Lichens and lichenized fungi

Lichens and lichenized fungi

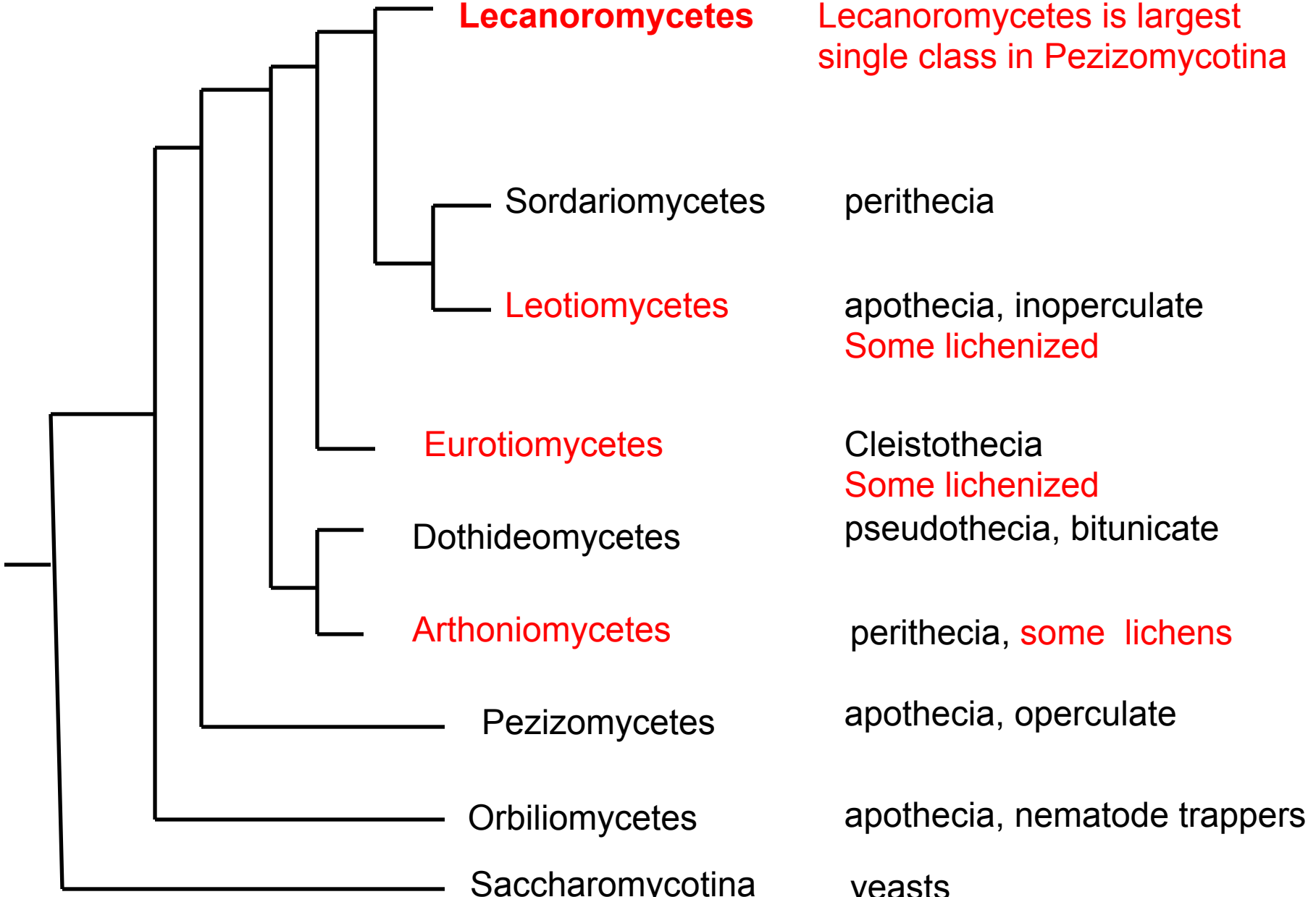
Lichens are dual (often triple) organisms involving two, and often three, different Kingdoms:

Fungi
Plants
Bacteria

"A self-supporting, stable association between an exhabitant fungal partner and inhabitant population of extracellularly located unicellular or filamentous algal or cyanobacterial cells."

The fungal partner in the lichen is the mycobiont
The algal and cyanobacterial partners are the photobionts

Pezizomycotina is the largest subphylum of Ascomycota



Lichen fungi are polyphyletic, like other nutritional or ecological fungal groups (e.g. mycorrhizal fungi, human or plant pathogens), but the majority of lichens belong to a single lineage.

lichenization has evolved multiple times (also lost?)

Lecanoromycetes is the largest, > 90% of lichen species
The largest class in terms of numbers of species, diversity
Ascocarps primarily apothecia but a few families have perithecial ascomata

Lecanoromycetes are exclusively lichenized
The largest class of ascomycete fungi, approximately 14,000 species
Total lichen biodiversity estimated 17,000-20,000 species

Only three genera of lichenized basidiomycetes: *Dictyonema* (Atheliaceae), *Multiclavula* (Clavariaceae) and *Lichenomphalia* (Tricholomataceae); the name *Lichenomphalia* is now used for lichenized *Omphalina*.

Licenized ascomycetes mainly class Lecanoromycetes (Pezizomycotina), however some lichenized species occur in other asocomycete classes—Leotiomycetes, Arthoniomycetes, and Eurotiomycetes.

Some ascomycete classes/orders contain both lichenized and nonlichenized spp. (Arthoniomycetes, Eurotiomycetes, Leotiomycetes)

Common basidiomycete lichens

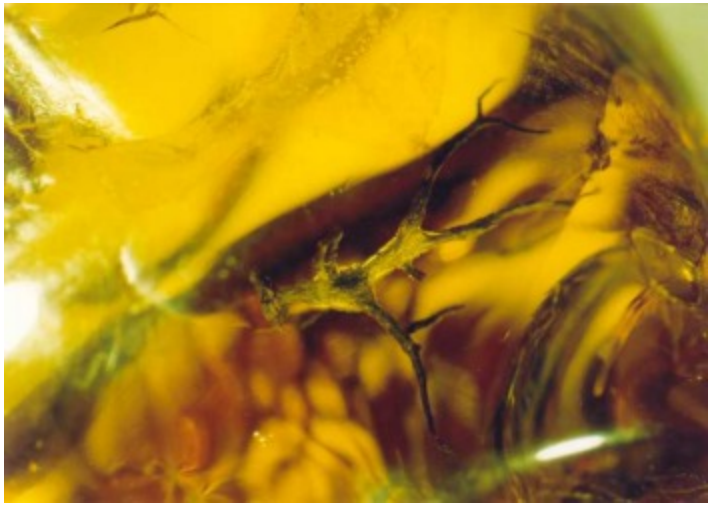
Lichenomphalia (formerly *Omphalina*)

