The development of plant life on land during Silurian and Devonian Periods (443-354 MY)

Jarðsaga 1
-Saga Lífs og Lands -
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Outline of the Silurian climate
Silurian development of life

- Land plants evolved in the moist regions near the Equator, and the earliest vascular plants occur in early-mid Silurian strata.
- A wide and rapid spread of jawless fish, but also the appearances of both the first known freshwater fish as well as the first fish with jaws
- The Silurian strata has fossils that are substantive evidence of life on land, particularly the arthropod groups.
- In the oceans, coral reefs made first appeared and expanded; there was a widespread radiation of crinoids and a continuation of the expansion of the brachiopods.
The Devonian configuration of Continents

Early Devonian  390 Ma
The Devonian climate

Generally dry conditions prevailed across much of North America, Siberia, China and Australia during the early Devonian. South America and Africa were covered by cool, temperate seas.
Late Devonian Climate

During the Late Devonian Pangea began to assemble. Thick coals formed for the first time in the tropical rainforests in the Canadian Arctic and in southern China. Glaciers covered parts of the Amazon Basin, which was located close to the South Pole.
Devonian development of Life

The Devonian was a time of great transition.

• On land, trees and forests appear for the first time. Very rapid development of plants and soils

• In the sea, ammonoids and fish evolve and quickly diversify. Major growth of reefs.

• The first insects, spiders, and tetrapods evolve.
When did land plants first develop?

- Maybe land plants first developed, as lichens, already during the Cambrian, prior to 500 MY. The clue to this might be the drop in atmospheric CO$_2$ observed after that time:
  - The pioneer lichens might have produced acids strong enough to dissolve rocks. When washed away by rainwater, the calcium released from the lichen-encrusted rocks eventually forms calcium carbonate limestone.
  - Land plants contain carbon that does not readily decompose. After the plant dies, some of its carbon remains locked up and can become buried in sediments/soils preventing those carbon atoms from returning to the atmosphere.
Problems needed to overcome for land plants

The basic requirements for the existence of large multicellular plants on land are very different from those in water:

• Air is much less dense than the tissues of a plant, so terrestrial plants need to develop a rigid stalk or stem to stand upright.

• A tall plant needs to be anchored by a root system or buried stem, which also serves the function of collecting water and nutrients from the soils.
Problems for land plants

• To achieve rigidity and to collect nutrients, the first plants first had to develop vascular tissue.

• The risk of desiccation - the plants would have to develop strategies to prevent drying out. Also, they shift from salt water to fresh water environment.

• To colonise new terrestrial habitats spores would have to be released in air not water

The prevailing hypothesis is that during the Late Ordovician-Silurian, 500-425 MY ago freshwater, green algae invaded the land.
The importance of plant colonization of land

The conquest of land by multicellular plants was of enormous importance for the further development of life. Without the plants no animals would ever have been able to survive on land. First food, then grazers...
Cooksonia sp

The earliest vascular land plants ("háplöntur") appeared about 425 MY ago in the Early-Mid Silurian. This form, *Cooksonia*, looked very simple: a stem which bifurcated a couple of times topped with small spheres in which the spores were formed.

No leaves, no flowers, no seeds. Roots? Probably horizontal growing stems, connected with the soil by root hairs, took the function of roots.

The plants were only a few cm high. For millions of years it was mainly this kind of plants that grew on land.
The first land plants

Cooksonia sp.
The enigmatic plant *Parka decipiens*

The *Parka decipiens* is a primitive sporangia (*gróplanta*) of Lower Devonian age. It is not well understood and the systematic place is uncertain.

Extremely large specimen of *Parka decipiens*. Lower Devonian, Scotland. Diameter 7,5 cm

*Parka decipiens* with irregular form. Diameter 1,9 cm

The chemical composition indicates a relationship with green algae. Maybe *Parka* belonged to a group of enigmatic plants, which tried to colonize the still barren land.
The *Baragwanathia* of Australia

The Cooksonian plants were only a few cm high. The late Silurian *Baragwanathia* of Australia is a much more robust plant consisting of up to 30 cm long axes with spirally arranged leaves. It is considered to be an early lycopod (*jafni*). Why Silurian plants in Australia seem more developed than elsewhere is a mystery. It has been used to suggest that land plants may be much older than Silur-Ordovician.
A visit to Rhynie

Rhynie in the Grampian Region of Scotland has become famous as one of the most important paleobotanical localities in the world.

