Lichens, surprising pioneering organisms

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Remarkable pioneers, lichens have conquered the most extreme environments. They are able to grow on the rocks of alpine peaks or those of rocky coasts swept by the spray, on the lava flows barely cooled, hung on the branches of trees in tropical forests but also on the roof tiles of houses or the stones of our old buildings! The lichen flora of our planet represents a great biodiversity with nearly 20000 species. Beyond the diversity of shapes and colours of lichens, their ability to withstand extreme conditions is a constant source of interest for scientists

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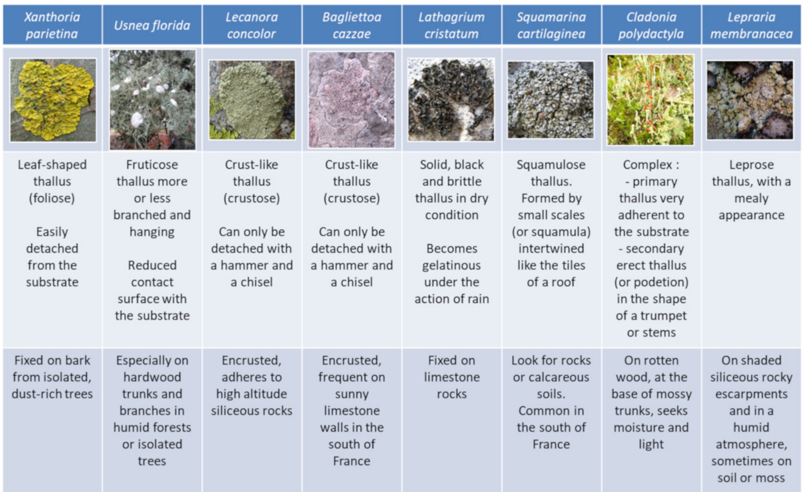
1. Lichens, various shapes and colour palettes in landscapes



Xanthoria parietina	Usnea florida	Lecanora concolor	Bagliettoa cazzae	Lathagrium cristatum	Squamarina cartilaginea	Cladonia polydactyla	Lepraria membranacea
Leaf-shaped thallus (foliose) Easily detached from the substrate	Fruticose thallus more or less branched and hanging Reduced contact surface with the substrate	Crust-like thallus (crustose) Can only be detached with a hammer and a chisel	Crust-like thallus (crustose) Can only be detached with a hammer and a chisel	Solid, black and brittle thallus in dry condition Becomes gelatinous under the action of rain	Squamulose thallus. Formed by small scales (or squamula) intertwined like the tiles of a roof	Complex : - primary thallus very adherent to the substrate - secondary erect thallus (or podetion) in the shape of a trumpet or stems	Leprose thallus, with a mealy appearance
Fixed on bark from isolated, dust-rich trees	Especially on hardwood trunks and branches in humid forests or isolated trees	Encrusted, adheres to high altitude siliceous rocks	Encrusted, frequent on sunny limestone walls in the south of France	Fixed on limestone rocks	Look for rocks or calcareous soils. Common in the south of France	On rotten wood, at the base of mossy trunks, seeks moisture and light	On shaded siliceous rocky escarpments and in a humid atmosphere, sometimes on soil or moss

Figure 1. Main types of lichens through some examples. Name (photo), characteristics of their thallus and their relationship with their substrate. [Source: Photos © J. Asta]

Lichens often go unnoticed, but in environments where they are abundant, such as at high altitudes or along the coast, they attract our attention thanks to the **colours** they are adorned with. All palettes are then found from black to white and all shades of blue, green, yellow, orange or red (Figure 1).

As for the shapes, there is nothing more varied. Unlike higher plants, lichens have **no roots, stems or leaves**. Their vegetative apparatus, called **thallus**, is characterized by a great diversity of shapes and more or less complex aspects, fixed in various way on the most diverse substrates (Figure 1):

Some thalli are **leaf** or flake-shaped, others are more or less **branched** - upright or hanging - and still others are **crust-shaped**, very adherent to the substrate;

Thalli are more or less firmly attached to a wide variety of substrates: **tree** trunks and branches, **rocks** and cliff walls (limestone or siliceous), ancient monuments, **soils**, roadsides, etc.;

Depending on the species, the contact area between lichens and their substrate may cover almost the entire thallus or can be reduced to a single point.