Common basidiomycete lichens

Multiclavula mucida Clavariaceae

The oldest putative fossil lichen comes from the Rhynie Chert 400 MYA (early Devonian)—approximate time of divergence of main phyla of fungi

Winfrenatia reticulata

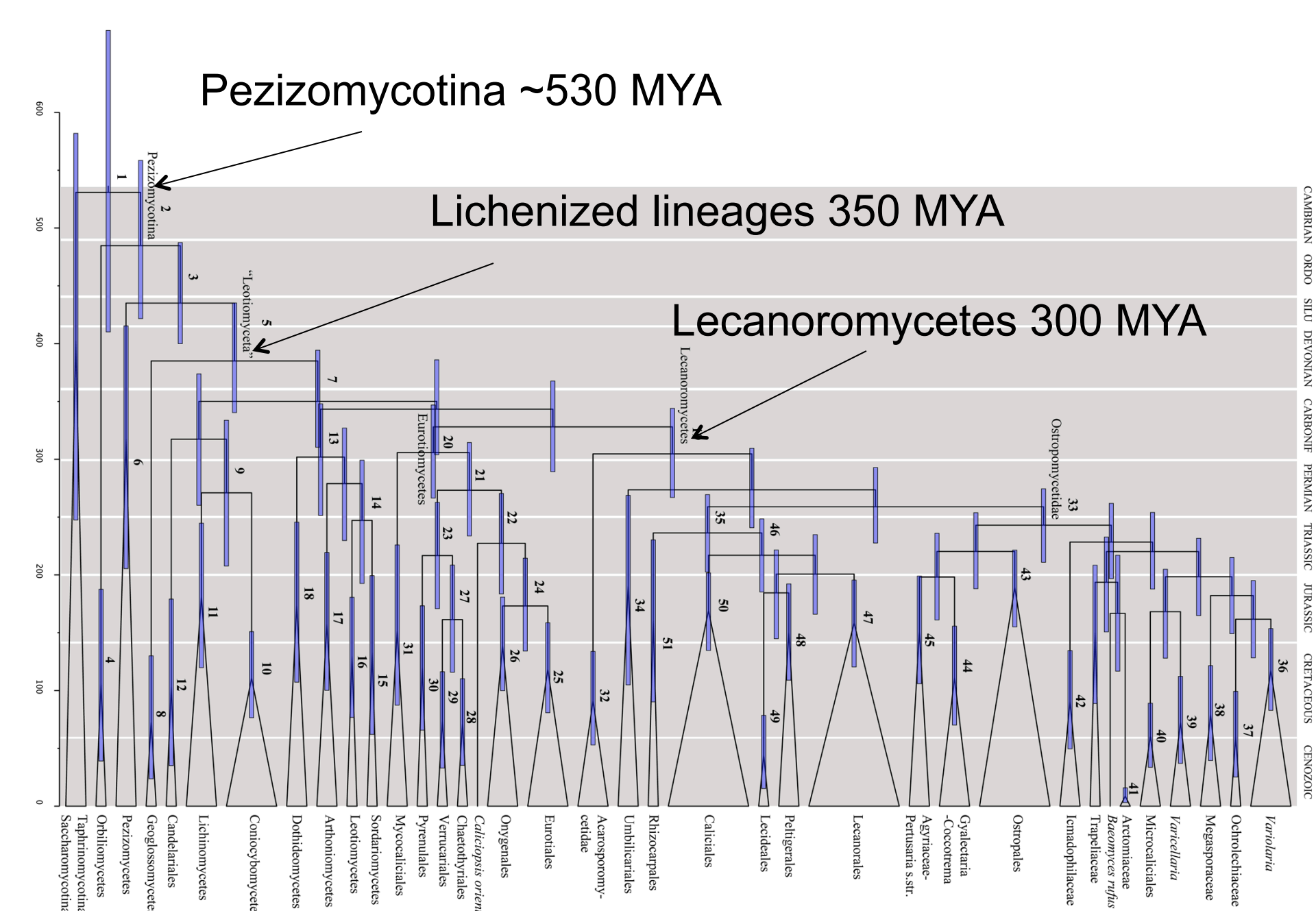


Usnea sp in Eocene amber

Winfrenatia photobionts were cyanobacteria
Mycobiont hyphae lack septa—possible Glomeromycota?

The main lichenized Ascomycota lineages appeared as early as the Carboniferous, 350 MYA, with successive radiations in the Jurassic and Cretaceous that generated the diversity in the main modern groups.

Lecanoromycetes divergered at around 300 MYA, expansions occurred during Jurassic and Cretaceous, 150—200 MYA, coinciding with diversification of Angiosperms



Prieto M, Wedin M (2013) Dating the Diversification of the Major Lineages of Ascomycota (Fungi). PLoS ONE 8(6): e65576. doi: 10.1371/journal.pone.0065576

http://www.plosone.org/article/info:doi/10.1371/journal.pone.0065576

Lichen systematics

Names and classification of lichens is based only on the mycobiont

Lichen names are integrated into the system of fungal nomenclature

13 of 46 ascomycete orders contain lichenized species

only 4 orders are exclusively lichenized

Class Lecanoromycetes, the majority of lichenized species

Four orders:

Lecanorales, 5700 spp

Peltigerales, 1200 spp

Teloschistales, 1200 spp

Class Lichinomyetes

One order:

Lichinales, 350 spp., all lichenized with cyanobacteria

No. of genes/ data set	No. of taxa	% of missing data
5	111	17
5+4	188	26
5+4+3	274	37

RAxML BP	PHYML BP	MrBayes PP
1	2	3
4	5	6
7	8	9

not applicable due to missing taxa

RAxML-BP/PHYML-BP ≥70% / MrBayes-PP ≥95%

RAxML-BP/PHYML-BP <70%/ MrBayes-PP <95%/ node does not exist

Primary photobiont:

- *Trebouxia* or *Asterochloris*
- *Trebouxia*
- *Asterochloris*
- *Myrmecia*
- *Cystococcus*
- *Trentepohlia*
- *Dictyochloropsis*
- *Coccomyxa*
- Other chlorococcoid algae
- Cyanobacteria
- Non-lichenized

Secondary photobiont:

- S /Sc — *Stigonema* /*Scytonema*
- N — *Nostoc*
- C — *Calothrix*

LECANORALES

PHYSCIINEAE

TELOSCHISTALES

TELOSCHISTINEAE

Caliciaceae?

Physciaceae?

