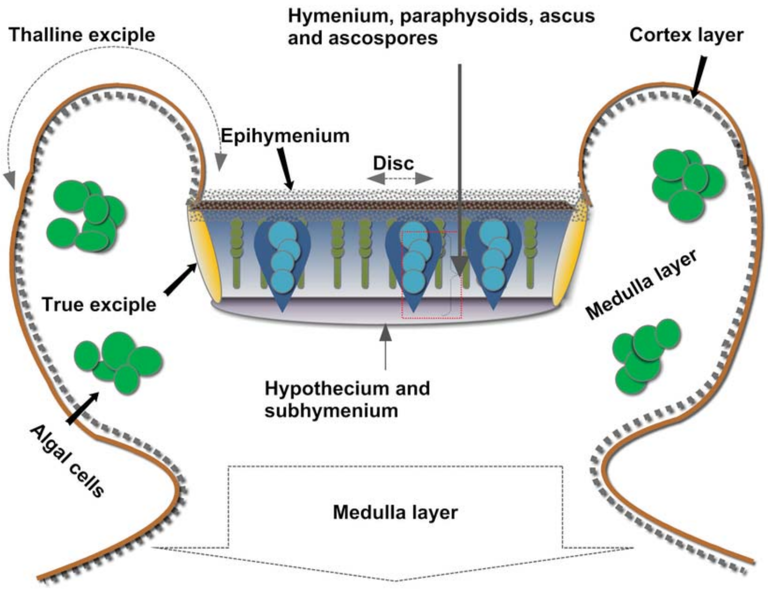


Fig. 6 — Detailed schematic presentation of the structures in the apothecium of *Circinaria fruticulosa* as seen in cross section.

Cortex and epinecral layer (**Fig. 7 A-B**)

The cortex in sphaerothallioid species of *Circinaria* has two different forms. In some species the cortex layer often appears without a distinct delimiting border between exterior and interior parts, and it is difficult to distinguish true paraplectenchymatous cortex layer from the prosoplectenchymatous tissue of medulla. Personal observations confirm that in some vagrant sphaerothallioid species the algal layer is compartmentalized into small groups which form a discontinuous layer, and subsequently it is interrupted by prosoplectenchymatous tissue of medulla. This kind of cortex formation is here referred to as an unevenly thickened cortex in which prosoplectenchymatous tissue, originating from anticlinal hyphae of the medulla, is included; for instance *C. alpicola*, *C. aschabadensis*, *C. cerebroides*, *C. emiliae*, *C. esculenta*, *C. gyrosa*, *C. jussuffii*, *C. lacunosa*, *C. rostamii*, *C. tominii* and *C. vagans* have this kind of a cortex (see **Fig. 7 B).** *C. digitata* (see the study **IV**), *C. fruticulosa* (see **Fig. 7 A**), *C. hispida* s.str. and *C. rogeri* (see the study **V**) have two distinct cortical layers.

Algal cells (**Fig. 7 C-D**)

A discontinuous algal layer was observed in subfruticose vagrant sphaerothallioid species, particularly those with a thick medulla and cortex layers. It seems that discontinuous algal layer is characteristic structure in some arid region lichens. For example such algal layer is also observed in the foliose vagrant species *Xanthoparmelia hueana* (Gyeln.) O. Blanco *et al.* and *X. semiviridis* (Nyl.) O. Blanco *et al.* therein algal cells packed into small clusters. Algal layer in sphaerothallioid species are forming group of small clusters with c. 100–200 × 150–250 µm broad. However, this kind of an algal layer was not found in *Circinaria arida*, *C. caesiocinerea*, *C. calcarea*, *C. contorta*, *C. gibbosa* and *C. leprosescens* which have a much thinner medulla layer (see paper **II**).

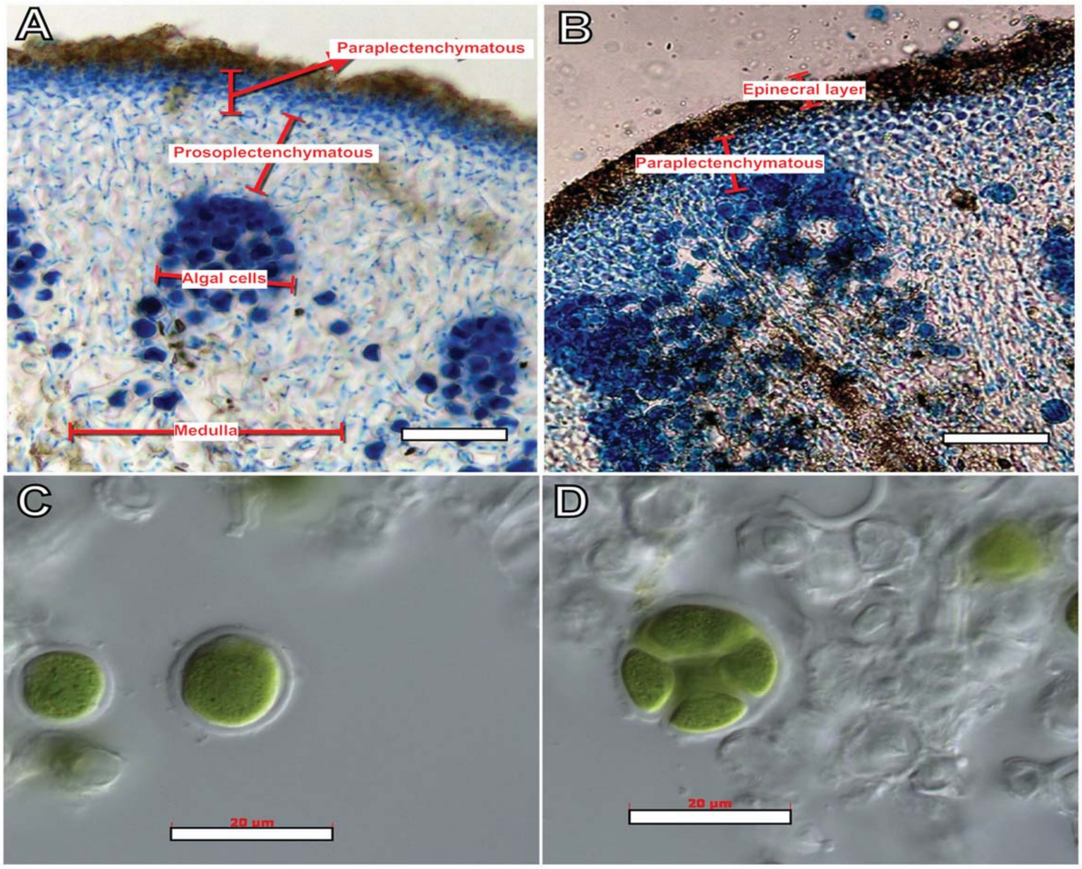


Fig. 7 — A: Cortex with prosoplectenchymatous tissue in *Circinaria fruticulosa* (*Sohrabi 10405A*, H); **B:** Cortex with paraplectenchymatous tissue in *C. alpicola* (*Litterski 4848*, H), stained by lactophenol cotton blue (LCB); **A-B,** scale = 50 µm. **C-D:** Photobiont chlorococcal (*Asterochloris* or *Trebouxia*) in *C. gyrosa* (*Sohrabi 10085*, IRAN), scale = 20 µm.

Medulla (Fig. 7 A)

The medulla is a well developed layer in most vagrant sphaerothallioid species, forming with prosoplectenchymatous tissue, irregularly to anticlinally oriented hyphae. Since vagrant *Circinaria* are substrate-free with more or less spherical in external morphology, the medulla layer is somewhat thicker than in crustose sphaerothallioid lichens species. For example, in *C. cerebroides* with a truffle-like thallus morphology (c. 25 mm wide) the medulla layer is well developed and thick, reaching to c. 20 mm in microtome sections, and in well-developed thalli 3–4 cm wide, the medulla layer is still thicker. The medulla in the strict sense is a fungal layer between the algal layer and the surface of the substrate (see also Henssen & Jahns 1974, Büdel & Scheidegger 2008).

True exciple or proper exciple (Fig. 6)

The true exciple of most sphaerothallioid species is fairly well-developed and composed of distinctly or indistinctly radiating hyphae. The anatomy of the true exciple provides some of the best characters to identify certain lichen species and genera (see Ekman 1996). In study **VII**, it is shown that in some sphaerothallioid *Circinaria* the innermost part of the true exciple forms a more or less distinct layer with an intricate texture. The thickness of this layer varies between closely related taxa; for example, it is less developed in *C. vagans* but slightly more developed in *C. gyrosa* and *C. rostamii*. However, the differences are too subtle and therefore not useful in the identification of species without support from other characters.

Hymenium and epihymenium (Fig. 6)

In this study mature apothecia of sphaerothallioid species were examined. The hymenium is hyaline and often gives an amyloid reaction with iodine. The thickness of the hymenium shows some minor variation among species, and it seems that it alone cannot be used in distinguishing species. The thickest hymenium was observed in *Circinaria fruticulosa* and *C. rogeri*. The epihymenium is partly pigmented with yellowish to greenish-brown crystals. This pigmentation is deposited in the apical part, and often reacts K± (fading in colour) and N+ (more or less changing to light green; *Aspicilia*-green *sensu* Meyer & Printzen 2000).

Paraphysoids (Paraphyses) (Fig. 8)

The term paraphysoids (“paraphysoïdes”) was recently adopted by Roux *et al.* (2011). The term was earlier used by Janex-Favre (1985) and Lumbsch (1997) in the same meaning for inter-ascal or pre-ascal hyphae which are derived from an ascolocular development forming a plectenchyma that resembles pseudoparaphyses (see also LIAS glossary contributors 2010, http://glossary.lias.net/). In the present work (studies **II**, **V**, **IV** and **VI**) the term “paraphyses” is used following previous studies by Owe-Larsson *et al.* (2007), but the term paraphysoids is adopted later (see study **VII**). Paraphysoids in sphaerothallioid *Circinaria* are mostly branched except in their uppermost parts (see **Fig. 8 E-G**), they differ in thickness, 2–4 × 5–7 µm in the lower parts, and have globose to subglobose cells in the uppermost parts, with cells up to 3–5 × 4–6 µm, often moniliform to submoniliform (*sensu* Magnusson 1939, Owe-Larsson *et al.* 2007).

Hypothecium and subhymenium (Fig. 6)

In studies **V**, **VI** and **VII** the delimitation of the hypothecium and subhymenium follows Owe-Larson *et al.* (2007). The hypothecium is typically hyaline, but in older specimens rather unclear and with a muddy colour. A very thin subhymenium is always present between the hymenium and the hypothecium. Both hypothecium and subhymenium are amyloid and I± blue.

Asci and ascospores (Fig. 8)

The asci belong to the *Aspicilia*-type (Hafellner 1989, Lumbsch 1997, see also Malcolm & Galloway 1997). The shape of an ascospore in sphaerothallioid species ranges from globose to subglobose (see **Fig. 8 C** and **I**). Only one type of ascospores was found. A rather large and globose to subglobose shape is usually found in both sphaerothallioid species (e.g., *Circinaria alpicola*, *C. aschabadensis*, *C. aspera*, *C. elmorei* s.lat., *C. gyrosa*, *C. sphaerothallina* and *C. vagans*, see the studies **IV**, **V**, **VI** and **VII**), and allied saxicolous species (e.g., *C. arida*, *C. calcarea*, *C. contorta*, *C. gibbosa*, see the studies **VI** and **VII**). The spore size has often been used as an important character for identifying species in all lichen groups including Megasporaceae (see Smith *et al.* 2009 for review). However, in the present study, it was shown that the ascospore size and the number of the spores per ascus are less variable and therefore have less taxonomic value (see **Fig. 9 B**). In study **VII** it was shown that *Aspicilia tibetica* does not belong to sphaerothallioid species. It has small ascospores in asci containing eight spores, characterized by their thick wall and ellipsoid shape (see study **II** for more detail).