2. Lichen symbiosis: an original combination

2.1. How do symbiosis works in a lichen?

"A lichen is the composite association of a fungus and a photosynthetic symbiont that results in a stable vegetative organism with a specific structure" (definition of a lichen by the *International Association for Lichenology*).

Studies conducted on **pure** symbiont **cultures**, then on the cultures of the two components together to carry out the **synthesis**, provided information on the physiology of the partners and their nutritional exchanges.

Using small filaments acting as roots, called the rhizinae, the fungus fixes the lichen to the substrate. In addition, due to its high biomass, it plays a **protective** role for the photosymbiont. Heterotrophic, the fungus provides the photosymbiont with **water**, **mineral salts** and certain vitamins such as **vitamin C** [1].

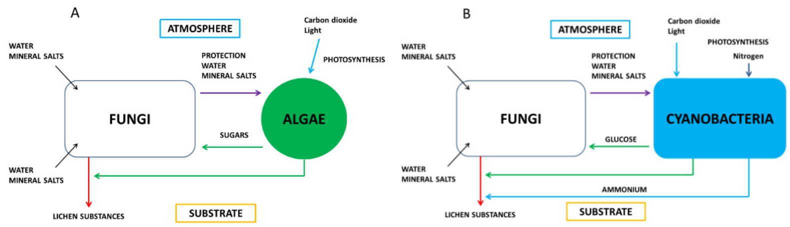


Figure 2. Trophic exchanges within a lichen between fungus and algae (A) and between fungus and cyanobacteria (B), at the interface between a substrate and atmosphere. [Source: © J. Asta]

Photosymbionts*, autotrophic for carbon, carry out photosynthesis and provide fungi with carbon-containing substances. Green algae produce, among other things, **polyols** [2], substances derived from sugars, as well as **vitamin B** (Figure 2A).

In the case of symbioses where algae are replaced by cyanobacteria, the latter form **glucose** (Figure 2B). The fungus transforms polyols and glucose into **mannitol*** and **arabitol***. In addition, cyanobacteria have the ability to fix the **atmospheric nitrogen** (see Plants that live on Air) that is released to the fungus as **ammonium**.

The combination of fungus and algae is very original: the fungus produces a large number of secondary metabolites (**lichen substances** or **lichen acids**), which is not the case with the fungus alone. More than 700 molecules have been discovered. [3] These compounds provide lichens with **various specific properties**: fixation on the substrate, maintenance of water balance, regulation of photosynthesis, protection against light radiation or temperature variations. These secondary metabolites allow lichens to settle on substrates that do not have organic matter (stones, rocks, lava, etc.).

Many applications have been made possible thanks to these many substances: in perfumery [4], in the pharmaceutical and medical field (see Focus Lichens and therapeutic applications), in the manufacture of dyes [5], etc.

2.2. Surprising discoveries

Figure 3. Lobaria pulmonaria [Source: Photo © J. Asta].

More than 800 species of **bacteria** have been found associated with *Lobaria pulmonaria* [6] (Figure 3), a lichen known for its interest in the pharmacopoeia (see Focus Lichens and therapeutic applications). These bacteria participate in many functions [7]: nitrogen, phosphorus and sulphur supply, defence against pathogens, resistance to certain abiotic factors (temperature, hygrometry, etc.), resistance to heavy metals, photosynthesis aid by supplying vitamin B12 to the algae, hormone synthesis (indoleacetic acid) for the growth of algae and fungi, degradation of the ageing parts of the thallus, etc.

The basic symbiotic fungus of a lichen is multicellular. Thus, the discovery of an additional mycosymbiont* consisting of specific **unicellular basidiomycetes*** in many lichen species belonging in particular to the family *Parmeliaceae* made the effect of a bomb in the community of lichenologists [8]. These **unicellular basidiomycetes** would be involved in the development of the structure of the thallus and the production of lichen secondary metabolites.

Lichen symbiosis is therefore not limited to a partnership between two or three components and the thallus can be considered as a true **complex ecosystem** (see Symbiosis and parasitism). Since the partners have constitutive characteristics that their non-symbiotic parents do not show, lichen symbiosis creates **biodiversity**: **systematic** biodiversity (with more than 20,000 species of lichens worldwide), **morphological** biodiversity (by creating new forms that do not exist in the mycosymbiont and photosymbiont as free organisms) and **biochemical** biodiversity (with the synthesis of lichen-specific secondary metabolites).