7 *Parmotrema tinctorum* (5)
89 *Parmotrema austrosinense* (5)
8 *Parmotrema reticulatum* (5)
2 *Flavoparmelia caperata* (5)
85 *Punctelia hypoleucites* (5)
9 *Punctelia rudecta* (5)
317 *Flavopunctelia flaventior* (5)
6 *Canoparmelia caroliniana* (5)
4 *Xanthoparmelia conspersa* (5)
206 *Myelochroa aurulenta* (5)
1370 *Melanelixia fuliginosa* (5)
Parmelia saxatilis
312 *Hypotrachyna caracensis* (5)
324 *Hypotrachyna degelii* (5)
Pleurosticta acetabulum
813 *Usnea antarctica* (5)
816 *Usnea sphacelata* (5)
5 *Usnea strigosa* (4)
1245 *Tuckermanopsis ciliaris* (5)
231 *Flavocetraria nivalis* (5)
1710 *Masonhalea richardsonii* (4)
198 *Vulpicida pinastri* (5)
Vulpicida juniperina
211 *Cetraria islandica* (5)
225 *Dactylina arctica* (5)
Evernia prunastri
10 *Menegazzia terebrata* (4)
235 *Asahinea scholanderi*
1243 *Pseudevernia consocians* (5)
195 *Hypogymnia physodes* (4)
Pseudevernia furfuracea
201 *Platismatia glauca* (4)
203 *Platismatia glauca* (5)
1044 *Imshaugia aleurites* (4)
205 *Bryoria trichodes* (5)
872 *Bryoria trichodes* (5)
209 *Alectoria ochroleuca* (5)
3 *Cladonia caroliniana* (5)
Cladonia rangiferina
1657 *Cetradonia* sp. (5)
1377 *Pycnothelia papillaria* (5)
Menus conglomeratus
Pilophorus cereolus
Pilophorus strumaticus
Cladia retipora
Heterodea muelleri
1244 *Lepraria lobificans*
325 *Lepraria lobificans* (5)
1792 *Lepraria incana*
Stereocaulon paschale (4)
Stereocaulon tomentosum
1281 *Squamarina cartilaginea** (4)
1701 *Squamarina gypsacea**
1693 *Lecanora achariana** (5)
877 *Lecanora contractula** (5)
1798 *Lecanora polytropa** (4)
*Lecanora concolor**
*Lecanora intumescens**
1275 *Lecidella elaeochroma** (4)
*Lecidella meiococca**
1374 *Lecidella euphorea** (4)
639 *Lecanora hybocarpa** (5)
Pyrrhospora quernea
1328 *Tephromela atra** (4)
780 *Tephromela atra** (5)
1373 *Tephromela atra** (5)
196 *Mycoblastus sanguinarius* (5)
1793 *Bacidia rubella**
*Bacidia rosella**
642 *Bacidia schweinitzii** (4)
213 *Toninia sedifolia** (4)
1845 *Bacidina arnoldiana* (4)
111 *Crocynia pyxinoides* (5)
Lecania cyrtella
86 *Ramalina complanata* (4)
966 *Ramalina complanata* (4)
777 *Niebla cephalota* (4)
108 *Lopezaria versicolor* (5)
1032 *Psora decipiens* (4)
219 *Psora ruhiformis* (4)
992 *Protoblastenia calva* (5)
1057 *Sphaerophorus globosus* (5)
226 *Sphaerophorus fragilis* (4)
Neophyllis melacarpa
Strangospora pinicola
Scoliciosporum umbrinum
1306 *Amandinea punctata* (4)
889 *Buellia frigida** (5)
Amandinea punctata
571 *Buellia stillingiana** (5)
Hafellia disciformis
1695 *Tholurna dissimilis*
1051 *Buellia fimbriata** (4)
573 *Buellia dialyta** (4)
207 *Pyxine sorediata* (4)
686 *Pyxine subcinerea* (5)
839 *Dirinaria applanata* (4)
*Calicium viride** (4)
1061 *Tornabaena scutellifera* (4)
320 *Heterodermia vulgaris* (5)
84 *Physcia aipolia* (5)
1308 *Phaeophyscia orbicularis* (5)
648 *Anaptychia palmulata* (5)
Anaptychia runcinata
220 *Physconia muscigena* (5)
1314 *Rinodina tephraspis** (5)
214 *Xanthoria elegans* (5)
Xanthoria parietina
200 *Xanthoria polycarpa* (5)
Xanthomendoza fallax (4)
*Caloplaca flavorubescens**
107 *Megalospora tuberculosa* (5)
102 *Letrouitia domingensis* (5)