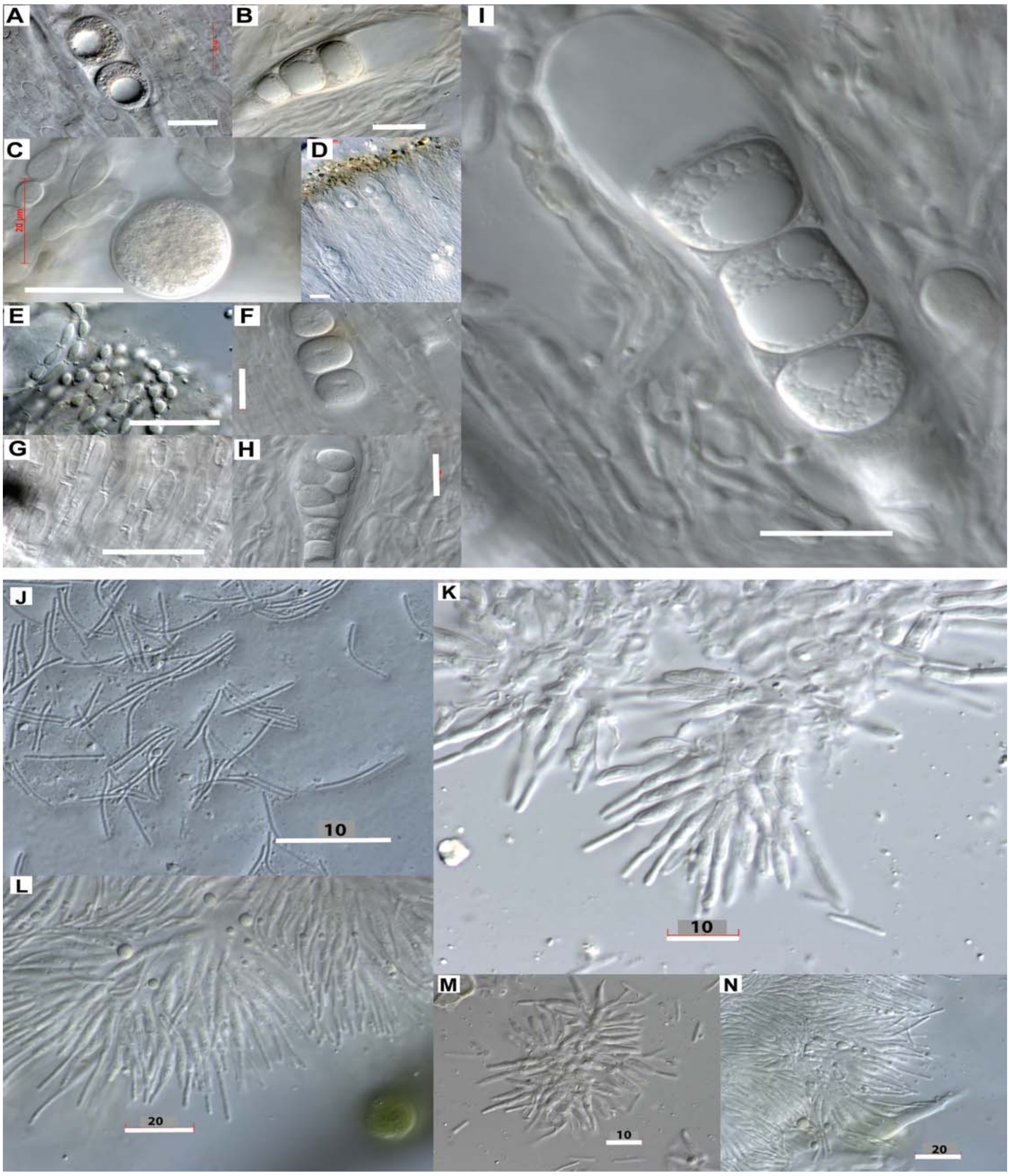


Fig. 8 — A–I. Details of asci, ascospores and paraphysoids in *Circinaria gyrosa* (*Sohrabi 10085*, IRAN); scale = 20 µm. **A**, **C**, **F:** a ± globose to subglobose ascospore; **B** & **I:** an ascus with its typical thickened apical cap, showing three ascospores per ascus; **H:** an exceptional case with eight ascospores in an ascus; **E:** (sub) moniliform paraphysoids with 3–9 ± globose uppermost cells; **G:** lower part of paraphysoids, 1–2.5 µm wide, simple to ±branched; **D:** epihymenium green to olive-brown or brown. **J–K.** Conidiogenous cells and conidia in *C. gyrosa* (*Sohrabi 10085*, IRAN); scale in the photos. **J:** conidia simple, bacilliform to filiform; **K:** conidiogenous cells with simple, bacilliform to filiform conidia cells in tip; **M–N.** Conidiogenous cells and conidia in *C. rogeri* (*Rosentreter 3516*, B); scale in the photos.

Pycnidia, conidia and conidiogenous cells (Fig. 8, 10)

According to Hawksworth (1988), conidium shape and size, rather than the structure of the conidiomata (pycnidia), or the method of conidiogenesis, are important characters in many genera including *Aspicilia* A. Massal., *Heterodea* Nyl. (Cladoniaceae), *Micarea* Fr. (Pilocarpaceae) and

Opegrapha Ach. (Opegraphaceae). In the present study many pycnidia among most of the examined specimens were observed, and conidia size appeared to be a reasonably informative character among the vagrant sphaerothallioid species. Pycnidia usually have a blackened ostiole and a hyaline wall (see **Fig. 10 A**), and they are typically covered with a white rim. They are also conspicuous and located in the thickened parts of the thallus, near the lobes or sometime in pseudocyphellae or beside the apothecia. Conidia are elongated (**Fig. 8**), filiform and somewhat curved. Study **VII** showed that conidia size is informative for species delimitation, but only in some cases. A graphic representation of the measurements of conidia in the vagrant and erratic sphaerothallioid species is presented in **Fig. 9 A.**

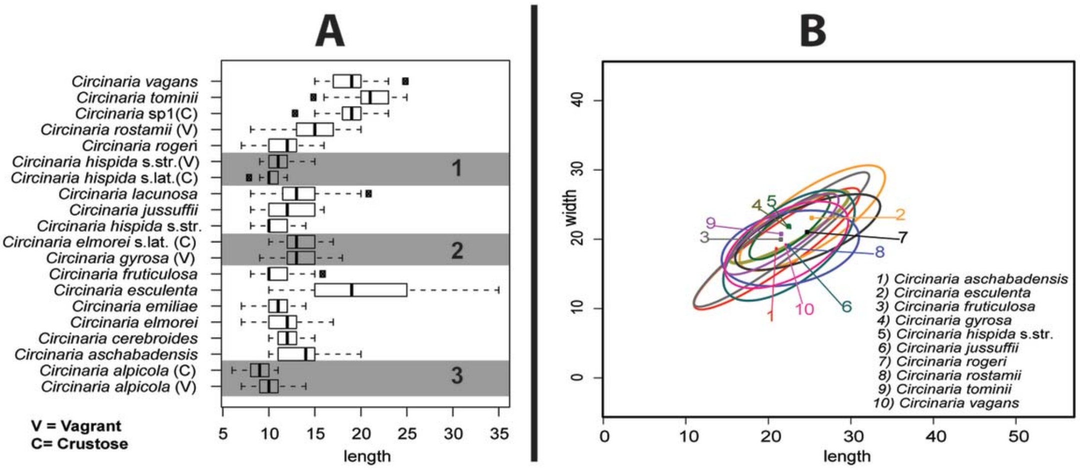


Fig. 9 — A. Variability in conidia size among the 'manna lichens' shown in boxplot**.** The measurements are expressed as mean ± SD (boxes) and extremes. Data obtained from measurements of conidia length in five pycnidia (= 30 conida) per species. 1: *Circinaria hispida* s.lat. (on pebbles) and *C. hispida* s.str. (vagrant form) show different conidia size. In study **VII** (MS154 & MS159) the specimens turned out to belong to the same species. 2: *C. elmorei* s.lat. on pebbles and vagrant *C. gyrosa* show similar conidia size. In study **VII** MS66 (vagrant) and HQ389201 (crustose) turned out to be different taxa. 3: Crustose and vagrant morphotypes of *C. alpicola* show slightly different conidium size. In study **VII** MS175 (crustose morphotype) & US2123 (vagrant morphotype) turned out to belong to the same species (see **Fig. 3** above). **B.** Ascospore size in the 'manna lichens', with 95% confidence ellipses obtained from ascospore measurements of five specimens per species (= 30 ascospore). Both graphs were implemented in R using boxplot and ellipse packages (see R Development Core Team 2008).

Pycnidia have been found in all sphaerothallioid species treated in study **VII**, except *Circinaria digitata* (see study **IV**). In the study **V**, the pycnidia for Eurasian species *C. fruticulosa* (syn. *A. fruticulosa*) was reported as "not found", however after examination and study of additional material it was found and described in the study **VII**. Pycnidia appear to be more or less similar to *Roccella*-type (*sensu* Vobis 1980; Vobis & Hawksworth 1981). Otherwise they are not comparable with other types proposed. Inside, the pycnidial cavity is lined by conidiogenous cells, which produce conidia terminally, and the hollow consists of a short conidiophore, a sub-cylindrical to cylindrical cell 5–7 × 2–4 µm, with one to three septa. Conidiophores might be particular to *Circinaria* and somewhat similar to those in *Arthonia galactites* (DC.) Dufour *sensu* Vobis (1980).

