

The Tetrapods Transition to Land

The Old Order (or, "Fish Out Of Water")

Fossils of Carboniferous amphibians were relatively well known by the turn of the century, as were their probable piscine (fish-like) ancestors, the Devonian lobe-finned fishes.

But there was a sizable anatomical gap between the two, and the transition between fish and tetrapod was frustratingly obscure.

Crossopterygians – Lobe Finned Fishes

Crossopterygians first arose in the Lower Devonian (360-408 mya) and became the dominant freshwater predators during the Late Paleozoic.

They diversified during the Middle Devonian into several major groups, of which only one group, the Actinistia (coelacanth) survived the great Permian (245-286 mya) extinction.

The fossil record of the coelacanth extends into the Cretaceous, but a modern survivor, *Latimeria chalumnae*, was discovered in 1938.

Crossopterygians together with the lungfishes (Dipnoi) form a group of bony fishes called the Sarcopterygii or lobe-finned fishes.

Note: **Lungfishes** first appeared about 400 million years ago and quickly underwent a period of rapid evolution during the Devonian often referred to as the "dipnoan renaissance."

The classification of and interrelationships within the Sarcopterygii are matters of much debate.

The traditional classification places the Crossopterygians and lungfishes into two separate subclasses (Crossopterygii and Dipnoi), but some members of the Crossopterygii appear to be more closely related to lungfishes than to other crossopterygians.

One conspicuous feature of Late Devonian geology was the prevalence of red sediments in Europe and North America

In 1916, Joseph Barrell argued that these oxidized sediments were evidence of a harsh landscape subject to severe droughts.

He also argued that this severe climate was a major driving force in the evolution of air-breathing vertebrates, including tetrapods.

Elaborations on the idea that Devonian droughts were the driving force for the evolution of tetrapods culminated in 1950s with a scenario proposed by Alfred Sherwood Romer - tetrapods evolved from crossopterygian lobe-finned fishes driven onto the land by drought.

As one pool or stream dried out, the fishes ventured onto land in search of other bodies of water.

Over time, natural selection would, over time, favor those fishes with more efficient terrestrial locomotion (i.e., with more leg-like limbs).

In other words, tetrapods evolved from fish out of water.

Ichthyostega

Preliminary reports on the anatomy of **Ichthyostega** during the 1950s reinforced Romer's hypothesis

This Late Devonian tetrapod apparently had well-developed limbs similar to those of some Carboniferous amphibians, but it also had a fish-like tail.

It was seen as a fully terrestrial tetrapod, but one almost certainly dependent on water for its aquatic young.

Although it was originally considered to be the transitional form between fishes and Carboniferous amphibians, its skull possesses several Primitive, fish-like features, whereas those of other early tetrapods (i.e., *Acanthostega* and *Ventastega*) were generally more derived.

Skeletal differences between *Acanthostega* and *Ichthyostega* suggest they had rather different life habits.

While *Acanthostega* was probably exclusively aquatic, *Ichthyostega* may have hauled itself onto the shore.

The forelegs may have been weight-bearing, but the forearms were unable to extend fully.

Clack has speculated that *Ichthyostega* hauled itself onto land by moving its forelegs in parallel while dragging its hindquarters.

The New Findings (or, "Fishes With Legs")

Until the 1980s, the fossil record of early tetrapods was essentially limited to *Ichthyostega*, a Late Devonian tetrapod from eastern Greenland.

But the early tetrapod record has expanded dramatically since 1987.

These enhanced records, together with findings from other scientific disciplines has engendered a new understanding of how tetrapods evolved.

Instead of fish escaping drought, the first tetrapods are now seen as fishes with legs.

Perhaps the most important findings to alter our understanding of tetrapods evolution followed the discovery and analysis of ***Acanthostega*** in the late 1980s and early 1990s. A skull roof of this tetrapod was first discovered by Gunar Save-Soederberg and Erik Jarvik in 1933, but the significance of this animal was not realized until after additional material was recovered by Jenny Clack in 1987.

Together with Michael Coates, Clack realized that this animal was clearly a tetrapod, but one that was not well adapted to land.

Its legs were ill-suited to support its weight and the wrists were absent.

Yet, it had well developed digits (fingers and toes).

Surprisingly, the forelimbs possessed eight digits rather than the anticipated five digits, while the hindlimbs possessed seven.

Additional features from the spine, ribs, pelvis and tail corroborated the notion that Acanthostega would not be able to support itself on land.

It also possessed internal fish-like gills. (in addition to its lungs.)

Acanthostega, with its four limbs, pelvic girdle and assorted other features, was clearly a tetrapod, but its lineage probably never left the water.

The unexpected characteristics of Acanthostega have led to reinterpretations of Ichthyostega by Per Ahlberg, Jennifer Clack and Michael Coates.