Parmeliaceae*

Cladoniaceae

N

Stereocaulaceae*

S/Sc

Lecanoraceae*

Mycoblastaceae*

Ramalinaceae*

Psoraceae

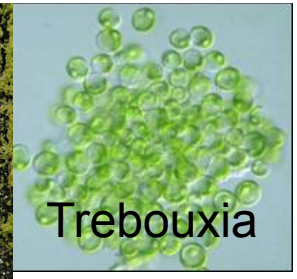
Sphaerophoraceae

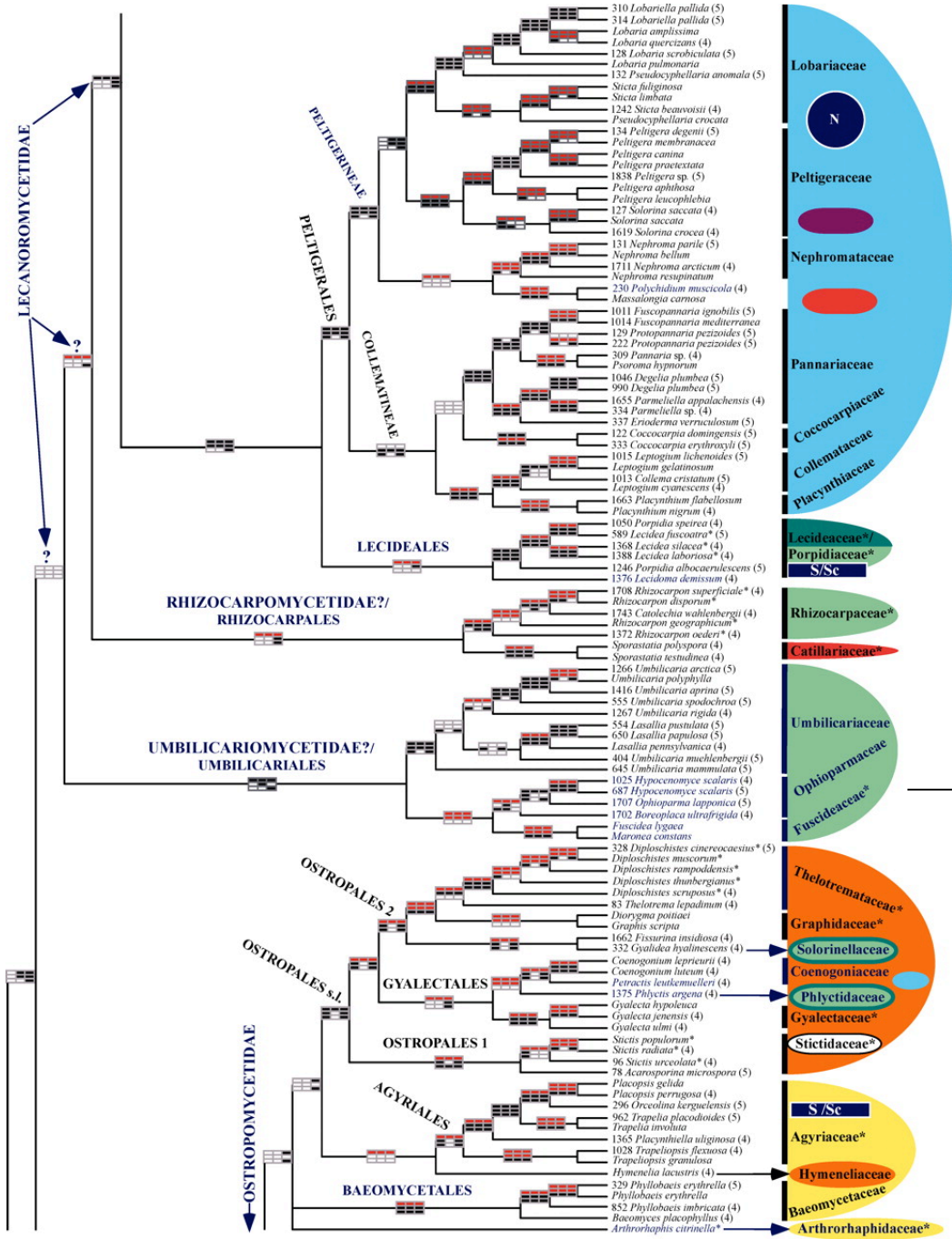
Physciaceae*

Teloschistaceae*

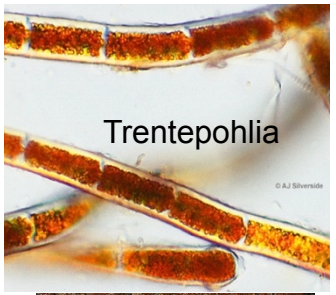
Megalosporaceae

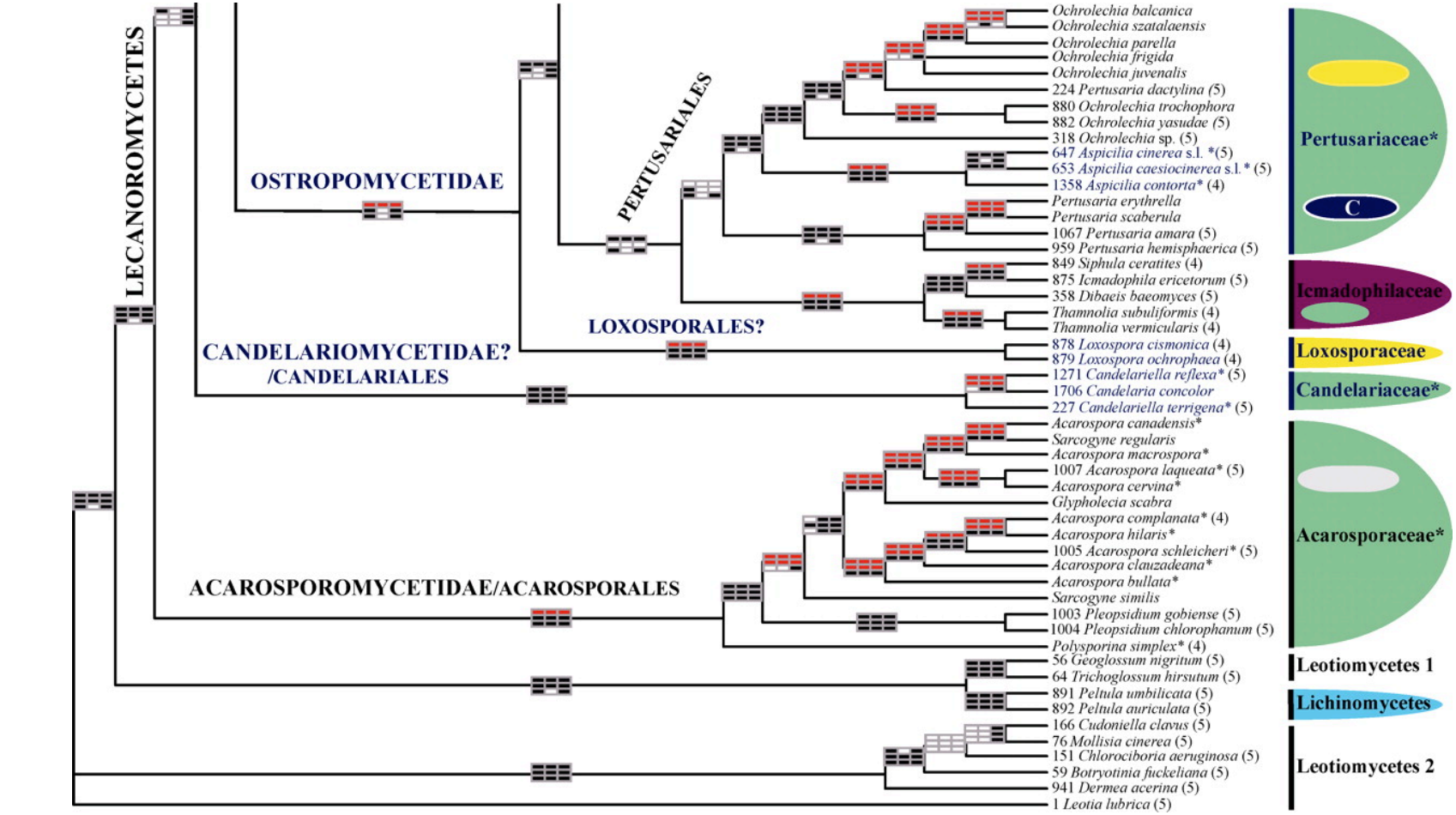
Letrouitiaceae




LECANOROMYCETIDAE
PELTIGERINEAE
PELTIGERALES
COLLEMATINEAE
LECIDEALES
RHIZOCARPOMYCETIDAE?/
RHIZOCARPALES
UMBILICARIOMYCETIDAE?/
UMBILICARIALES
OSTROPALES 2
OSTROPALES s.l.
GYALECTALES
OSTROPALES 1
AGYRIALES
BAEOMYCETALES
OSTROPOMYCETIDAE
310 Lobariella pallida (5)
314 Lobariella pallida (5)
Lobaria amplissima
Lobaria quercizans (4)
128 Lobaria scrobiculata (5)
Lobaria pulmonaria
132 Pseudocyphellaria anomala (5)
Sticta fuliginosa
Sticta limbata
1242 Sticta beauvoisii (4)
Pseudocyphellaria crocata
134 Peltigera degenii (5)
Peltigera membranacea
Peltigera canina
Peltigera praetextata
1838 Peltigera sp. (5)
Peltigera aphthosa
Peltigera leucophlebia
127 Solorina saccata (4)
Solorina saccata
1619 Solorina crocea (4)
131 Nephroma parile (5)
Nephroma bellum
1711 Nephroma arcticum (4)
Nephroma resupinatum
230 Polychidium muscicola (4)
Massalongia carnosa
1011 Fuscopannaria ignobilis (5)
1014 Fuscopannaria mediterranea
129 Protopannaria pezizoides (5)
222 Protopannaria pezizoides (5)
309 Pannaria sp. (4)
Psoroma hypnorum
1046 Degelia plumbea (5)
990 Degelia plumbea (5)
1655 Parmeliella appalachensis (4)
334 Parmeliella sp. (4)
337 Erioderma verruculosum (5)
122 Coccocarpia domingensis (5)
333 Coccocarpia erythroxyli (5)
1015 Leptogium lichenoides (5)
Leptogium gelatinosum
1013 Collema cristatum (5)
Leptogium cyanescens (4)
1663 Placynthium flabellosum
Placynthium nigrum (4)
1050 Porpidia speirea (4)
589 Lecidea fuscoatra* (5)
1368 Lecidea silacea* (4)
1388 Lecidea laboriosa* (4)
1246 Porpidia albocaerulescens (5)
1376 Lecidoma demissum (4)
1708 Rhizocarpon superficiale* (4)
Rhizocarpon disporum*
1743 Catolechia wahlenbergii (4)
Rhizocarpon geographicum*
1372 Rhizocarpon oederi* (4)