In 1912 the Scottish geologist William Mackie discovered an occurrence of Lower Devonian plant-bearing cherts near this small village. Recent radiometric datings of these rocks give an age of 396 ± 12 million years.

http://www.uni-muenster.de/GeoPalaeontologie/Palaeo/Palbot/erhynie.html
The occurrence of the Rhynie cherts is related to volcanic activity related to the Taconic-Acadian orogeny, and they have been formed as hot spring deposits. Several different types of chert \((\text{SiO}_2)\) can be recognised, varying from vuggy, sinter-like cherts, often with upright standing plant axes to more massive chert types formed during flooding events with silica-rich waters. Similar deposits are nowadays being formed around hot springs, e.g., in Iceland (Geysir area) and Yellowstone National Park.
Preservation of Rhynie plants

Plants are known in various modes of preservation, often truly excellent. The silicification process must have occurred very quickly, within a few days or even much less, because even very delicate plant structures and also very short-lived life and developmental stages have been preserved, like germinating spores. The higher land plants often show many details of their anatomy. In several cases whole life cycles can be studied.
Rhynie fossil flora

In addition to vascular plants, many fungi, algae and even the earliest well documented lichens have been described from the Rhynie Chert.

Lichens are example of a symbiosis of a fungus and algae or cyanobacteria. Also other examples of interactions between fungi, land plants and animals, e.g. parasitism have been documented from the Rhynie Chert.
The Rhynie plants

The vascular land plants were 10 to 40 cm high.

• Except for one species, all higher land plants were leafless and all had bifurcating aerial axes with terminally and/or laterally attached sporangia.

• All species had clonal growth which means that aerial axes (daughter plants) developed from the rhizomatic axes of the mother plant.

*Aglaophyton major*, one of the most common plants in the Rhynie Chert
The Rhynie plants...

- Each species had its characteristic growth form, which indicates that each was well adapted to a specific habitat.
- Some species had long-living aerial axes whereas others had seasonal aerial axes.
- Two species lived entirely subaerial, two had a subterranean rhizome, whereas ones species had roots which penetrated the soil. Adaptations of these early land plants to the substrate and the available groundwater were apparently still limited.
Asteroxylon

*Asteroxylon mackiei*, up to 40 cm high, and one of the earliest lycopods (*jafnar*). Is the only plant from the Rhynie Chert which had already small leaf-like structures. It had root-like organs which could reach up to 20 cm deep. The development of leaves considerably increased the photosynthetic surface. The plant was probably better able to regulate humidity by keeping dew drops between the leaves. *Asteroxylon* perhaps was better able to regulate its water household than the other Rhynie Chert plants.
Fungi and non-vascular plants

Apart from vascular plants, many other organisms have been documented from the Rhynie Chert.

A spore of *Aglaophyton* infected by fungi

Mycoparasitism, a fungal parasite on another fungus living in *Horneophyton*

Another remarkable form is *Winfrenatia*, the oldest lichen, being a symbiosis between a fungus and a cyanobacteria.
Faunal remains

The Rhynie Chert is not only famous for the well preserved plant remains but also as the locality that has yielded remains of one of the earliest land faunas. The colonization of land by plants and animals took place almost simultaneously.

Plant-animal interactions are primarily documented by many different types of coprolites (forntað) which show an enormous variation in their shape and composition. These demonstrate that at least some types of animals primarily fed on dead plant material. This indicates that in early terrestrial ecosystems also animals played an important role in the recycling of organic matter and the formation of soils. Some plant axes show wound and wound repair tissue, suggesting that animals also consumed living plant material.
Fossil faunal remains

A trigonotarbid (spider) showing the body, several legs and the mouth parts

The oldest known mite (áttfætlumaur)

Í dag eru bekktar rúmlega 75.000 tegundir af áttfætlum og er fjölda nýrra tegunda lýst árlega, jafnvel um 1.000 tegundir á hverju ári. Langflestar tegundir áttfætlina eru innan ættbálks köngulóa eða um 35.000 tegundir, en til áttfætlumaura teljast um 30.000 tegundir. Margir fræðimenn telja að heildarfjöldi tegunda áttfætlina sé nálægt einni milljón. (af Vísindavef HÍ: http://visindavefur.hi.is/svar.asp?id=3210)
Rhynie ranks among the world's most important fossil plants localities because it is the oldest locality with a completely preserved flora.

- Plants are anatomically preserved, including many life stages and growth forms. Because of the excellent preservation the Rhynie Chert is one of the very few fossil ecosystems that is known in such detail.

- Interactions between different life forms, symbiosis, parasitism and feeding can be reconstructed.
Mosses – an innovative solution to the problems of living on land...

The mosses found their own solutions to surviving on land, which places them between algae and vascular plants: They do not have roots for taking up water and nutrients, and they do not have vascular tissue. Therefore, they are dependant on humid environments in the same way as the algae. They resist drying out by slowing metabolism.

_Polytricum moss_

Since mosses lack vascular tissue, they cannot grow in height. The oldest macro-fossils of mosses are from the Silurian.
Artistic impression of Early Devonian landscape
Remarkably rapid Silurian-Devonian evolution
In order to grow big, strong roots are needed to defy gravity and winds.
Red Hill: a well known Late Devonian fossil site

The sediments at Red Hill, Pennsylvania, are alluvial mudstones, deposited in a wide, meandering, lowland river. The sediments belong to the Catskill Delta, a complex of Middle to Late Devonian alluvial, deltaic and marine deposits produced by the erosion of the Acadian Orogeny.