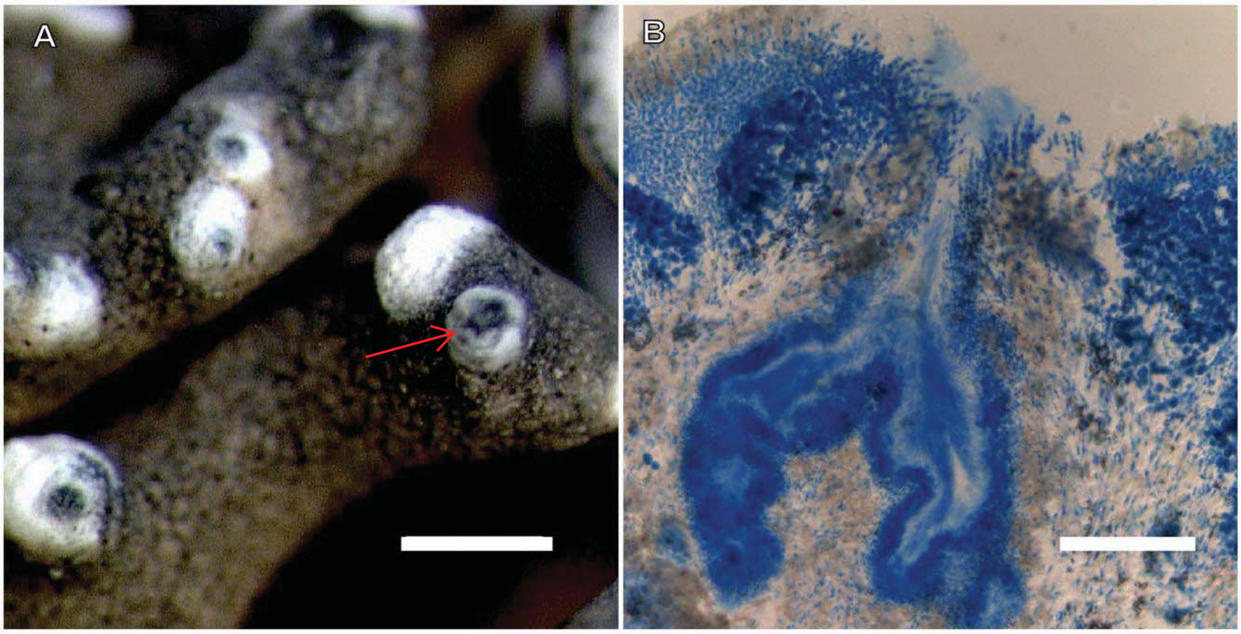


Fig. 10 — A. Pycnidia in *Circinaria rogeri* (Rosentreter 4874, SRP, see also Fig 2 B in study **V**), scale = 0.5 mm. **B.** Cross section of pycnidia in *C. tominii* (*Baranov* s.n., H) stained by lactophenol cotton blue (LCB), scale = 50 μm.

Ecology and distribution

All species studied are mainly from the temperate region of the Holarctic ecozone in the Northern Hemisphere (*sensu* Takhtajan 1986). *Circinaria* species with a vagrant growth form are distributed in the temperate zone between latitudes 30º to 60º (**Fig. 11**). They are found from the lowlands of the Caspian Sea (Mereschkowsky 1911a, b, 1921) to the high latitudes of Tian-Shan Mountains (see studies **IV** and **VII**; Litterski 2002). The group is well diversified in the arid and semiarid areas of the Eurasia (**Fig. 12**). The largest number of vagrant *Circinaria* species is found in the Central Asian steppes (**IV** and **VII**), with only a few representatives in the western North America. Middle East steppes and deserts, and South European forest steppes (Crespo & Barreno 1978, Hafellner *et al.* 2004) are also areas showing high diversity. In the temperate zone with an arid climate (including xeric and semi-xeric habitats), many species that belong to other groups with vagrant growth form may also occur; for example vagrant growth forms have been reported for some species in *Xanthoparmelia* (Vain.) Hale (see Pérez 1997b, Litterski 2002, Blanco *et al.* 2005, Leavitt *et al.* 2011), *Dermatocarpon* Eschw. and *Rhizoplaca* Zopf (Rosentreter & McCune 1992, Rosentreter 1993, Arup & Grube 2000). Some deformed vagrant *Circinaria emiliae* and *Dermatocarpon* spp. somewhat resemble each other by their external morphologicy even though they belong to unrelated lineages of lichenized fungi. Since vagrancy can be assumed to be a response to drought stress (Honegger 2001), and the mentioned taxa belong to evolutionarily distant lineages of lichenized fungi, this phenomenon obviously represents morphological convergence.

In study **VII** it is shown that a number of species including *Circinaria alpicola*, *C. aschabadensis*, *C. cerebroides*, *C. digitata*, *C. esculenta*, *C. fruticulosa*, *C. lacunosa* and *C. vagans* are confined to the Irano-Turanian region, some with a very restricted distribution; for instance, *C.*

aschabadensis from Kopet-Dag Mountain and *C. alpicola* and *C. cerebroides* from the high mountains of Tian-Shan, *C. tominii* from Chuy Desert in Altai Republic in Russia can be regarded as endemic in these particular areas. Some species, such as *C. jussuffii* and *C. gyrosa*, have a limited distribution in the Mediterranean area. It must be noted that of all the Mediterranean climate zones in different parts of the Old World, vagrant taxa have only been found in the North Sahara, Middle East and South Europe. *Circinaria hispida* s.str. is the only widespread taxon among other sphaerothallioid species, as it is known from both Eurasia (Old World) and North America (New World). No vagrant *Circinaria* species have been reported from Australian deserts (Eldridge & Rosentreter 1997).

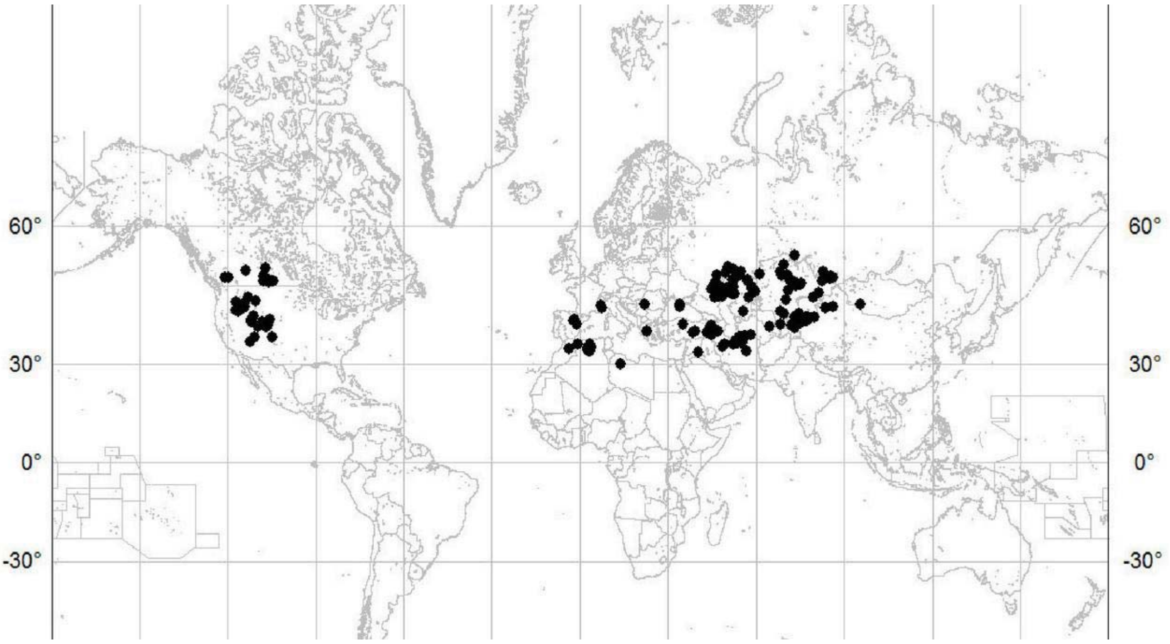


Fig. 11 — Known world distribution of 'manna lichens' determined from examined specimens in papers **V** and **VII**. The outline map was produced by PanMap software.

Fig. 12 — A–B. Population of *Circinaria esculenta* near Lake Inder in Kazakhstan (Photo by *O. Vondrákova* & *J. Vondrák)*. **C.** Population of *C. alpicola* in Ak-Saj, Kyrgyzstan (photo by *B. Litterski*). **D–F.** Habitats of *Circinaria* in Iran. **D**: *C. gyrosa* in open juniper forest in Shah kuh and Jahan Nama district in Golestan province; **E:** *C. rostamii* in dry steppe with *Astragalus* spp. and *Artemisia* spp. in the Kiamaki Wildlife Refuge in East Azerbaijan province; **F:** *C. fruticulosa* (*Sohrabi 10405B*) in Kaleybar district, 35 km S of Kaleybar along road to Ahar; scale = 5 mm.

Results and Discussion

Nomenclature

Type specimens are scientifically important and support the stabilization of nomenclature (see also Daston 2004). Examination of type material is critical for determining correct circumscription of taxa (Speers & Edwards 2008). ‘Manna lichens’ is one the oldest known groups of lichens and it contains several old names mostly described during past two centuries. In addition to pre-Linnean names by J. Amman, J. J. Dillenius and others (see Elenkin 1910d, Savicz & Elenkin 1950) the oldest validly published name in the group is *Lichen esculentus* Pall., introduced in 1776 by the German naturalist Pallas. The name *Lichen esculentus* and its combinations (e.g., *Aspicilia esculenta*, *Lecanora esculenta* and *Sphaerothallia esculenta*) are still used in many textbooks and popular publications. According to ICBN, the application of names is determined by the identity of their type specimens (herbarium specimens or illustrations). Therefore, the typification of such important and widely used names can have a significant effect on their usage. Careful scrutiny of the protologue for each of the names used for ‘manna lichens’, coupled with the study of herbarium specimens, allowed us to designate epitype for *Aspicilia esculenta* and lectotypes for several species, variants and forms of ‘manna lichens’ (see study **I**).

In the course of herbarium studies (**I–VII**) it was found that *Lichen esculentus* and its combinations have been used in very wide sence, including several distinct species. The same was true with *Lecanora fruticulosa* and its combinations. Occasionally even saxicolous specimens, sometimes referred to *Lecanora desertorum* (nom. illeg.), were called ‘manna lichens’. Some infraspecific taxa poposed by earlier authors (e.g., Berkeley 1849, Reichardt 1864, Steiner 1910 and Szatala 1957) proved to be distinct species, while most of them turned out to be environmental modifications. The tracing of original material and subsequent typification were laborious tasks. Still some of the original material particularly that of K.S. Mereschkowsky could not be located.

In some studies, the names *Aspicilia fruticulosa* and *A. fruticulosofoliacea* have been given to some vagrant, sphaerothallioid specimens (see Barreno *et al.* 1998; Sancho *et al.* 2000). Molecular characters, as well as an evaluation of the type specimens, confirmed that the Spanish species represent a distinct population, which belongs to a new species, *C. gyrosa*. In study **V**, the distinct morphology of *C. fruticulosa* led to the resolution of a taxonomic problem between the North American and Eurasian specimens of this species. Finally, both molecular and morphological characters confirmed that *A. fruticulosa sensu* Rosentreter (1993) and Brodo *et al.* (2001) in North America is a new species, and it was described as *A. rogeri* (syn. *Circinaria rogeri*)

Generic and species concepts

Since our current knowledge of the independent presence of genera in nature is in a state of flux, their delimitations remain rather subjective. It is well accepted that a genus is a monophyletic assemblage, a cluster of one or several distinctive species. Traditionally it is also an adopted concept in the biological classification system. The generic concepts in lichenized fungi in general have been unsettled since the late 1960s (e.g., Nimis 1998; DePriest 1999; Rambold & Triebel 1999; Lumbsch & Leavitt 2011). In studies **I–V,** the generic name *Aspicilia* was accepted, and three new species (*A. tibetica*, *A. digatata*, and *A. rogeri*) were described. A phylogenetic analysis of the family Megasporaceae resulted in a new generic classification in Nordin *et al.* (2010) and in study **VII**. In study **VI** the new generic names were adopted and the older name *Circinaria* was resurrected. Nordin *et al.* (2010) outlined a possible basis for the future circumscription of *Circinaria*, characterized by a crustose, subfruticose and subfoliose thallus, and the presence of aspicilin (in some species). A number of other important characters, such as the presence of pseudocyphellae, cortex with two layers, and conidia size, were taken into account in study **VII.** It became clear in study **VII** that *Circinaria* might not be a good generic name for sphaerothallioid species. The name *Sphaerothallia* Nees as an oldest name after *Circinaria* was another alternative which has been used a few times for 'manna lichens' (see Nees von Esenbeck 1831, Reichardt 1864, Szatala 1957, Follmann & Crespo 1974). The results in study **VII** show that sphaerothallioid species (e.g., *C. cerebroides, C. esculenta, C. emiliae, C. fruticulosa, C. gyrosa, C. hispida* s.str., *C. lacunosa, C. rostamii, C. sphaerothallina* and *C. vagans*) are nested in the same clade together with the crustose species *C. arida*, *C. calcarea*, *C. contorta*, *C. gibbosa* and *C. leprosescens*. Therefore, some necessary nomenclatural changes were proposed.