Sporastatia polyspora (4)
Sporastatia testudinea (4)
1266 Umbilicaria arctica (5)
Umbilicaria polyphylla
1416 Umbilicaria aprina (5)
555 Umbilicaria spodochroa (5)
1267 Umbilicaria rigida (4)
554 Lasallia pustulata (5)
650 Lasallia papulosa (5)
Lasallia pennsylvanica (4)
404 Umbilicaria muehlenbergii (5)
645 Umbilicaria mammulata (5)
1025 Hypocenomyce scalaris (4)
687 Hypocenomyce scalaris (5)
1707 Ophioparma lapponica (5)
1702 Boreoplaca ultrafrigida (4)
Fuscidea lygaea
Maronea constans
328 Diploschistes cinereocaesius* (5)
Diploschistes muscorum*
Diploschistes rampoddensis*
Diploschistes thunbergianus*
Diploschistes scruposus* (4)
83 Thelotrema lepadinum (4)
Diorygma poitiaei
Graphis scripta
1662 Fissurina insidiosa (4)
332 Gyalidea hyalinescens (4)
Coenogonium leprieurii (4)
Coenogonium luteum (4)
Petractis leutkemuelleri (4)
1375 Phlyctis argena (4)
Gyalecta hypoleuca
Gyalecta jenensis (4)
Gyalecta ulmi (4)
Stictis populorum*
Stictis radiata* (4)
96 Stictis urceolata* (4)
78 Acarosporina microspora (5)
Placopsis gelida
Placopsis perrugosa (4)
296 Orceolina kerguelensis (5)
962 Trapelia placodioides (5)
Trapelia involuta
1365 Placynthiella uliginosa (4)
1028 Trapeliopsis flexuosa (4)
Trapeliopsis granulosa
Hymenelia lacustris (4)
329 Phyllobaeis erythrella (5)
Phyllobaeis erythrella
852 Phyllobaeis imbricata (4)
Baeomyces placophyllus (4)
Arthrorhaphis citrinella*
Lobariaceae
N
Peltigeraceae
Nephromataceae
Pannariaceae
Coccocarpiaceae
Collemataceae
Placynthiaceae
Lecideaceae*/
Porpidiaceae*
S/Sc
Rhizocarpaceae*
Catillariaceae*
Umbilicariaceae
Ophioparmaceae
Fuscideaceae*
Thelotrematacеae*
Graphidaceae*
Solorinellaceae
Coenogoniaceae
Phlyctidaceae
Gyalectaceae*
Stictidaceae*
S /Sc
Agyriaceae*
Hymeneliaceae
Baeomycetaceae
Arthrorhaphidaceae*


Nostoc


Trentepohlia



Pertusaria

Icmadophila

Candelaria

Acarospora

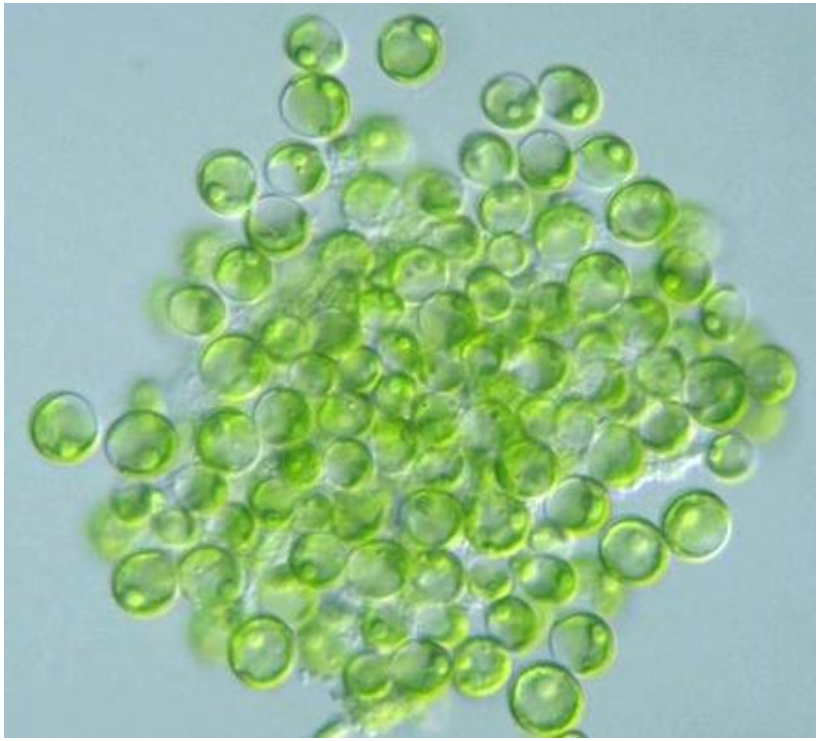
Lichen photobionts

Chlorococcalean (single celled algae)
Coccomyxa, Trebouxia, Myrmecia

24 genera of green algae are lichenized, but *Trebouxia* accounts for >75% of known lichens