Numerous plant and animal fossils found in the Red Hill sediments
Within 50 MY of first appearance, plants had evolved to trees

Some Late Paleozoic lycopods (*jafnar*) grew to tree-like proportions, and during Late Devonian large trees with strong, woody stems for the first time occurred.

The Archaeopteris

- From its first appearance in Late Devonian *Archaeopteris* quickly became a dominant flora component, and formed the first true forests.

- *Archaeopteris* remained dominant until the end of the Devonian, at which time it mysteriously became extinct.
Archaeopteris was the first tree, with trunk diameters of >1 m, and it stood up to 30 m high. The success can be attributed to several evolutionary innovations:

- It grew in much the same way as do modern trees, with lateral buds in its trunk and branches, and became a truly perennial plant. Some individuals apparently lived for at least 40-50 years.
- It developed a massive root system that would have been useful for structural support and the uptake of nutrients and water; root system depths in excess of 1 m have been reported for this tree.
- It developed broad leaves, that improved sunlight capture. As a perennial plant it probably shed its leaves in autumn to hinder drying out in winter.
The ferns (*burknar*) start developing in Late Devonian...

Modern ferns are spore-producing plants common in a wide range of tropical to temperate environments. Most grow as small to medium-sized bushes, but some are trees while others are aquatic. With approximately 12,000 living species they are second in diversity only to the flowering plants (angiosperms).

*Rhacophyton ceratagium* was an early fern, a tall shrub with a central main stem 1-1.5 m in height.
...and so do the sphenophytes ("elftingar")

The sphenophytes, another group of sporangias, appeared in the Late Devonian, diversified rapidly and expanded during the Carboniferous. Were important during the Mesozoic, but are a small group of plants today (~30 living species).
Calamites, a Devonian sphenophyte
The seed plants arrive in the Late Devonian

Today, the seed plants are some of the most important organisms on earth. Life on land as we know it is shaped largely by the activities of seed plants. This large and important group appeared early in the evolution of vascular plants, and throughout the Late Paleozoic shared dominance of the land flora with ferns, lycophytes, and sphenopsids. Since the beginning of the Mesozoic, however, most trees and forests have consisted of seed plants.

*Archaeosperma arnoldii*
The development of the seed: A step in the liberation from the aquatic environment

- All spore plants have a complex reproductive cycle (Stanley, fig. 3-22). A sperm of a spore plant needs moisture to reach the egg; that restricts them to habitats that are damp at least for part of the year.
- Since fertilization is an internal process in seed plants, environmental moisture is not necessary. The seed is released as a durable structure that can sprout into a plant when conditions become favorable.

By the end of the Devonian, a variety of early seed plants arrived. These include *Sphenopteris* a plant with fern-like leaves, but which bore seeds.
The first seed plants were seed ferns (*fraeburknar*), a rather heterogeneous, completely extinct group which was, however, very successful in the late Palaeozoic.
Overview of plants emerging in Devonian times
A Late Devonian Forest

A Late Devonian forest would have been a very different environment from present-day forests: dominated by ferns, lycopods and sphenophytes; very quiet...
Devonian life on land – first amphibians and wingless insects
Origin of insects and millipeds

The history of the insects is closely connected to the evolution of plants. Insects and millipeds have many similarities in the way they are built:

• They breathe with tubes that bring the oxygen into the body from breathing holes in the skin
• They have an outer skeleton of chitin that never calcifies
• The head consists of four segments that have grown together (fused)
• The head has antennae and jaws

The insects probably developed from millipeds early in the Devonian, about 380 million years ago. The oldest and most primitive insect belong to the group Apterygota - vængleysingjar, and lack wings.
Devonian insects

Fossil evidence of Devonian detrivorous invertebrates is extremely sparse, but investigations of several Silurian-Devonian sites suggest there a variety of detritivores were already well established by the Late Devonian. These include millipedes (*púsunðfætlur*) and springtails (*stökkskottur*). A variety of invertebrate predators have also been found in Late Silurian and Devonian deposits. Scorpions, trigonotarbids (extinct, spider-like), spiders and centipedes (*margfætlur*) have been found.
Development of millipedes

The fossil record of millipedes dates back to at least the Early Devonian of Scotland and possibly as early as the Late Silurian (also in Scotland). The earliest North American record for millipedes comes from the Middle Devonian of eastern Canada.

Millipedes belong to a group of myriapod arthropods called the Diplopoda (=double feet); the name comes from the presence of two pairs of feet per body segment. They typically inhabit damp terrestrial habitats.
References, useful web sites

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