2.3. Consequences of symbiosis

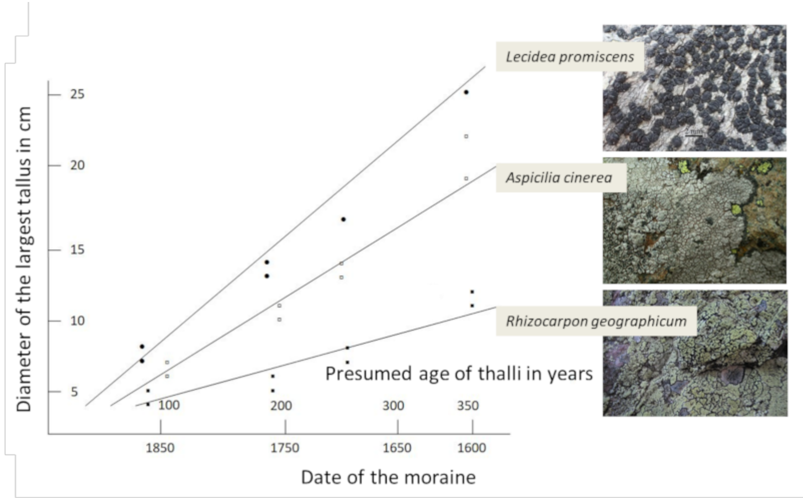


Figure 4. Relationship between the diameter of the thalli and their presumed age, evaluated by the date of the moraines that support them, for three crustose species (from Beschel [10], modified). On the abscissa, the numbers 1600 to 1850 represent the approximate date of establishment of the moraine, the numbers 100 to 350 represent the presumed age of the thallus, in years, deduced from the previous dates; on the ordinate the numbers 5 to 25 represent for each species, the diameter of the largest thallus, in cm. The three lines refer to three species of crust-like lichens. [Sources: Lecidea promiscens & Aspicilia cinerea © J.M. Sussey; Rhizocarpon geographicum © J. Asta].

Symbiosis has remarkable consequences on the lichens' ability to adapt to extreme conditions, their longevity and their particular **growth**. Indeed, lichen growth is generally **very slow**, ranging from 0.1 to 1 mm per year. Crustose lichens grow the slowest [9]

Crust-like lichens, whose thallus can sometimes reach several tens of centimetres, would thus be **centuries old**. The low growth of lichens and their long life span are the basis of **lichenometry**, a method which, based on the knowledge of their growth rate and the measurement of the largest thalli, consists in evaluating the age of the lichens and consequently the age of the substrate [10]. In the case of *Rhizocarpon geographicum*, the measurement of thalli allowed to evaluate the age of glacial moraines on which this species developed at 300-400 years (Figure 4, [10]).

3. Lichens and their ecology

Lichens have colonized almost every environment from sea rocks to the highest altitudes, from arid deserts to high latitude regions. Only on the high seas, in highly polluted areas and on living animal tissues are they lacking. The development of each species requires particular ecological conditions determined by the types of supports, climatic factors and relationships with other living beings.

3.1. Types of substrates and habitats

Figure 5. Lichens can grow on different artificial substrates: wooden fences, metal cisterns, old leather, cement posts, etc. [Source: Photos © J. Asta]

Lichens are more or less dependent on their substrate according to their morphology: very close dependence in the case of crustose lichens, less so for foliiose and fruticose lichens. Lichens are found on trees (**corticolous** lichens), soil (**terricolous** lichens), rocks **(saxicolous** lichens), mosses, old wood, evergreen leaves. Some species even develop as parasites on other lichens. But they can also be found on a wide variety of surface substrates (old walls, wooden or metal fences or posts, railway rails, old leather, plastic, glass, etc., Figure 5).

The substrate conditions the water economy and the installation of the thallus by **mechanical** and **physical factors** (histological structure and bark porosity, rock density and heterogeneity, stability, structure, grain size and soil porosity) and by **chemical factors** (pH and mineral chemical composition or organic substances of the various substrates).