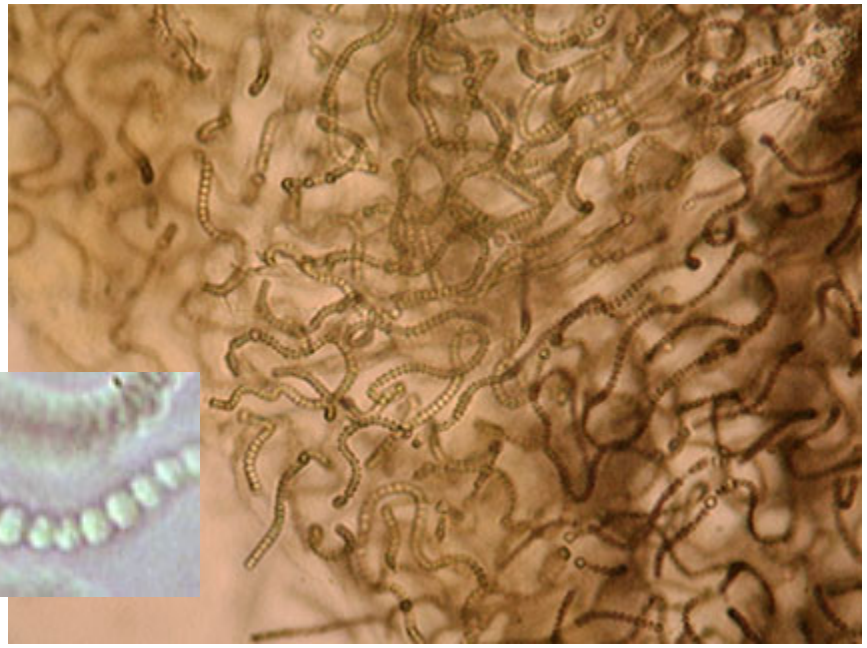
Filamentous algae
Trentepohlia, Phycopeltis
Cyanobacteria
Calothrix, Nostoc, Scytonema, Stigonema
Cyanophycophilous lichens: Approx. 10% of lichens have a cyanobacterium as the only or primary photobiont; most of these belong to *Nostoc*

Secondary compounds produced
lichen acids
polyketide derivatives (depsides and depsidones, anthraquinones and xanthones)
terpenes
pulvinic acid derivatives



Trebouxia

Green alga



Nostoc

Cyanobacteria

Fewer genera/species of algae and cyanobacteria are represented in lichens than fungi

Most belong to genera that have free living species

~25 genera of algae

Cephaleuros, Coccomyxa, Myrmecia, Trentepohlia

*Trebouxi*a is primarily lichen-forming alga, rarely found free-living

15 of cyanobacteria

Calothrix, Gloeocapsa, Nostoc, Scytonema, Stigonema

More than one algal strain or species can be involved in formation of the same lichen thallus (but not different fungi)

Diphycophilous lichens have a primary photobiont green alga and secondary cyanobacterial photobiont in specialized organs (cephalodia)

Cephalodia may also establish independent of the primary photobiont as an distinct lichen (*Lobaria* and *Dendriscocaulon*)

Photobiont/mycobiont interface is wall-to-wall or intracellular haustoria

Many families are exclusively lichenized

Some families (and genera) contain both lichenized and non lichenized members (and lichenicolous spp.)

e.g. *Arthonia, Omphalina* (= *Lichenomphalia*)

Suggests lichenization has been repeatedly acquired and lost

Mycobionts can be cultured independently from spores or thallus fragments, tend to be very slow growing, do not form ascomata

Resynthesis has been accomplished for only a few lichens

Lichen ecology

Habitats

- epiphytes of trees
- bare soil (soil crusts)
- bare rock (saxicolous)
- freshwater streams (Hydrothyria)
- marine intertidal
- endolithic (Antarctica)

Worldwide distribution (terrestrial)

may be dominant autotroph in polar, subpolar, alpine and subalpine habitats

Particularly diverse in temperate rainforests, N and S hemisphere

Long lived, often slow-growing

used to date glacial moraines, used as indicators of air pollution

Poikilohydric and homiohydric organisms

Like homiotherms and poikilotherms for temperature regulation

Lichens are poikiolhydric
- thalli absorb and lose water passively
- precipitation, fog, dew, high RH
- water potential of lichen is lower than that of the atmosphere
- lichens absorb water from non saturated atmosphere
- requires low temperature (<20 C) and high RH (> 75%)

Water content of lichens varies passively with environment
Adapted to cycles of wetting and drying
Polyols protect proteins and membranes from dessication, maintain low water potential so lichen thalli rapidly absorb water from ambient air

Air-dried water content can be as low as 15-30% of oven dry wt.
Fully hydrated can be 200 - >2000%

25% hydration is sufficient to support net photosynthesis

Lichen Secondary metabolites

Comprise 40% or more of the thallus dry weight
> 400 secondary metabolites identified
Metabolites are unique to the association, not produced by either partner when grown alone
produced by fungus
Useful for taxonomy/systematics before DNA sequences

Lichen acids
Unknown bioloical function, defenses against other organisms?
Protect against ROS?