There is no general agreement among biologists about the unique "species concept". The issue is highly controversial and constantly debated, even between taxonomists. Species concept and species delimitation have been recently reviewed in general by, for example, de Queiroz (2007), and in lichens by (e.g., Purvis 1997; Grube & Kroken 2000; Crespo & Lumbsch 2010; Lumbsch & Leavitt 2011). The species concept used in this study is a pragmatic one (see also McDade 1995), relying mostly on morphological characters, or other recognizable patterns of discontinuity, and assuming that these patterns reflect the essential genetic integrity of the species. In some publications on lichens the use of this approach has been referred to as a so-called 'taxonomic' species concept (for review see Kärnefelt 1979, Cronquist 1988).

Phylogeny

In a three-gene analysis (nrLSU, mtSSU, RPB1) by Lumbsch *et al.* (2007) the Megasporaceae, including *Megaspora*, *Lobothallia* and *Aspicilia*, formed a monophyletic group with a high support value. The family was accepted by Lumbsch & Huhndorf (2007) and in Index Fungorum (CABI Bioscience, CBS & Landcare Research 2007). Based on extensive sampling and analysis of two independent loci (nrLSU and mtSSU) the monophyly of Megasporaceae was also found by Nordin *et al.* (2010). According to the new circumscription of the family it consists of five genera, *Aspicilia*, *Circinaria*, *Lobothallia*, *Megaspora*, and *Sagedia*.

Compared to previous studies, sampling of the genera *Circinaria*, *Lobothallia* and *Megaspora* was extended in study **VII**. The inclusion of the genus *Circinaria* in the family Megasporaceae was confirmed. The genus *Sphaerothallia* is nested in *Circinaria*, and thus the necessary new combinations for 15 sphaerothallioid species are proposed in study **VII**.

To conclude, a major revision of the family Megasporaceae is also required. The morphological characters currently used to separate the genera within the family are apparently not sufficient if the current classification is to reflect natural, phylogenetic relationships. Useful characters still remain to be discovered, and therefore comprehensive studies of morphology will be necessary. Species concepts need to be critically revised in *Circinaria* as well as in some other genera of Megasporaceae. *Circinaria hispida* s.str. (vagrant morphotype = type specimen) with multiple samples included was shown to be non-monophyletic. All groups that were studied include species that are vagrant. The vagrancy was shown to have evolved repeatedly in the genus *Circinaria* and seems to be more stable in some species such as *C. cerebroides, C. digitata, C. esculenta, C. fruticulosa*, *C. gyrosa*, *C. lacunosa*, *C. rostamii* and *C. vagans*. The preliminary results show that some crustose species (e.g., *C. aspera*, *C. elmorei* s.lat., *C. sphaerothallina*) and crustose morphotype of the erratic *C. alpicola*, *C. aschabadensis* and *C. hispida* s.lat., are grouped with many subfruticose to subfoliose species. All of these, based on sequence level data, seem to be correctly placed together with fruticose and subfoliose species in *Circinaria* (see study **VII**).

In study **VII** phylogeny of some crustose and vagrant morphotypes of the erratic species (e.g., *C. alpicola, C. aschabadensis* and *C. hipida*) was verified. Their crustose and vagrant morphotypes were found to be identical based on sequence regions used. For example, nrITS sequences of vagrant and crustose morphotypes in *C. alpicola, C. aschabadensis, Circinaria* sp.1 and *Circinaria* sp. 2 are identical and belong to a single species. This result suggests that a detailed study of the genetic similarity between vagrant and crustose species would be an exciting challenge; in particular between 'manna lichens', in order to understand their different growth forms. For a clearer picture, more intensive sampling of different species, including those which are truly vagrant and those with thalli on pebbles will be desirable.

Interestingly, of the five genera of Megasporaceae, only *Circinaria* includes species with a vagrant growth form, but this form is not found in *Aspicilia*, *Lobothallia*, *Megaspora* and *Sagedia*. The genetic basis for the origin of this peculiar life-from is unknown. Many questions concerning the evolution of vagrant sphaerothallioid species remain open for the future.

Additional remarks

Online catalogue of the lichen family Megasporaceae

As stated by Nimis & Vignes Lebbe (2010) "The correct identification of organisms is fundamental not only for the assessment and the conservation of biodiversity, but also in agriculture, forestry, the food and pharmaceutical industries, forensic biology, and in the broad field of formal and informal education at all levels". The identification of lichens is essential in several applied fields, such as biomonitoring (particularly air and soil pollution), biological soil crust studies, and biodeterioration of stone monuments. Identification is often difficult for non-specialists and technicians who are consistently dealing with lichen monitoring techniques (Nascimbene *et al.* 2010).

The fast development of the internet and wireless networks have created many possibilities for prompt identification of lichens by using several tools such as LIAS 1996-2011 (http://lias.net/; Rambold 1997), ITALIC (http://dbiodbs.univ.trieste.it/; Nimis & Martellos 2008), Consortium of North American Lichen Herbaria (NALH; http://symbiota.org), KeyToNature (see Randlane *et al.* 2010 for review, http:// www.keytonature.eu/) and EOL (http://www.eol.org). These databases contain useful information, including descriptions, photos, and distribution maps for lichens. Recently, in order to speed up cataloguing of an estimated 10,000 undescribed species of lichens, the Field Museum lichenologists (including T. Lumbsch and R. Lücking) used a special monograph style in bringing together 100 new species from all around the globe in a single publication (see Lumbsch *et al.* 2011). The first set of species information (e.g., the Latin diagnoses and descriptions) was published in accordance with ICBN and subsquently full data and many colour photographs from all new species were presented in EOL.

Following rapid developments in cyber applications for taxonomy and biodiversity studies, MYCO-LICH (www.myco-lich.com) was created during 2009 and 2010 (Sohrabi & Ghobad-Nejhad 2010). The website is still under development and comprises mainly biodiversity and taxonomic information on Iranian lichenized, lichenicolous and other fungi. It provides support to the identification process by offering online keys, medium to high-resolution pictures and ecological information, and online geographical distribution maps for species. In this thesis two peer reviewed publications (**IV** and **V**) and a manuscript (**VII**) include the cross-links to the MYCO-LICH and facilitate the tracking of updated information on recently published species. Some minor changes can be published i.e., range extensions, newly obtained photographs and other useful taxonomic observations. These will be uploaded in the online catalogue of the lichen family Megasporaceae in the following address: http://www.myco-lich.com/online-lichen-catalogue/megasporaceae.

Taxonomists currently spend significant time and resources determining where existing types are located and obtaining access to this material. Having an online index to type material including where it is located would greatly increase the efficiency of the taxonomic process (Speers & Edwards 2008). For this reason, online photographs of some of the type specimens (*Aspicilia tibetica*, *Circinaria arida*, *C. digitata*, *C. elmorei* and *C. rogeri*) of the publications **I, II, IV, V** and **VI** are available on the MYCO-LICH website. After proper publication of the taxonomic novelties of paper **VII**, additional photographs from the type material of new species will be uploaded.

References

Al-Aswad, M.B., Ahmad, M. & D.M. Sabir (1977) Über das Artenspektrum Manna erzeugender Aphiden. Anzeiger für Schädlingskunde, Pflanzenschutz, Umweltschutz 50: 164–165.

Andreeva, E.I. (1987) *Flora sporovykh rasteniy Kazakhstana,* vol. 11, *Lichenes,* 3, *Lecanorales – Physciales.* Nauka Kazakhskoy SSR, Alma-Ata [Almaty]. [in Russian]

Aptroot, A. (1998) Aspects of the integration of the taxonomy of lichenized and non-lichenized Pyrenocarpous Ascomycetes. The Lichenologist 30: 501–514.

Arup, U. & M. Grube (2000) Is *Rhizoplaca* (Lecanorales, lichenized Ascomycota) a monophyletic genus? Canadian Journal of Botany 78: 318–327.

Aucher-Éloy, P.M.R. (1843) *Relations des voyages en Orient de 1830 à 1838*. Revues et annotées M. le Comet Jaubert, 2 parties, Paris.

Barreno, E., Puche, F., Atienza, V., Pérez Rovira, P., Gimeno, C. & J.G. Segarra (1998) Flora no vascular de interés conservacionista. In: Laguna Lumbreras, E., Crespo Villalba, M.B., Mateo Sanz, G., López Udias, S., Fabregat Llueca, C., Serra Laliga, L., Herrero-Borgoñon Pérez, J.J., Carretero Cervero, J.L., Aguilella i Palasí, A. & R., Figuerola Lamata (eds.), Flora endémica rara o amenazada de la Comunidad Valenciana. Generalitat Valenciana, Conselleria de Medio Ambiente, València, pp. 363–373.

Berkeley, M.J. (1849) On *Lichen esculentus*. Gardeners' Chronicle. 1849: 611–612.

Blanco, O., Crespo, A. & J.A. Elix (2005) Two new species of *Xanthoparmelia* (Ascomycota: Parmeliaceae) from Spain. The Lichenologist 37: 97–100.

Bridson, G.D.R., Townsend, S.T., Polen, E.A. & E.R. Smith [eds.] (2004) *BPH-2: Periodicals With Botanical Content*, comprising a second edition of Botanico-Periodicum-Huntianum. Hunt Institute for Botanical Documentation, Pittsburgh.

Brodo, I.M., Sharnoff, S.D. & S. Sharnoff (2001) *Lichens* of *North America*. Yale University Press, New Haven and London.

Brummitt, R.K. (2001) *World geographical scheme for recording plant distributions.* Ed. 2, Hunt Institute for Botanical Documentation, Pittsburgh.

Büdel, B. & D.C.J. Wessels (1986) *Parmelia hueana* Gyeln., a vagrant lichen from the Namib Desert, SWA/Namibia. I, Anatomical and reproductive adaptations. Dinteria 18: 3–12.

Büdel, B. & C. Scheidegger (2008) Thallus morphology and anatomy. 40–68 pp., In: T. H. Nash [ed.]: *Lichen Biology.* Cambridge University Press, Cambridge.

CABI Bioscience, CBS & Landcare Research (2007) Index Fungorum (www.indexfungorum.org). Accessed 11 December 2011.

Cannon, P.F. & P.M. Kirk (2007) *Fungal families of the world*. Wallingford, CABI.

Castresana, J. (2000) Selection of conserved blocks from multiple alignments for their use in phylogenetic analysis. Molecular Biology and Evolution 17: 540–552.

Clauzade, G. & C. Roux (1984) Les genres *Aspicilia* Massal. et *Bellemerea* Hafellner et Roux. Bulletin de la Société Botanique du Centre-Ouest: Nouvelle Serie: Numero Special,15: 127–141.