Some species indicate the presence of calcium carbonate (**calcicolous** species) in the substrate. Others are looking for a more acidic substrate, on soil, rock or bark (**acidophilous** species). Some species are indicative of metallic elements and develop only on this type of substrate or tolerate a certain amount of metals in soil or rock. The presence of **iron** on a rock is identified by the **rust-coloured** of the lichen thalli that cover it. The richness in soluble **minerals**, particularly **nitrogen**, is most often linked to the presence of bird droppings and favours the establishment of particular lichens (e.g. *Xanthoria elegans*).

3.2. Influence of climatic factors

The atmosphere is a very important set of factors because it provides some of the water, carbon dioxide and mineral salts used by lichens.

3.2.1. Water

Water plays a crucial role in the ecology of lichens because the degree of hydration of the thallus determines the fundamental functions. Some organisms can move quickly from the state of active life when wet to the state of slowed life when dry and vice-versa (**reviviscence** phenomenon). In the dry state, the water content is estimated at between 15 and 20% of the dry weight, while in the wet state, the content can reach 200 to 350%. Gelatinous thallus lichens, rich in mucilage [11], have the highest water contents (up to 3500% by dry weight). Soaking with liquid water takes less than 1 to 2 minutes, while absorption of steam is slower and sometimes takes several weeks. Conversely, dessication takes place very quickly.

Figure 6. Xanthoria elegans [Source: Photo © J. Asta]

In the dry state, gas exchanges are practically impossible to detect, but as soon as the lichens are moistened, respiration and photosynthesis resume very quickly. Studies carried out at high altitude on *Xanthoria elegans* [12] (Figure 6) have shown that after hydration, respiration resumes in the following second and photosynthesis in the minute. Resumption of respiration is prepared during dehydration by the accumulation of 6-P gluconate and the preservation of nucleotides. The high concentration of polyols (see ref. [2]) in the two symbionts of *Xanthoria elegans* contributes to the protection of cellular constituents and to the preservation of the integrity of intracellular structures during drying. After hydration, 6-P gluconate is immediately metabolized and provides the necessary substrates for respiration. There is also significant photosynthetic activity of the wet thallus of *Xanthoria elegans* at low temperatures, which could help this lichen take advantage of brief hydration opportunities at higher elevations, such as snowmelt, thus promoting its growth in the harsh conditions of high mountain climates.

This explains why, on highly exposed substrates, like on high altitude rocks, photosynthesis only takes place for a few hours in the morning after dew, or after a rain. Due to its high resistance, *Xanthoria elegans* is one of the species that can grow at the highest altitude (it is found at more than 7000 m in the Himalayas).

A number of lichens colonize small stones on the ground or live very close to the ground, on small boulders. They are subjected to very different climatic conditions from those experienced by species on the surfaces of the largest blocks, characterized in particular by greater thermal and water amplitudes and a supply of moisture by morning dew. Some species only settle on overhanging walls and are always **protected from rain**. Conversely, others can withstand flooding for a longer or shorter period of time and develop in **fresh** or **marine water**. Thus, on rocky coasts, the typical layering of lichen vegetation can be observed from the top of the boulders to the algae located at depth (see Biodiversity on rocky coasts: zoning and ecological relationships).

Some lichens support a certain atmospheric salinity and settle in the spray zone. Some maritime lichens on the Chilean coast are covered with a salt crust that plays a hygroscopic role by tripling the rate of water absorption.

3.2.2. Light and temperature

Figure 7. Flavoparmelia soredians [Source: Photo © J. Asta]

Light acts on photosynthesis and the possible excess of photosynthesis over respiration. Some lichens prefer illuminated stations or can tolerate full sunlight. On the other hand, some grow at more shaded stations, for example, under forest cover or, for saxicolous lichens, overhanging rock faces.

Figure 8. Cetraria islandica [Source: Photo © J. Asta]

When dry, lichens are very resistant to **extreme temperatures**. At high altitudes, lichens can withstand long periods of very low or very high temperatures, for example, on the surface of rocks where solar radiation causes temperatures of up to 50°C. The distribution of some species is conditioned by temperature variations over a long period of time: there is currently a northward extension of the lichen range in relation to global warming (e.g. *Flavoparmelia soredians*, Figure 7) (this is a quite general property as seen for birds in **How do birds adapt to a changing climate?**).