Properties of lichen secondary metabolites

Antibiotics, anti fungal

- Usnic acid in commercial antiseptic creams

Anti tumor

- Usnic acid and various lichen polysaccharides investigated for anti tumor properties

Anti viral

- Some sulfonated deriviatives of lichen poly saccharides inhibit HIV attachment to T lymphocytes

Poisons

- Letharia vulpina, pulvinic acid

Skin irritation “woodcutters eczema”

Perfume

- Evernia prunastri, Pseudevernia furfuracea collected for extraction

Dyes

- traditional dyes, Harris tweeds

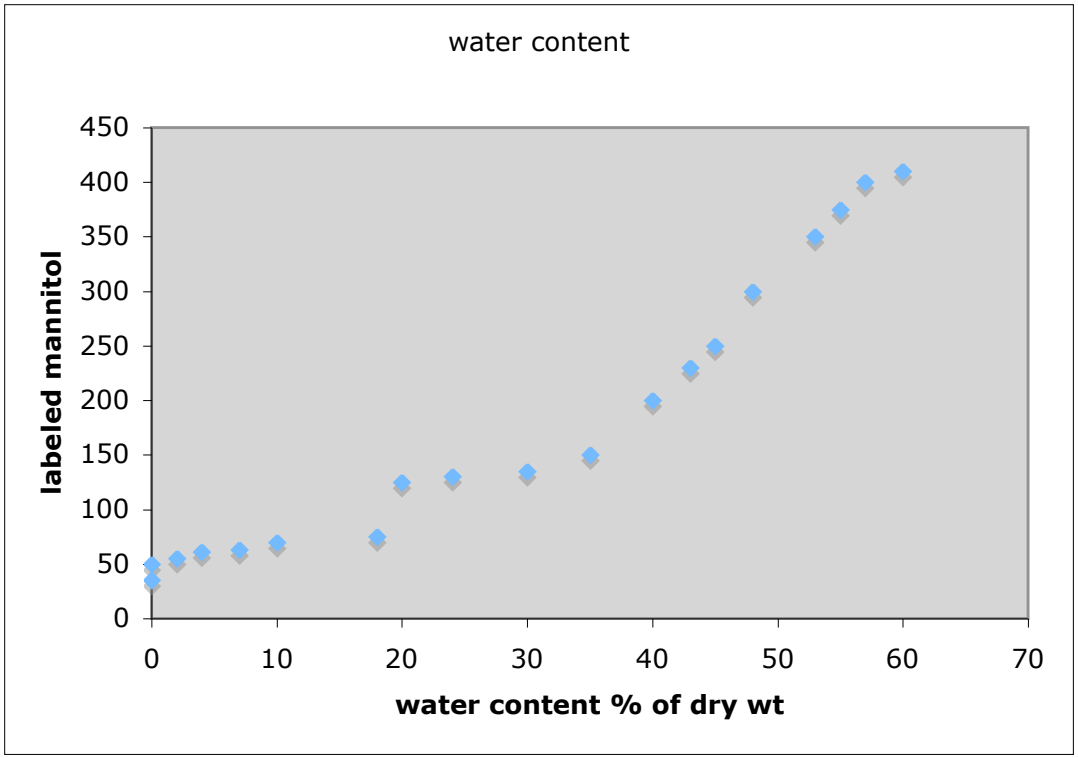
Cycles of hydration - desiccation

Photosynthesis is limited by hydration
More photosynthate retained by photobiont at lower water content

more photosynthate transferred to mycobiont at higher water content

glucose converted to mannitol

alternating wet and dry cycles allow for balanced distribution of fixed carbon between the two symbionts



Temperature

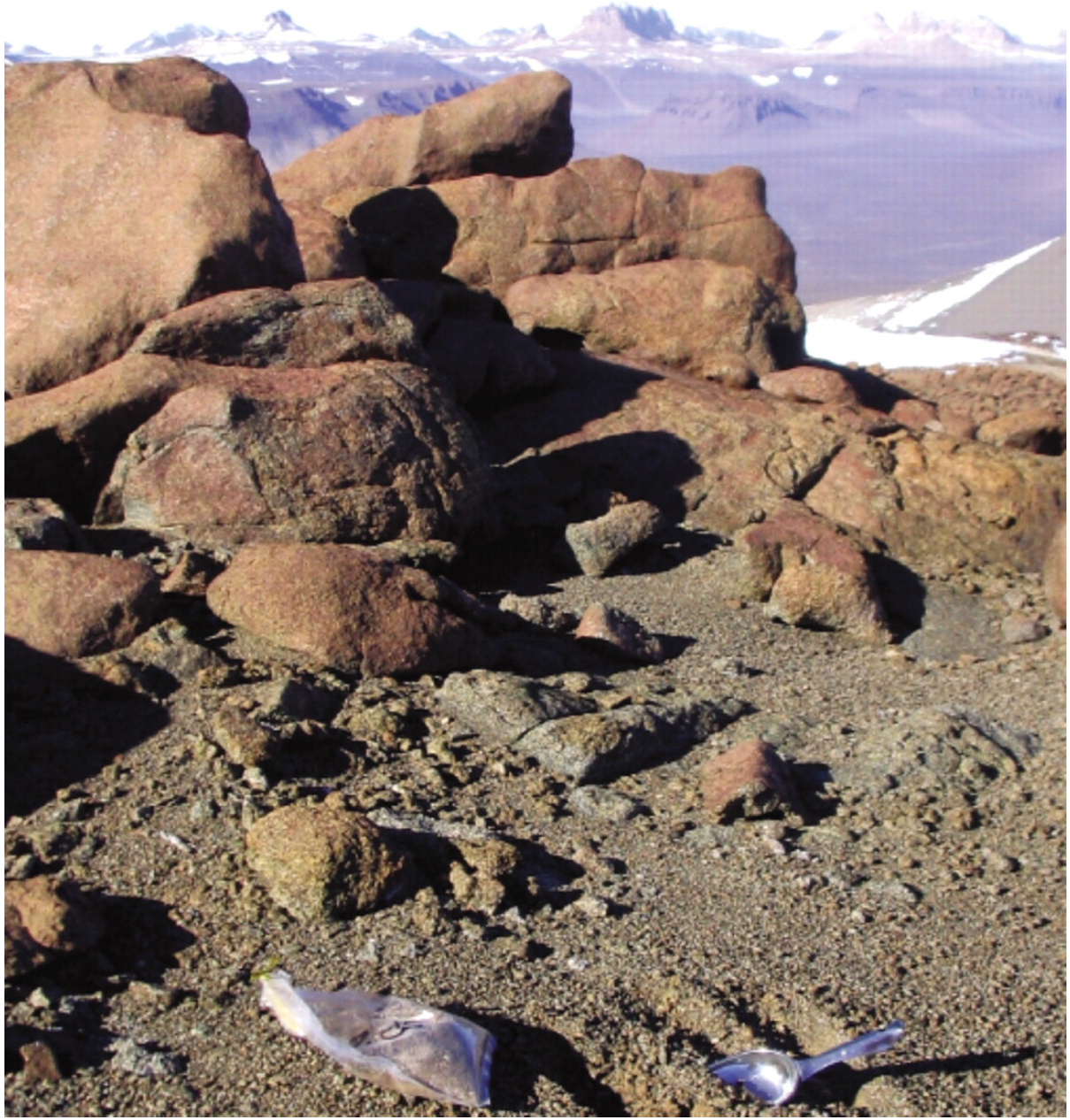
Extremophiles
Lichens are the dominant life form on about 8% of land area
-polar, alpine