Crespo, A. & E. Barreno (1978) Sobre las comunidades terrícolas de líquenes vagantes (Sphaerothallio – Xanthoparmelion vagantis al. nova). Acta Botanica Malacitana 4: 55–62.

Crawford, S. (2007) Ethnolichenology of *Bryoria fremontii:* wisdom of elders, population ecology, and nutritional chemistry. M.Sc. thesis, University of Victoria, Canada.

Crespo A. & H.T. Lumbsch (2010) Cryptic species in lichen-forming fungi. IMA Fungus 1: 167–170.

Cronquist, A. (1988) *The Evolution and Classification of Flowering Plants*. New York, Allen Press.

Crum, H. (1993) A lichenologist's view of lichen manna. Contributions from the University of Michigan Herbarium 19: 293–306.

Daston, L. (2004) Type specimens and scientific memory. Critical Inquiry 31: 153-182.

DePriest, P.T. (1999) Development of Mason E. Hale’s list of epithets in the parmelioid genera (lichen-forming Ascomycotina): a bibliographic review. The Bryologist 102: 442–461.

De Queiroz, K. (2007) Species concepts and species delimitation. Systematic Biology 56: 879–886.

Donkin, R.A. (1980) *Manna: an historical geography*. Biogeographica 17. Junk, The Hague, Boston & London.

Donkin, R.A. (1981) The "manna lichen:" *Lecanora esculenta*. Anthropos 76: 562–576.

Edgar, R. C. (2004) MUSCLE: multiple sequence alignment with high accuracy and high throughput. Nucleic Acids Research 32: 1792–1797.

Ekman, S. (1996) The corticolous and lignicolous species of *Bacidia* and *Bacidina* in North America. Opera Botanica 127: 1–148.

Eldridge, D. & R. Rosentreter (1997) Terricolous *Aspicilia* in semi-arid eastern Australia: how many species are there? Australasian Lichenology 41: 18–19.

Elenkin, A. (1901a) Wanderflechten der Steppen und Wüsten. Izvestiya Imperatorskago S.-Peterburgskago Botanicheskago Sada. 1: 16–38, 52–72, 4 tables. [in Russian].

Elenkin, A. (1901b) “Wanderflechten” der Wüsten und Steppen. Trudy Imperatorskago S.-Peterburgskago Obshchestva Estestvoispytatelei Vypusk 3, Otdelenie Botaniki. 32: 151–154, 156–157. [in Russian].

Elenkin, A. (1901c) Lichenes florae Rossiae. Nos. 1–50. Fasc. 1. Trudy Imperatorskago S.-Peterburgskago Botanicheskago Sada 19: 1–52.

Elenkin, A. (1901d) Lichen manna (*Lichen esculentus* Pall.) (Historical survey of literature). Trudy Imperatorskago S.-Peterburgskago Botanicheskago Sada 19: 53–99. [in Russian].

Elenkin, A. (1901e) Lichenes florae Rossiae et regionum confinium orientalium. Fasc. 1. Nos. 1–50. Petropoli. [Exsiccate Labels].

Elenkin, A. (1907) Lichenes florae Rossiae Mediae [Flora Lishaynikov Sredney Rossii], part 2. K. Mattisen, Yur’ev. [Aus dem Naturhistorischen Museum der Gräfin K. P. Scheremetjeff in Michailowskoje, Gouvernement Moskau 4]. [in Russian]

Errera, L. (1893) Sur le pain du ciel “provenant” de Diarbekir. Bulletin de l’Académie Royale des Sciences, des Lettres et des Beaux-Arts de Belgique, sér 3., 26: 83–91.

Esnault, J. (1985) Le genre *Aspicilia* Mass. (Lichens) en Algérie: étude des caractères taxonomiques et de leur variabilité. Doctoral Thesis, Laboratoire de Botanique L. Daniel, Université de Rennes I.

Evans,W.C., Trease, G.E. & D. Evans (2002) Pharmacognosy, ed. 15th. Baillière Tindall, London.

Eversmann, D. (1831) *Lichenum esculentum* Pallasii et species consimiles adversaria. Nova Acta Physico-Medica Academiae Caesareae Leopoldino-Carolinae Naturae Curiosorum Exhibentia 15: 351–358.

Felsenstein, J. (1985) Confidence limits in phylogenies: an approach using the bootstrap. Evolution 39: 783–791.

Felsenstein, J. (2004) *Inferring phylogenies*. Sinauer Associates Inc., Sunderland, Massachusetts.

Feuerer, T. & D.L. Hawksworth (2007) Biodiversity of lichens, including a world-wide analysis of checklist data based on Takhtajan's floristic regions. Biodiversity and Conservation 16: 85–98.

Flagey, C. (1896) Catalogue des lichens de l'Algérie. In: Battandier, J.A. & L. Trabut [eds.]: *Flore de l'Algérie,* Part 2, Vol. 3, 1(1): 1–140. Jourdan, Alger & Savy, Paris.

Follmann, G. & A. Crespo (1974) Observaciones acerca de la distribución de líquenes españoles. II. *Sphaerothallia fruticulosa* (Eversm.) Follm. & Crespo. Anales del Instituto Botánico A. J. Cavanilles 31: 325–333.

Frost, D.R., Grant, T., Faivovich, J., Bain, R.H., Haas, A., Haddad, C.F.B., De Sá, R.O., Channing, A., Wilkinson, M., Donnellan, S.C., Taxworthy, C.J., Campbell, J.A., Blotto, B.L., Moler, P., Drewes, R.C., Nussbaum, R.A., Lynch, J.D., Green, D.M. & W.C. Wheeler (2006) The Amphibian tree of life. Bulletin of the American Museum of Natural History 297: 1–371.

Gardes, M. & T.D. Bruns (1993) ITS primers with enhanced specificity for basidiomycetes-application to the identification of mycorrhizae and rusts. Molecular Ecology 2: 113–118.

Gargas, A., DePriest, P.T., Grube, M. & A. Tehler (1995) Multiple origins of lichen symbioses in fungi suggested by SSU rDNA phylogeny. Science 268: 1492–1495.

Giribet, G., Wheeler, W.C. & J. Muona (2002) DNA multiple sequence alignments. 107–114 pp., In: DeSalle, R., Giribet, G. & W.C. Wheeler [eds]: *Molecular Systematics and Evolution*: Theory and Practice. Birkhäuser Verlag. Basel.

Göbel, F. (1830) Chemische Untersuchung einer in Persien herabgeregneten Substanz, der *Parmelia esculenta.* Schweigger's Journal für Chemie und Physik 60: 393–399.

Goloboff, P., Farris, J.S. & K. Nixon (2008a) T.N.T.: Tree Analysis Using New Technology, Version 1.1. Available from: http://www.zmuc.dk/public/phylogeny/TNT/ (11 December 2011).

Goloboff, P., Farris, J.S. & K. Nixon (2008b) TNT, a free program for phylogenetic analysis. Cladistics 24: 774–786.

Grant, T. & A.G. Kluge (2003) Data exploration in phylogenetic inference: scientific, heuristic, or neither. Cladistics 19:379–418.

Grube, M. & D.L. Hawksworth (2007) Trouble with lichen: the re-evaluation and re-interpretation of thallus form and fruit body types in the molecular era. Mycological Research 111: 1116–1132.

Grube, M. & S. Kroken (2000) Molecular approaches and the concept of species and species complexes in lichenized fungi. Mycological Research 104: 1284–1294.

Hafellner, J. (1991) Die Gattung *Aspicilia*, ihre Ableitungen nebst Bemerkungen über cryptolecanorine Ascocarporganisation bei anderen Genera der Lecanorales (Ascomycetes lichenisati). Acta Botanica Malacitana 16: 133–140.

Hafellner, J., Nimis, P.L. & M. Tretiach (2004) New records of *Aspicilia hispida* from Italy and Greece. Herzogia 17: 95–102.

Hafellner, J. (1989) The genus *Aspicilia* and cryptolecanorine ascocarp organization in other genera of lichenized fungi. 19–21 pp., In abstract book: 8th Simposios Ciencias Criptogamicas. Libro de Resumenes. Melilla, 23–26 de Septiembre de 1989. Dpto. Biología Vegetal, Universidad de Malaga, Malaga

Hawksworth, D.L. & D.J. Hill (1984) *The lichen-forming fungi*. Blackie, Glasgow and London.

Hawksworth, D.L., Kirk, P.M., Sutton, B.C. & D.N. Pegler (1995) *Ainsworth & Bisby's Dictionary of the Fungi*. 8th ed. CAB International, Wallingford.

Hawksworth, D.L. (1988) Conidiomata, conidiogenesis, and conidia. 181–193 pp., In: M. Galun [ed.]: CRC Handbook of Lichenology. Volume I. CRC Press, Inc., Boca Raton.

Heckman, D.S., Geiser, D.M., Eidell, B.R., Stauffer, R.L., Kardos, N.L. & S.B. Hedges (2001) Molecular evidence for the early colonization of land by fungi and plants. Science 293: 1129–1133.

Henssen, A. & H.M. Jahns (1974‘1973’) *Lichenes*. Georg Thieme Verlag, Stuttgart.

Hibbett, D.S., Binder, M., Bischoff, J.F., Blackwell, M., Cannon, P.F., *et al.* (2007) A higherlevel phylogenetic classification of the Fungi. Mycological Research 111: 509–547.

Honegger, R. (1996) Mycobionts. 24–36 pp., In: Nash, T.H. [ed]: *Lichen Biology*. Cambridge University Press, Cambridge.

Honegger, R. (2001) The symbiotic phenotype of lichen-forming ascomycetes. In: Hock, B [ed.]: *The Mycota IX*. Fungal Associations. Springer-Verlag, Berlin, Heidelberg, pp. 165–188.

Högnabba, F. (2007) *Phylogenetic studies of cyanobacterial lichens*. Doctoral thesis, Yliopistopaino, Helsinki.

Huelsenbeck, J.P., Ronquist, F., Nielsen, R. & J.P. Bollback (2001) Bayesian inference of phylogeny and its impact on evolutionary biology. Science 294: 2310–2314.

Huelsenbeck J.P. & F. Ronquist (2001) MrBayes: Bayesian inference of phylogenetic trees. Bioinformatics 17: 754–755.

Huelsenbeck, J.P. & F. Ronquist (2003) MrBayes 3.0 beta 4. bayesian analysis of phylogeny. Program available in: http://mrbayes.csit.fsu.edu/ , Accessed date 11 December 2011.

Ivanova, N.V. & J. Hafellner (2002) Searching for the correct placement of *Megaspora* by use of ITS1, 5.8S and IS2 rDNA sequence data. Bibliotheca Lichenologica 82: 113–122.

Janex-Favre, M.C. (1985) Developpement et structure des apothecies de *l'Aspicilia calcarea* (discolichen). Cryptogamie, Bryologie et Lichénologie 6: 25–45.

Jørgensen, P.M. (1996) On the nomenclature of lichen phototypes. Taxon 45: 663–664.

Kappen, L. (1988) Ecophysiological relationship in different climatic regions. 37–100 pp., In: M. Galun, [ed]: *Handbook of Lichenology*, Vol. 2. CRC Press, Boca Raton.

Kärnefelt, I. (1979) The brown fruticose species of *Cetraria*. Opera Botanica 46: 1–150.