Work conducted at altitude was carried out on the **effect of UV radiation** on *Cetraria islandica* (Figure 8) during the summer [13]. The radiation showed no significant effect on photosynthetic pigments and on respiration measured at night. On the other hand, UVBs resulted in a significant decrease in the concentration of 8 out of 12 phenolic compounds. This means that in *Cetraria islandica*, phenolic compounds have considerable resistance to UV rays and explain the ability of this lichen to withstand high altitude radiations.

3.2.3. The action of the wind

It is done in two ways:

an indirect, physiological action, which results in an increase in the rate of dehydration.

a direct, mechanical action, which plays a role in the dissemination of thallus fragments and vegetative propagules.

A very particular example is that of some folicose soil lichens from desert to semi-desert steppes. Their photosynthetic activity can only be done in the wet state when they expose their upper cortex to light. In the dry state, they roll up on themselves. In this form, they are then easily transported and spread by the wind, hence the term "erratic" lichens.

Experiments carried out under conditions simulating those of space (vaccum, high UV radiation) have shown the extreme resistance of spores of different lichen species, particularly those of *Xanthoria elegans*. [14]

3.3. Relations with other living organisms

3.3.1. Relationships between lichens, and between lichens and plants

Figure 9. Lichens on rocks being covered with mosses [Source: Photo © J. Asta]

On the bark or rocks, crustose lichens are generally the first to settle, followed by folose and fruticose lichens. On block tops, it is not uncommon to see that bryophytes and vascular plants then settle - depending on ecological conditions (Figure 9). Soil lichens cannot be maintained in sites where the upper vegetation is too dense. Indeed, due to their small size, they are hindered by the shade and dead leaves of higher plants.

3.3.2. Action of animals and humans

Animals and humans cause the fragmentation of thalli on the ground by trampling and modifying chemically the environment as they enrich it with ammonia, nitrates, etc. Man himself plays a special role:

by creating new substrates (walls, mortars, cement, tiles, quarry size fronts, etc.) where a specific lichen flora can settle;

by disrupting the climate (drying out the atmosphere, increasing ambient temperature, pollution by dust or tar, etc.), but also by removing stations favourable to the establishment of lichens (forests reduction because of clearing, hedges and trees destroyed by the extension of cities, moors, dry grasslands, etc.).

The time required for the recolonization of a slab eroded to the rock by bryophytes and lichen groups can be more than a century. The transplant technique has been successfully implemented, either to replace an already extinct lichen flora (like

Lobaria transplant [15]) or in anticipation of a reconstitution if trees are to be cut down.

4. Lichens, pioneer species?

4.1. How do lichens colonize new substrates?

Through their ability to adapt to living in extreme conditions, lichens can colonize substrates that are low in nutrients and are considered as **true pioneers**.

The dispersal of spores formed by lichen is one of the first steps in colonization (see Focus Lichens: hybrid organisms). Indeed, once mature, the lichen spores are violently ejected outside the asci and fall on the substrate. They germinate by emitting mycelial filaments that branch quickly. For a lichen to recover, the mycelium thus formed must meet an algae partner. Recognition is most often carried out using molecules such as **lectins*** that impregnate the cell walls. A young undifferentiated thallus is then formed, which gradually acquires the adult form and, most of the time, forms reproductive organs.

4.1.1. Rock colonization

Lichens are installed on rocks by mechanical and chemical action:

On **limestone rocks**, oxalic acid from lichens promotes the dissolution of calcium carbonate, which is transform into calcium oxalate by thalli.

On **acidic rocks**, lichen substances physically attack the rock by dissociating minerals.