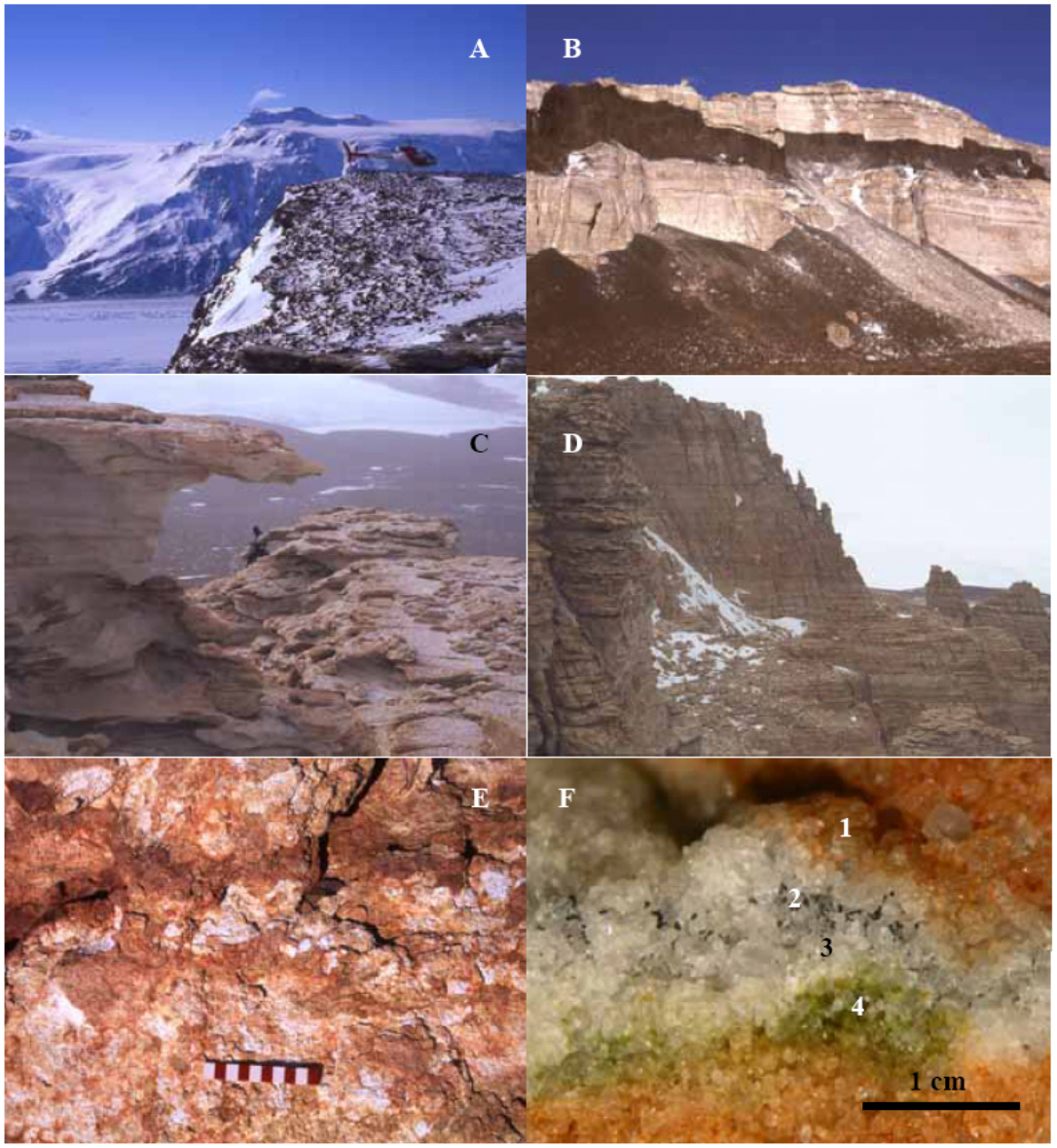
Psychrotolerant/psychrophilic, dominant terrestrial organisms of Antarctica
can survive at temps < - 50 C
grow at temps near 0 C
endolithic lichens in porous rocks
Thermotolerant, grow in deserts where temps > 55C

Grow on exposed substrates
rock sufaces often 20 - 30 C higher than air temp

Heat tolerance depends on hydration, dry lichens tolerate temps > 70 C
Can survive freezing of -196 C and then rehydrate and photosynthesize

High solute concentration, polyols, polyamines prevent ice crystal formation
protect proteins, membranes





Endolithic fungi in Antarctica

Stratified microbial communities in porous sandstone

Fig. 1. Landscapes at sample locations. A. Timber Peak, Northern Victoria Land, Antarctica. B. Layered Beacon sandstone and dolerite in the University Valley, Southern Victoria Land, Antarctica. C, D. Sandstone sculptured by the activity of cryptoendolithic microrganisms in Battleship Promontory. E. Patchwork-like effect of sandstone surface resulting from biogenous weathering. F. Typical stratification in sandstone colonised by lichen dominated community: (1) silicified, reddish brown crust; (2) black zone colonised by lichenised and non-lichenised fungi; (3) white zone colonised by lichenised fungi and lichenised algae; (4) green zone colonised by non-lichenised algae and cyanobacteria.

Nitrogen fixation

About 10% of lichen species have cyanobacteria as primary or secondary photobiont

Cephalodiate lichens (cyanobacteria secondary photobiont in cephalodia)

heterocysts are specialized cells for N fixation
maintain low O_2 content

Higher frequency of heterocysts in the cyanobacteria in cephalodia

Most N_2 fixed by cephalodial photobiont is absorbed by the mycobiont

Lichens may be the major source of fixed N in several terrestrial ecosystems

> 50% for old-growth Douglas-fir

Peltigera membranacea, a diphycophilous lichen
Cyanobacteria in cephalodia

Chimeras

Two “species” with different photobionts and distinct morphology found together in the same composite thallus

Different “photomorphs” result from interactions of one mycobiont and different photobionts

Green alga

cyanobacteria

Peltigera britannica chimera

Thallus organization

Non stratified—photobiont distributed throughout the thallus, not in a specific layer or structure

Stratified—photobiont occurs in a distinct layer

six general forms:

fruticose, foliose, crustose, squamulose, leprose, filamentous

combinations of growth forms occur in e.g. *Cladonia, Stereocaulon* (squamulose/fruitcose)

Fruticose *Cladina* (*Cladonia*)

Fruitcose *Cladia*

Fruticose Cladia

Squamulose

Cladonia

Squamulose/fruticose *Cladonia*

Crustose *Caloplaca*