Kelly, L.J., Hollingsworth, P.M., Coppins, B.J., Ellis, C.J., Harrold, P., Tosh, J. & R. Yahr (2011) DNA barcoding of lichenized fungi demonstrates high identification success in a floristic context. New Phytologist 191: 288-300.

Kiple, F.K. & K. Coneè Ornelas [eds.] (1999) *The Cambridge World History of Food.* Cambridge University Press, Cambridge.

Kirk P.M., Cannon P.E., Winter D.W. & J.A. Stalpers [eds.] (2008) *Dictionary of the Fungi*. 10th ed. CAB International, Wallingford.

Krempelhuber, A. (1867) *Lichen esculentus* Pall., ursprünglich eine steinbewohnende Flechte. Verhandlungen der Zoologisch-Botanischen Gesellschaft in Wien 17: 599–606.

Larkin, M.A., Blackshields, G., Brown. N.P., Chenna, R., McGettigan, P.A., McWilliam, H., Valentin, F., Wallace, I.M., Wilm, A., Lopez, R., Thompson, J.D., Gibson, T.J. & D.G. Higgins (2007) Clustal W and Clustal X version 2.0. Bioinformatics 23: 2947–2948.

Laundon J.R. & D.L. Hawksworth. (1988) Proposal to conserve *Aspicilia* Massal. against several names (Lichenized Ascomycotina: Hymeneliaceae). Taxon 37: 478–489

Leavitt, S.D., Johnson, L., Goward, T. & L. St Clair (2011) Species delimitation in taxonomically difficult lichen-forming fungi: an example from morphologically and chemically diverse *Xanthoparmelia* (Parmeliaceae) in North America. Molecular Phylogenetics and Evolution 60: 317–332.

Lemey, P., Salemi, M. & Vandamme, A.M. (eds.) (2010) *The Phylogenetic Handbook: a Practical Approach to Phylogenetic Analysis and Hypothesis Testing*. 2nd Edition, Cambridge University Press, Cambridge.

LIAS (1996–2011) A global information system for lichenized and non-lichenized ascomycetes: www.lias.net. Accessed date: 11 December 2011

LIAS glossary contributors (2010) LIAS glossary. http://glossary.lias.net/ Accessed date: 11 December 2011.

Link, H.F. (1848) Ueber eine dem *Lichen esculentus* Pall. nahestehende Flechte aus der Wüste Sahara. Botanische Zeitung (Berlin) 1848: 53, 665.

Link, H.F. (1849) Ueber den *Lichen Jussufii* aus Algier. Botanische Zeitung (Berlin) 1849: 729.

Litterski, B. (2002) Vagrant lichens in Kyrgyzstan. Bibliotheca Lichenologica 82: 77–82.

Lohtander, K., Myllys, L., Sundin, R., Källersjö, M. & A. Tehler (1998) The species pair concept in the lichen *Dendrographa leucophaea* (Arthoniales): analyses based on ITS sequences. The Bryologist 101: 404–411.

Lumbsch H.T. (1997) A comparison of ascoma ontogeny supports the inclusion of the Eigleraceae in the Hymeneliaceae (Lecanorales). The Bryologist 100: 180–192.

Lumbsch, H.T. (2002) Analysis of phenolic products in lichens for identification and taxonomyc. 281–295 pp., In: Kranner, I., Beckett, R.P. & A.K. Varma [eds.]: *Protocols in Lichenology*. *Culturing, Biochemistry, Ecophysiology and Use in Biomonitoring.* Springer-Verlag, Berlin, Heidelberg.

Lumbsch, H.T., Ahti, T., Altermann, S., Amo de Paz, G., Aptroot, A., Arup, U., Bárcenas Peña, A., Bawingan, P.A., Benatti, M.N., Betancourt, L., Björk, C.R., Boonpragob, K., Brand, M., Bungartz, F., Cáceres, M.E.S., Candan, M., Chaves, J.L., Clerc, P., Common, R., Coppins, B. J., Crespo, A., Dal-Forno, M., Divakar, P.K., Duya, M.V., Elix, J.A., Elvebakk, A., Fankhauser, J.D., Farkas, E., Ferraro, L.I., Fischer, E., Galloway, D.J., Gaya, E., Giralt, M., Goward, T., Grube, M., Hafellner, J., Hernández J.E., Herrera Campos, de los Ángeles, M., Kalb, K., Kärnefelt, I., Kantvilas, G., Killmann, D., Kirika, P., Knudsen, K., Komposch, H., Kondratyuk, S., Lawrey, J.D., Mangold, A., Marcelli, M.P., McCune, B., Messuti, M.I., Michlig, A., Miranda Gonzáles, R., Moncada, B., Naikatini, A., Nelsen, M.P., Øvstedal, D.O., Palice, Z., Papong, K., Parnmen, S., Pérez-Ortega, S., Printzen, C., Rico, V.J., Rivas Plata, E., Robayo, J., Rosabal, D., Ruprecht, U., Salazar Allen, N., Sancho, L., Santos de Jesus, L., Santos Vieira, T., Schultz, M., Seaward, M.R.D., Sérusiaux, E., Schmitt, I., Sipman, H.J.M., Sohrabi, M., Søchting, U., Søgaard, M.Z., Sparrius, L.B., Spielmann, A., Spribille, T., Sutjaritturakan, J., Thammathaworn, A., Thell, A., Thor, G., Thüs, H., Timdal, E., Truong, C., Türk, R., Umaña Tenorio. L., Upreti, D.K., Van Den Boom, P., Vivas Rebuelta, M., Wedin, M., Will-Wolf, S., Wirth, V., Wirtz, N., Yahr, R., Yeshitela, K., Ziemmeck, F., Wheeler, T. & R. Lücking (2011) One hundred new species of lichenized fungi: a signature of undiscovered global diversity. Phytotaxa 18: 1–127.

Lumbsch, T.H., Feige, G.B. & K.E. Schmitz (1994) Systematic studies in the Pertusariales. I: Megasporaceae, a new family of lichenized ascomycetes. Journal of the Hattori Botanical Laboratory 75: 295–304.

Lumbsch, H.T. & H.W. Kothe (1988) Anatomical features of *Chondropsis semiviridis* (Nyl.) Nyl. in relation to its vagrant habit. The Lichenologist 20: 25–29.

Lumbsch T.H. & S.M. Huhndorf (2007) "Outline of Ascomycota – 2007". Myconet (The Field Museum, Department of Botany, Chicago, USA) 13: 1–58. Issued in 31 December. Availbel via http://archive.fieldmuseum.org/myconet/outline.asp, Accessed date: 11 December 2011.

Lumbsch, H.T., Schmitt, I., Lücking, R., Wiklund, E. & M.,Wedin (2007) The phylogenetic placement of Ostropales within Lecanoromycetes (Ascomycota) revisited. Mycological Research 111: 257–267.

Lumbsch, H.T. & S.D. Leavitt (2011) Goodbye morphology? A paradigm shift in the delimitation of species in lichenized fungi. Fungal Diversity: DOI: 10.1007/s13225-011-0123-z

Lutzoni, F., Pagel, M. & V. Reeb (2001) Major fungal lineages are derived from lichen symbiotic ancestors. Nature 411: 937–940.

Lutzoni, F., Kauff, F., Cox, J.C., McLaughlin, D., Celio, G., Dentinger, B., Padamsee, M., Hibbett, D., James, T.Y., Baloch, E., Grube, M., Reeb, V., Hofstetter, V., Schoch, C., Arnold, A.E., Miadlikowska, J., Spatafora, J., Johnson, D., Hambleton, S., Crockett, M., Shoemaker, R., Sung, G.H., Lücking, R., Lumbsch, H.T., O'Donnell, K., Binder, M., Diederich, P., Ertz, D., Gueidan, C., Hansen, K., Harris, R.C., Hosaka, K., Lim, Y.W., Matheny, B., Nishida, H., Pfister, D., Rogers, J., Rossman, A., Schmitt, I., Sipman, H., Stone, J., Sugiyama, J., Yahr, R. & R. Vilgalys (2004) Assembling the fungal tree of life: Progress, classification, and evolution of subcellular traits. American Journal of Botany 91: 1446–1480.

Lutzoni, F. & J. Miadlikowska (2009) Lichens: Quick Guide. Current Biology 19: R502–R503.

Lücking, R., Hodkinson, B.P., Stamatakis, A. & R.A. Cartwright (2011) PICS-Ord: Unlimited Coding of Ambiguous Regions by Pairwise Identity and Cost Scores Ordination. BMC Bioinformatics 12: 10. doi:10.1186/1471-2105-12-10.

Lücking, R., Rivas Plata, E., Chaves, J.L., Umaña, L. & H.J.M. Sipman (2009) How many tropical lichens are there... really? Bibliotheca Lichenologica 100: 399–418.

Magnusson, A.H. (1939) Studies in species of *Lecanora*, mainly the *Aspicilia gibbosa* group. Kungliga Svenska Vetenskaps-Akademiens Årsbok, Stockholm, ser. 3, 17: 1–182.

Malcolm, W.M. & D.J. Galloway (1997) *New Zealand Lichens: Checklist, Key, and Glossary*. Museum of New Zealand Te Papa Tongarewa, Wellington.

McDade, L.A. (1995) Species concepts and problems in practice: insight from botanical monographs. Systematic Botany 20: 606–622.

McNeill, J., Barrie, F.R., Burdet, H.M., Demoulin, V., Hawksworth, D.L., Marhold, K., Nicolson, D.H., Prado, J., Silva, P.C., Skog, J.E., Wiersema, J.H. & N.J. Turland [eds.] (2006) *International Code of Botanical Nomenclature (Vienna Code) adopted by the Seventeenth International Botanical Congress Vienna, Austria, July 2005.* Regnum Vegetabile 146. Gantner Verlag, Ruggell, Liechtenstein.

Mereschkowsky, C. (1911a) Contributions á la connaissance des lichens du gouvernement de Wladimir. Protokoly Zasedanij Obscestva Estestvoispytatelej pri Imperatorskom Kazanskom Universitete 42: 1–26. [in Russian]

Mereschkowsky, C. (1911b) Excursion lichénologique dans les steppes Kirghises (Mont Bogdo). Protokoly Zasedanij Obshchestva Estestvoispytatelej pri Imperatorskom Kazanskom Universitete 43(5): 1–42. [in Russian]

Mereschkovsky, C. (1921) Diagnoses of some lichens. Annals and Magazine of Natural History, including Zoology, Botany, and Geology, ser. 9, 8: 246–290.

Meyer B. & C. Printzen (2000) Proposal for a standardized nomenclature and characterization of insoluble lichen pigments. The Lichenologist 32: 571–583

Miadlikowska, J., Kauff, F., Hofstetter, V., Fraker, E., Grube, M., Hafellner, J., Reeb, V., Hodkinson, B. P., Kukwa, M., Lücking, R., Hestmark, G., Garcia Otalora, M., Rauhut, A., Büdel, B., Scheidegger, C., Timdal, E., Stenroos, S., Brodo, I., Perlmutter, G., Ertz, D., Diederich, P., Lendemer, J.C., May, P., Schoch, C. L., Arnold, A. E., Gueidan, C., Tripp, E., Yahr, R., Robertson, C. & F. Lutzoni (2006) New insights into classification and evolution of the Lecanoromycetes (Pezizomycotina, Ascomycota) from phylogenetic analyses of three ribosomal RNA- and two protein coding genes. Mycologia 98: 1088–1103

Müller K.F. (2005) The efficiency of different search strategies in estimating parsimony jackknife, bootstrap, and Bremer support. BMC Evolutionary Biology 5: 58. (doi: 10.1186/1471-2148-5-58)

Myllys, L., Lohtander, K., Källersjö, M. & A. Tehler (1999) Sequence insertions and ITS data provide congruent information on *Roccella canariensis* and *R. tuberculata* (Arthoniales, Euascomycetes) phylogeny. Molecular Phylogenetics and Evolution 12: 295–309.