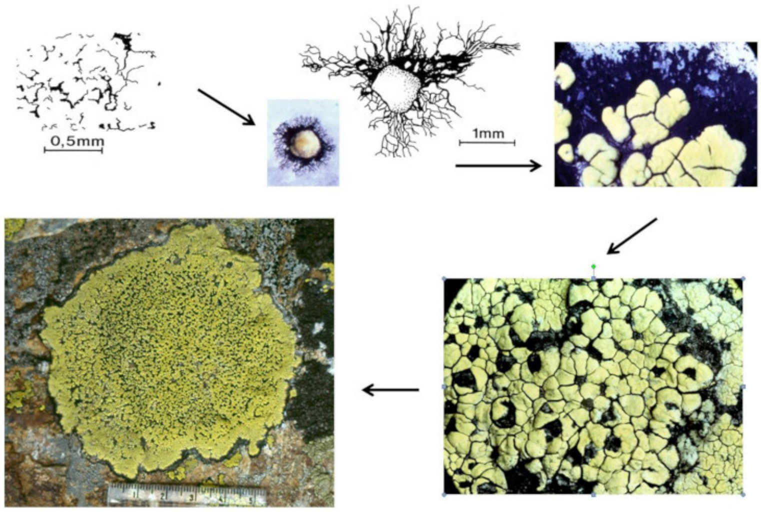


Figure 10. Colonization of quartzite by Rhizocarpon geographicum, crustose lichen. Follow the arrows: germination of the fungus spores, formation of a black hypothalle and the first areola containing the algae, development of other areolaes on the highly developed hypothallus, confluence of the areolaes, sometimes, confluence of the thallium. [Source: Photos J. Asta] from ref. [16].

A study on the action of lichens on **historic monuments** showed that the penetration of mycelial filaments of the lichen thallus into a granitic substrate could reach up to 2 mm. [16] The thalli are then able to truly "digest" the silica and incorporate it.

Lava emitted during eruptions is quickly colonized by lichens. Let us mention *Stereocaulon vesuvianum*, a species with green algae and cyanobacteria, whose first location was found on the volcanic deposits of Vesuvius, *Dyctionema pavonia*, which develops for example on the flank of the Soufrière volcano in Guadeloupe.

Work carried out on **quartzite*** colonization in alpine environments has made it possible to understand the colonization strategy of *Rhizocarpon geographicum* (Figure 10) [17]. The crustose thallus of this species consists of compartments containing fungi and algae (or **areolae**). The fungus spores germinate by forming a black mycelium **(hypothallus)** that grows radially and on which an initial areolae is formed. Other areolae appear on the hypothallus and confluent. The first formed thalli can in turn confluence and give rise to whole thalli that can reach sizes of 15 cm in diameter [16].

4.1.2. Soil colonization

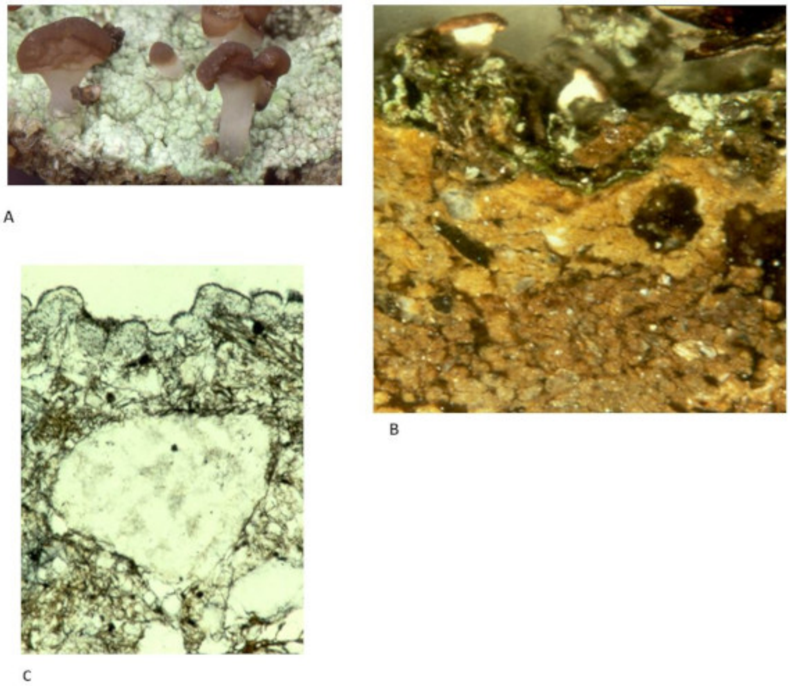


Figure 11. Soil colonization by Baeomyces rufus. A: Overview of the lichen showing the thallus and brown apothecia (small mushroom-shaped structures). B: Overview of a complete sequence of a sample of Baeomyces rufus colonizing a mainly mineral substrate (thick section). C: Cut of the lichen-sol complex (thin cut): the Baeomyces thallus follows the irregularities of the substrate and has small curved scales. There are many mycelial (black) filaments that penetrate between the minerals in the soil. [Source: Photo © J. Asta]. According to ref.[18].

Lichen species such as *Baeomyces*, *Cladonia*, are true pioneers on soil.

Observations conducted in the mountains showed that slopes initially bare for the construction of a ski slope were colonized by two organisms: a lichen, *Baeomyces rufus* and a moss, *Pogonatum urnigerum*. *Baeomyces,* begins to develop on the surface of the bare substrate and forms a very important mycelial felting that plays a role in stabilizing the surface soil (Figure 11) [18]. The *Pogonatum* moss has a different strategy and develops more deeply than the lichen. A real lichen-moss complex is created which favour the formation of a more elaborate soil [18].

In *Cladonia,* the basal part of the podetions* lyses, letting out mycelial filaments that gradually incorporate themselves into the earthy particles. A real lichen-soil complex is then formed, which is most often enriched with bacterial colonies and which, as in the previous case, will encourage subsequent colonization by higher plants. [19]

In some parts of the world, lichens constitute a significant part of ecosystems. While the global ratio between lichenic and phanerogamic flora* averages 0.1 to 1, it can exceed 100 in the Arctic regions. In these tundra areas or in northern temperate forests, several varieties of lichens - particularly reindeer lichen, *Cladonia rangiferina* - are a popular food for many wildlife (caribou - or reindeer-, moose, mouflon, etc.) and occasionally for some domestic animals (see Focus Lichen-animals interactions).

Figure 12. Biological crust on the soil of the Natural Bridges National Monument, Utah (USA). [Source photo: Nihonjoe (CC BY-SA 3.0)]

In arid and semi-arid areas, soil lichens contribute to the formation of "**biological crusts**" that colonize desert soils (Figure 12). The various organisms that make up them (lichens, cyanobacteria, fungi, bryophytes and algae) live in intimate association in the upper millimetres of the soil surface. These crusts represent an area of about 50 million km^2, the equivalent of 5 times the surface area of Europe. They play a fundamental role in the protection and fertilization of soils, the fight against erosion and desertification. It is estimated that they alone fix 7% of carbon dioxide, a value that corresponds to that emitted annually by the combustion of fossil fuels by humans on Earth. [20]

4.2. The origin of lichens and the colonization of land

Like many other living disciplines, lichenology is confronted with the question of origins. About fifty years ago, it was still thought that the first definite remains of lichens, found in Rhineland lignites and Baltic amber, dated only to the tertiary era. Thus, one of the first fossilized lichens, *Anzia electra*, found in Baltic amber from Germany (Tertiary, Lower Miocene, 20 Ma) already shows a small foliated thallus with narrow lobes, a spongy layer, a two-layer medulla and rhizinae.

It is certain that the lichens did not constitute themselves from the outset but underwent an evolution of which we are only beginning to know a few stages. [21]

Among the lichen constituents, **cyanobacteria*** appeared **3800 Ma** in the first traces of terrestrial life (stromatolites) found in Australia in particular. At the origin of the chloroplasts of eukaryotic cells following an endosymbiosis (see Symbiosis and evolution: at the origin of the eukaryotic cell) they allowed plants to carry out photosynthesis.

Fungi, on the other hand, are difficult to fossilize, and the first real fungus appear in the **Precambrian**. Fossils already showing a possible association between a fungus and an algae have been discovered in the Precambrian of South Africa (from -2700 to -2300 Ma). Subsequently, fungi have transformed parallel to the plant world and symbiotic associations (mycorrhizae, lichens) are the result of a long evolution of interactions with photosynthetic organisms.

Ancient traces of lichens have been found in the fossiliferous formation of Dushanto (China, Guizhou Province) dating from the early **Ediacaran** period (635-551 Ma). These exceptionally preserved microfossils show thin filaments associated with cells that have been interpreted as cyanobacteria or green algae similar to current organisms. A probably lichenized fungus, *Cosmochlaina*, discovered in England in the Middle Ordovician (460 Ma) shows an intact cortex and a second cortical layer in electron microscopy. But the photosymbiont was not found. [22]

Two Lower Devonian fossils found in England, *Cyanolichenomycitis devonicus* and *Chlorolichenomycitis salopensis,* are considered the **first true lichens** to be found due to their structural similarity to existing lichens. Indeed, the first fossil shows a heteromeric thallus with a thick cortex on the surface and a medulla filled with cyanobacteria colonies resembling the current Nostocs. These fossils are interpreted as lichens belonging to the *Pezizomycotina*, with an anatomical structure similar to that of current *Lecanoromycetes*. [23]

The lichen symbiosis is probably much older than the proven lichen samples. The discoveries are hampered by the fact that the lichen components are difficult to fossilize and the samples found are often of poor quality. However, it is to be hoped that current investigation methods (dating, molecular biology, etc.) that continue to be improved will provide valuable information for future fossil lichen discoveries.