Nannfeldt, J.A. (1932) Studien über die Morphologie und Systematik der nicht-lichenisierten inoperculaten Discomyceten. Nova Acta Regiae Societatis Scientiarum Upsaliensis, ser. 4, 8: 1–368.

Nascimbene, J., Nimis, P.L. & S. Martellos (2010) An integrated system for producing user-specific keys on demand: an application to Italian lichens. 151–156 pp., In: Nimis P.L. & R. Vignes Lebbe [eds.]: *Tools for Identifying Biodiversity: Progress and Problems*. Edizioni Università di Trieste (EUT Publisher), Trieste, Italy.

Nash, H.T. (2008) Introduction. 1–8 pp., In: Nash T.H. [ed.]: *Lichen Biology*. Cambridge University Press, Cambridge.

Nees von Esenbeck, T.F.L. (1831) Über die Flechten, welche unser Freund und College, Herr Prof. Eversmann, in den Kirgisischen Steppen gesammelt hat. Nova Acta Physico-Medica Academiae Caesareae Leopoldino-Carolinae Naturae Curiosorum Exhibentia 15: 359–362.

Nelson, A. (1951) *Medical Botany*. E. and S. Livingstone, Ltd., Edinburgh.

Nimis, P.L. (1998) A critical appraisal of modern generic concepts in lichenology. The Lichenologist 30: 427–438.

Nimis, P.L. & S. Martellos (2008) ITALIC — the information system on Italian lichens. Version 4.0. University of Trieste, Department of Biology, IN4.0/1 (http:// dbiodbs.univ.trieste.it/). Accessed date: 11 December 2011.

Nimis P.L. & R.Vignes Lebbe [eds.] (2010) Tools for identifying biodiversity: progress and problems. Edizioni Università di Trieste (EUT Publisher), Trieste, Italy.

Nordin, A., Tibell L. & B. Owe-Larsson (2007) A preliminary phylogeny of *Aspicilia* in relation to morphological and secondary product variation. Bibliotheca Lichenologica 96: 247–266.

Nordin, A., Tibell, L. & B. Owe-Larsson (2008) *Aspicilia berntii*, a new name for a poorly known species. The Lichenologist 40: 127–133.

Nordin, A., Savić S. & L. Tibell (2010) Phylogeny and taxonomy of *Aspicilia* and Megasporaceae. Mycologia 102: 1339–1349.

Nylander, J.A.A. (2002) MrModeltest v1.0b. Program distributed by the author. Department of Systematic Zoology, Uppsala University. http://darwin.uvigo.es/software/jmodeltest.html. Accessed date: 11 December 2011.

Orange, A., James, P.W. & F.J. White (2001) *Microchemical methods for the identification of lichens.* The British Lichen Society, London.

Owe-Larsson, B., Nordin, A. & L. Tibell (2007) *Aspicilia.* 61–108 pp., In: Nash, T.H., Gries, C. & F., Bungartz [eds.]: *Lichen Flora of the Greater Sonoran Desert Region.* 3. Lichens Unlimited, Arizona State University, Tempe, Arizona.

Oxner, A.N. (1971) *Aspicilia.* 146–217 pp., In: Kopaczevskaja, E.F., Makarevicz, M.F., Oxner, A.N. & K.A., Rassadina [eds.]: *Handbook of the lichens of the USSR*, vol. 1. Nauka, Leningrad. [in Russian].

Pallas, P.S. (1776) *Reise durch verschiedene Provinzen des Russischen Reiches* 3. Kayserliche Academie der Wissenschaften, St. Petersburg.

Perez-Llano, G.A. (1944) Lichens — their biological and economic significance. Botanical Review 10: 1–65.

Pérez, F.L. (1994) Vagant cryptogams in a paramo of the high Venezuelan Andes. Flora 189: 263–276.

Pérez, F.L. (1997a) Geoecology of erratic globular lichens of *Catapyrenium lachneum* in a high Andean Paramo. Flora 192: 241–259.

Pérez, F.L. (1997b) Geoecology of erratic lichens of *Xanthoparmelia vagans* in an equatorial Andean paramo. Plant Ecology 129: 11–28.

Pitra, A. (1868) Ueber *Chlorangium esculentum*. Hedwigia 7: 7–12.

Poelt, J. (1969) *Bestimmungsschlüssel Europäischer Flechten*. Verlag von J. Cramer, Lehre.

Printzen C. (2010) Lichen systematics: The role of morphological and molecular data to reconstruct phylogenetic relationships. Progress in Botany 71: 233–275.

Purvis, O.W. (1997) The species concept in lichens. 109–134 pp., In: Claridge, M.F., Dawah, H.A. & M.R. Wilson [eds.]: *Species: Units of Biodiversity*. Systematics Association Special Volume Series 54, Chapman & Hall, London.

R Development Core Team (2008). R: A language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria. ISBN 3-900051-07-0, URL http://www.R-project.org. Accessed date: 11 December 2011.

Rabenhorst, L. (1871) Uebersicht der von Herrn Prof. Dr. Haussknecht im Orient gesammelten Kryptogamen, Lichens. Hedwigia 12: 177–180.

Rambold, G. (1997) LIAS — the concept of an identification system for lichenized and lichenicolous ascomycetes. Bibliotheca Lichenologica 68: 67–72.

Rambold, G. & D. Triebel (1992) The Inter-lecanoralean Associations. Bibliotheca Lichenologica 48:1–201

Rambold, G. & D. Triebel (1999) Generic concepts in lichenized and lichenicolous ascomycetes since 1950 — a historical approach. Symbolae Botanicae Upsalienses 32(2): 123–164.

Randlane, T., Saag**,** A., Martellos, S. & P.L. Nimis (2010) Computer-aided, interactive keys to lichens in the EU project KeyToNature, and related resources. Bibliotheca Lichenologica 105: 37–42

Rannala, B. & Z. Yang (1996) Probability distribution of molecular evolutionary trees: a new method of phylogenetic inference. Journal of Molecular Evolution 43: 304–311.

Reichardt, H.W. (1864) Ueber die Mannaflechte, *Sphaerothallia esculenta* Nees. Verhandlungen der Zoologisch-Botanischen Gesellschaft in Wien 14: 553–560.

Richardson, D.H.S. (1974) *The Vanishing Lichens. Their history, biology and importance*. Hafner Press (Macmillan Publishing Co.), New York.

Room, A. (2009*) Alternate Names of Places: a worldwide dictionary*. McFarland & Company, Inc., Publishers

Rosentreter, R. (1993) Vagrant lichens in North America. The Bryologist 96: 333–338.

Rosentreter, R. & B McCune, (1992) Vagrant *Dermatocarpon* in Western North America. The Bryologist 95: 15-19.

Ronquist, F. & J.P. Huelsenbeck (2003) MrBayes 3: Bayesian phylogenetic inference under mixed models. Bioinformatics 19: 1572–1574.

Rosenberg, M.S. (2009) Sequence alignment: Concepts and history. 1–22 pp., In: Rosenberg M.S. [ed.]: *Sequence Alignment: Methods, Models, Concepts and Strategies*. University of California Press, Berkeley.

Roux, C., Nordin A., Tibell L. & M. Sohrabi (2011) Quelques espèces d'*Aspicilia* peu connues ou nouvelles des Pyrénées-Orientales (France). Bulletin de la Société Linnéenne de Provence 14: 177–227.

Sancho, L.G., Schroeter, B. & R. Del-Prado (2000) Ecophysiology and morphology of the globular erratic lichen *Aspicilia fruticulosa* (Eversm.) Flag. from central Spain. Biblioth Lichenol 75: 137–147

Santesson, R. (1952) Foliicolous lichens I. A revision of the taxonomy of the obligately foliicolous, lichenized fungi. - Symbolae Botanicae Upsalienses 12: 1–590.

Savicz, V.P. & A.A. Elenkin (1950) Introduction to the lichen flora of the Asiatic part of the USSR. - Plantae Cryptog., Trudy Botanicheskogo Instituta Imeni V. L. Komarova Akademii Nauk SSSR. Ser. 2, 6: 181–343.

Schmitt, I. Yamamoto, Y. & H.T. Lumbsch (2006) Phylogeny of Pertusariales (Ascomycotina): resurrection of Ochrolechiaceae and new circumscription of Megasporaceae. Journal of the Hattori Botanical Laboratory 100: 753–764.

Schoch, C.L., Sung, G.H., López-Giráldez, F., Townsend, J.P., Miadlikowska, J., Hofstetter, V., Robbertse, B., Matheny, P.B., Kauff, F., Wang, Z., Gueidan, C., Andrie, R.M., Trippe, K., Ciufetti, L.M., Wynns, A., Fraker, E., Hodkinson, B. P., Bonito, G., Yahr, R., Groenewald, J. Z., Arzanlou, M., de Hoog, G.S., Crous, P.W., Hewitt, D., Pfister, D.H., Peterson, K., Gryzenhout, M., Wingfield, M.J., Aptroot, A., Suh, S.O., Blackwell, M., Hillis, D.M., Griffith, G.W., Castlebury, L.A., Rossman, A.Y., Lumbsch, H.T., Lücking, R., Büdel, B., Rauhut, A., Diederich, P., Ertz, D., Geiser, D.M., Hosaka, K., Inderbitzin, P.,Kohlmeyer, J.,Volkmann-Kohlmeyer, B., Mostert, L., O'Donnell, K., Sipman, H., Rogers, J.D., Shoemaker, R.A., Sugiyama, J., Summerbell, R.C., Untereiner, W., Johnston, P., Stenroos, S., Zuccaro, A., Dyer, P., Crittenden, P., Cole, M.S., Hansen, K., Trappe, J.M., Lutzoni, F. & J.W. Spatafora (2009) The Ascomycota Tree of Life: A phylum wide phylogeny clarifies the origin and evolution of fundamental reproductive and ecological traits. Systematic Biology 58: 224–239.

Seaward, M.R.D. & H.J.M. Sipman (2006) An updated checklist of lichenized and lichenicolous fungi for Egypt. Willdenowia 36: 537–555.

Seaward, M.R.D., Sipman, H.J.M. & M. Sohrabi (2008) A revised checklist of lichenized, lichenicolous and allied fungi for Iran. Sauteria 15: 459–520.

Sipman, H.J.M. & A. Aptroot (2001) Where are the missing lichens? Mycological Research 105: 1433–1439.

Smith, C.W., Aptroot, A., Coppins, B.J., Fletcher, A., Gilbert, O.L., James, P.W. & P.A. Wolseley (2009) *The Lichens of Great Britain and Ireland.* British Lichen Society. London.

Sohrabi, M. & M. Ghobad-Nejhad [eds.] (2010) MYCO-LICH: Online Mycology-Lichenology of Iran. http://www.myco-lich.com. Accessed date: 11 December 2011.

Sohrabi, M., Owe-Larsson, B., Nordin, A. & C. Roux [eds.] (2010) Online catalogue of the lichen family Megasporaceae. http://www.myco-lich.com. Accessed date: 11 December 2011.

Søchting, U. (1997) Two major anthraquinone chemosyndromes in Teloschistaceae. Bibliotheca Lichenologica 68: 135–144.

Speers, L. & J.L. Edwards (2008) International infrastructure for enabling the new taxonomy: The role of the Global Biodiversity Information Facility (GBIF). 87–94 pp., In: Wheeler Q.D. [ed.]: *The new taxonomy,* Systematics Association Special Volume Series 76. Boca Raton: CRC Press.

Stafleu, F.A. & R.S. Cowan (1981) Taxonomic literature. A selective guide to botanical publications and collections with dates, commentaries and types, ed. 2, 3 (Lh-O). Regnum Vegetabile 105: 1–980.

Steiner, J. (1910) Lichenes Persici coll. a cl. Consule Th. Strauss. Annales Mycologici 8: 212–245.

Stenroos, S.K. & P.T. DePriest (1998) SSU rDNA phylogeny of cladoniiform lichens. American Journal of Botany 85: 1548–1559.

Swofford, D.L. (2002) PAUP*. Phylogenetic Analysis Using Parsimony (*and Other Methods). Version 4. Sinauer Associate, Sunderland. Massachusetts. Program available in: http://paup.csit.fsu.edu/, Accessed date: 11 December 2011.

Szatala, O. (1957) Prodromus einer Flechtenflora des Irans. Annales Historico-Naturales Musei Nationalis Hungarici, ser. 2, 8: 101–154.

Talavera, G. & J. Castresana (2007) Improvement of phylogenies after removing divergent and ambiguously aligned blocks from protein sequence alignments. Systematic Biology 56: 564–577.

Takhtajan, A. (1986) *Floristic Regions of the World*. [Translated by Crovello T.J. & A. Cronquist]. University of California Press, Berkeley.

Taylor, T.N., Hass, H. & H. Kerp (1997) A cyanolichen from the Lower Devonian Rhynie Chert. American Journal of Botany 84: 992–1004

Taylor, T.N., Hass, H., Remy, W. & H. Kerp (1995) The oldest fossil lichen. Nature 378: 244.

Taylor, W.A., Free, C., Boyce, C., Helgemo, R. & J. Ochoada (2004) SEM analysis of Spongiophyton interpreted as a fossil lichen. International Journal of Plant Sciences 165: 875–881.

Tehler, A. & M. Wedin (2008) Systematics of lichenized fungi. 336–352 pp., In: Nash, T.H. [ed.]: *Lichen Biology*. Cambridge University Press, Cambridge.

Temina, M., Kondratyuk, S., Zelenko, S.D., Nevo, E. & S. Wasser (2005) *Lichen-forming, Lichenicolous, and Allied Fungi of Israel*. Verlag Gantner, Ruggell, Liechtenstein.

Thiers, B. (2011) [continuously updated]. Index Herbariorum: A global directory of public herbaria and associated staff. New York Botanical Garden's Virtual Herbarium. http://sweetgum.nybg.org/ih/ Accessed date: 11 December 2011.

Thor, G. & J. Nascimbene (2010) An annotated checklist and bibliography of lichens and lichenicolous fungi of Libya. Cryptogamie, Mycologie 31: 67–95.

Turker, M. (2009) Ageing. (Published Online). In: Encyclopedia of Life Sciences. (ELS). John Wiley & Sons, Ltd: Chichester. http://www.els.net [doi: 10.1002/9780470015902.a0001479.pub2] Accessed date: 11 December 2011.

Vilgalys, R. & M. Hester (1990) Rapid genetic identification and mapping of enzymatically amplified ribosomal DNA from several Cryptococcus species. Journal of Bacteriology 172: 4238–4246.

Visiani, R. (1865) Relazioni di una nuova specie di Manna caduta in Mesopotamia nel marzo passato. Atti del Reale Istituto Veneto di Scienze, Lettere ed Arti. Venice, ser. 3, 10: 284–306.

Vobis, G. (1980) Bau und Entwicklung der Flechten-Pycnidien und ihrer Conidien. Bibliotheca Lichenologica 14: 1–141.

Vobis, G. & D.L. Hawksworth (1981) Conidial lichen-forming fungi. 245–273 pp., In: G. T. Cole & B. Kendrick [eds.]: *Biology of Conidial Fungi*. Volume 1. Academic Press, New York.

Webster, J. & R. Weber (2007) Introduction to Fungi. Cambridge University Press. Cambridge.

Wedin, M., Wiklund, E., Crewe, A., Döring, H., Ekman, S., Nyberg, Å., Schmitt, I. & H.T. Lumbsch (2005) Phylogenetic relationships of Lecanoromycetes (Ascomycota) as revealed by analyses of mtSSU and nLSU rDNA seqaence data. Mycological Research 109: 159–172.

Wheeler, W.C. (1996) Optimization alignment: the end of multiple sequence alignment in phylogenetics? Cladistics 12: 1–9.

White, T.J., Bruns, T.D., Lee, S. & J. Taylor (1990) Amplification and direct sequencing of fungal ribosomal RNA genes for phylogenetics. 315–322 pp., In: Innis, M.A., Gelfand, D.H., Sninsky, J.J. & T.J. White [eds.]: *PCR Protocols.* Academic Press, San Diego.

Yuan, X., Xiao, S. & T.N. Taylor (2005) Lichen-like symbiosis 600 million years ago. Science 308: 1017-1020.

Zohary, M. (1982) *Plants of the Bible*. Cambridge University Press, Cambridge.

Zoller, S., Scheidegger C. & C. Sperisen (1999) PCR primers for the amplification of mitochondrial small subunit ribosomal DNA of lichen-forming ascomycetes. The Lichenologist 31: 511–516.

Acknowledgments

The completion of this thesis required hard work, but I did not go through this without generous support. I enjoyed companionship and involvement of several people. My sincere thanks are due to my supervisors Prof. Jaakko Hyvönen and Prof. Soili Stenroos for providing opportunities for me to finalise the task. They allowed me to work independently, yet were ready to answer my numerous questions and patiently read my manuscripts. They helped me to find ways to use advanced methods and facilities for phylogenetic analyses. I would also like to acknowledge the help and advice by Prof. Teuvo Ahti (Helsinki), Dr. Björn Owe-Larsson, Dr. Anders Nordin (both from Uppsala), Dr. Harrie Sipman (Berlin), Dr. Claude Roux (Marseille) and Dr. V. Rico (Madrid) in the taxonomy of *Aspicilia* s.lat. Without their encouragement and advice this study would not have been possible.

I thank all lichenologists working in the Botanical Museum in Helsinki for valuable discussions and insights. I am indebted to Prof. Teuvo Ahti who kindly helped me from my first day in the Botanical Museum. His deep knowledge in lichenology and his enormous private library that was freely available have been invaluable for my study. I thank Dr. Orvo Vitikainen, Dr. Leena Myllys, Roland Skytén, Sampsa Lommi, Dr. Filip Högnabba and Saara Velmala (all from Helsinki) for their kind help in many ways and for sharing their knowledge with me.

I also want to thank the co-authors of published work, Dr. Walter Obermeyer (Graz), Dr. Birgit Litterski (Greifswald), Dr. Ulrik Søchting (Copenhagen) and Prof. Leif Tibell (Uppsala), for their help during the preparation of the manuscripts.

Dr. Filip Högnabba, Dr. Masoomeh Ghobad-Nejhad and Saara Velmala were of considerable help during the work in the MES-lab. Pirkko Harju helped me to use TLC equipment and microtome. Sirkka Sällinen in the library always helped me when I could not find what I was looking for. The Botanical Museum generously provided me space and microscopes to study since October 2005, for which I am grateful to the directors, Prof. Pertti Uotila and Dr. Marko Hyvärinen. Sincere thanks are also due to all the other colleagues in the Botanical Museum who have made it such a nice place to work in, particularly Dr. Alexander Sennikov for being a source of support in the nomenclature and translation of the Russian texts, as well as Dr. Neil Bell for helping me with the English language and in learning phylogeny programs.

I am obliged to Prof. Pier Luigi Nimis (Trieste), Prof. Mark Seaward (Bradford), Dr. Volker John (Bad Dürkheim), Dr. Roger Rosentreter (Boise, Idaho), Dr Mikhail Andreev (Saint-Petersburg), Dr. Tiina Randlane (Tartu), Dr. Ayhan Şenkardeşler (Izmir), Dr. Mehmet Candan (Eskişehir), Dr. Steven Leavitt (Chicago), Dr. Vagn Alstrup (Copenhagen) and Dr. David Glenny (Lincoln), Dr. Eugene Yurchenko (Minsk) Dr. Toby Spribille (Graz), Dr. Jan Vondrák and Olga Vondrákova (both from Průhonice) and Vitaly Kulakov (Volgograd), for being the source of support and sending useful information or valuable specimens. I also acknowledge curators of the following herbaria (B, CANL, CANB, FH, FR, G, CBFS, GZU, H, LE, IRAN, MAF, S, SRP, TU, TUR, UPS, US, and W) who kindly provided important material for my study. This thesis would have been much more limited without inclusion of Iranian material. I have had the opportunity to collect extensively in Iran. Prof. Rasoul Zare, Dr. Mehrdad Abbasi, Mohammad Reza Asef and Faezeh Aliabadi (all from the Iranian Research Institute of Plant Protection, Tehran, Iran) have been very generous in hosting me during my visits to Iran in 2007 and 2008.

I also would like to express my sincere thanks to Prof. Nils Hallenberg (Gothenburg) for his kind advice and fruitful discussions during visits that I made together with my wife to Gothenburg, and during our field work in Iran. I also express my special gratitude to Prof. Mark Seaward who generously read the manuscript, made a number of valuable comments and revised the English.

I thank Dr. Ekaterina Kuznetsova, Nadezhda Alexeeva and Irina Stepanchikova (all from Saint-Petersburg State University, Russia), for their kind help in translating many Russian labels of the LE specimens.

Finally I express my warm thanks to my parents Rostam and Leila, brothers Yaghub, Yousef, Reza, and my sisters Reihaneh and Batoul, for their great patience and for supporting me in many ways. Last but not least, I wish to thank my wife Masoomeh, for her patience and constant support during my studies.

This thesis has been mainly funded by awards from the Iranian Ministry of Science and Technology (IMST) for which I am most grateful, as I am for financial support provided by Societas pro Fauna et Flora Fennica (SFFF) and Finnish Biological Society Vanamo.

Errata

Paper	**page**	**changes**
Paper **I**	Page 631	Change “Syntype material” to “corresponding material”
Paper **II**	Page 495	Add “(Fig. 4), ”after “Distribution and ecology”
Paper **III**	Page 628	Change “Jamshid, F.” to “Fatehi, J.”
Paper **IV**	Page 40	Change “SPR” to “SRP”
Paper **IV**	Page 41	Change “ DQ41” to “ DQ40” in all following numbers: (DQ4~~1~~1556–DQ4~~1~~1563, DQ411567–DQ4~~1~~1568, DQ4~~1~~1570–DQ4~~1~~1571 replace wiith DQ401556–DQ401563, DQ401567–DQ401568, DQ401570–DQ401571)
Paper **VI**	Page 244	Remove “& M. Sohrabi” and change to “& Sohrabi”