It seems highly probable that the colonization of the surface of rocks or soil by various types of microorganisms and lichens in appropriate climatic zones was one of the first steps in the conquest of land by living organisms during the Devonian (see The First Terrestrial Ecosystems). The current existence of biological crust gives an idea of some of the primitive forms of this colonization, but many others have been possible. Currently, existing terrestrial vegetation areas in the most extreme ecosystems (Arctic, Antarctic, Alpine, desert and steppe) are dominated by lichens wherever there is little or no competitive pressure from higher plants due to harsh environmental conditions. When they appeared, the higher plants were then able to settle on rocks and sediments partly altered by the activity of microorganisms and lichens. They then participated themselves in the formation of a soil, on which they were able to root and develop and which they feed with their own organic debris.

5. Messages to remember

Lichens grow in all environments except the high seas, on the tissues of live animals and in highly polluted areas.

Lichen symbiosis is more complex than previously thought: the structure of the thallus shows not only the presence of two basic partners (a fungus + a green algae and/or a cyanobacterium) but also that of many bacteria and a unicellular fungus recently discovered.

Lichens are reviviscent: after desiccation, they are able to return to active living as soon as they are rehydrated.

In the presence of algae only, the fungus produces lichen substances that facilitate the fixation of lichen on the substrate and help to protect it.

Lichens grow very slowly and some lichens can live for several centuries.

Lichens are pioneers: they have the ability to settle on substrates that are very low in nutrients and can withstand extreme temperature and light conditions.

The first known lichens date back to the Devonian.

Notes and references

Cover image. Rock covered with *Xanthoria elegans* (foreground) in the Lautaret alpine garden; the Meije (3 984 m) is in the background [Source: Photo © J. Joyard & M. Neuburger].

[1] Sometimes, the fungus can behave as a saprophyte by pulling organic substances from the environment or live as a parasite on another lichen.

[2] Present throughout the plant world, fungi, lichens and many algae, polyols are derived from oses. About 30% of primary carbon production on earth is through the synthesis of polyols in plants and algae. In plants, polyols are involved in tolerance to abiotic and biotic stresses and are a form of transport and storage of carbon skeletons.

[3] Some of these lichen metabolites are toxic. For example, in *Letharia vulpina* - an altitude cortex species recognizable by its mustard-yellow colour and growing mainly on larch and cembro pine - the vulpinic acid present gives lichen its toxicity. *Letharia vulpina* was once used as a mixture with bait to make wolves and foxes disappear. However, it should be noted that the effects were reinforced by the introduction of crushed glass into the bait.

[4] Lichens, already known as perfume fixatives since the Middle Ages, are still widely used in perfumery today. Two corticulose species, *Pseudevernia furfuracea*, *Evernia prunastri* (incorrectly called "oak moss"), which owe their fixing properties to their high atranorin content, are harvested in large quantities, mainly in Central Europe and imported into Grasse (France). Local perfumeries extract a concentrate called "absolute oak moss" which is used to make many perfumes. Each year, 6,000 to 8,000 tons of lichens are harvested in southern France, Morocco and other countries. These intensive removals threaten the survival of the species. Ideally, they should be replaced by synthetic products, but so far no one has been able to reproduce their complex biochemical nature.

[5] Since ancient times, various dyes have been extracted from lichens, such as the orseilles from the *Roccella*, which give red hues. Other lichens give brown to red tones *(Umbilicaria pustulata*), yellow tones *(Letharia vulpina*, *Flavoparmelia caperata),*

orange yellow to pink tones *(Xanthoria parietina*...), green (various *Cladonia*)... Remember that the "sunflower" liqueur which turns red or blue according to the acidity or basicity of the solution to be tested is extracted from different lichens *(Roccella, Dendrographa*...). Despite the use of chemical dyes, some Irish tweeds are still coloured with lichens.

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[7] This great diversity of bacteria associated with lichens and their essential functions in lichen symbiosis suggests that the concept of microbiota (a term that refers to all bacteria living in and with living organisms) can very logically be extended to lichens.

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