They found an animal that was less adept to life on land than the one depicted by Erik Jarvik, but they also found one that was probably less aquatic than Acanthostega.

Ichthyostega's forelimbs were more robust than those of Acanthostega and were probably able to lift the front half of the body.

However, its hindlimbs were relatively small and probably functioned more like paddles than legs.

Like Acanthostega, it had seven digits on its hindlimbs, but it lacked evidence of internal fish-like gills.

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Information from other Fossils

The shoulders of Tulerpeton and Hynerpeton suggest that these two tetrapods were more adept on land than Ichthyostega.

On the other hand, Elginerpeton and Obruchevichthys were probably more fish-like than Acanthostega.

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In addition to the new findings on Late Devonian tetrapods, paleontologists have also learned more about their closest fishy relatives, Panderichthys and Elpistostege.

These Early Frasnian fishes share a variety of features with the early tetrapods.

In fact, the fossil skull of one species, Elpistostege, was originally classified as a tetrapod.

But they differ from early tetrapods in several crucial ways, including the possession of fins rather than feet.

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The span between the Panderichthys and Late Famennian tetrapods such as Acanthostega and Ichthyostega is about 18 million years.

But there's a 20 million year gap in the fossil record following the close of the Famennian, after which time the record shows a host of more evolved Carboniferous amphibians.

Most early tetrapod remains have been recovered from North America, northern Europe, northern Britain and European Russia.

All of the early tetrapod localities were tropical to sub-tropical. In addition, with the exception of Tulerpeton, which was recovered from estuarine deposits, all of the Late Devonian tetrapods and the panderichthids inhabited freshwater habitats.

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These freshwaters and their surrounding landscapes had undergone a dramatic transformation.

The harsh, infertile, unstable and unpromising freshwater and terrestrial environments of the Middle Silurian gave way to ones that were profoundly modified by the emergence and evolution of vascular plants.

Invasion of Plants during the Devonian

Life, prior to this global transformation, flourished only in the oceans, while the land and its freshwaters were inhospitable wastelands.

Even estuaries, which today contain some of the earth's most productive ecosystems, were marginal habitats.

The vascular plants or Trachaeophytes may have evolved as early as the middle Ordovician, but their earliest confirmed records come from Middle Silurian rocks in Northern Europe and Upper Silurian rocks from Australia, Bolivia and China.

These early plants consisted of lycophytes (club mosses and their relatives) and plants of unknown affinities.

Most were small (<10 cm or 4 in.) and they were probably restricted to the water's edge. The variety of plants increased dramatically in the Early Devonian and the first forests appeared by the late Middle Devonian.

By the Late Devonian, plants were poised to colonize drier land.□

Other life forms accompanied vascular plants in the colonization of the land.

Non-vascular embryophytes (hornworts, liverworts, lichens and mosses), lichens and terrestrial algal may have preceded the trachaeophytes, but they apparently never achieved the trachaeophytes' diversity and abundance.

The first fossil Ascomycetes (mushrooms) have been recovered from Early Devonian rocks in Northern Europe, but they may have been present much earlier.

The evolution of mycorrhizal associations (the symbiosis of soil fungi and plants) probably greatly enhanced the radiation of land plants.

Invertebrates, first recorded from Ludlow (early Late Silurian) rocks in Wales, colonized the land relatively early. Significantly, the Ludlow invertebrates were broadly similar to those found in the Middle Devonian Gilboa and the Late Devonian Red Hill localities.

Although the colonization of the land is an obviously important part of the Devonian Transformation, the impact of terrestrial plant communities on aquatic ecosystems was also profound.

By the Middle to Late Silurian (430-415 million years ago), estuaries became more productive and diverse, while freshwater habitats were being colonized by small invertebrates.

Thus began an upstream progression of ecological development that culminated in the Late Devonian and Early Carboniferous.

The expansion of life into estuaries, streams and their adjoining landscapes generated a positive feedback loop in which the environment became less harsh, more stable and thus more hospitable to life.

One of the major aspects of this feedback loop was the enhanced weathering of soils caused by plants and their associated fungi.

This enhanced weathering resulted in the reduction of soil particle sizes and the increased leaching of plant and microbial nutrients.

Moreover, accumulations of plant organic matter, combined with the increased proportion of finer soil particles, increased the soils capacity to store water.

Improved water storage would have reduced erosion and moderated water flows in streams and estuaries.

Flooding becomes less destructive and more beneficial.

The combination of more moderate flows and increasingly dense stands of tracheophytes would have stabilized the banks of streams and estuaries.

Increased bank stability, combined with inputs of fine sediments, would in turn stabilize shallow water habitats and engendered the development of wetlands.

The growth of vascular plants in and adjacent to the shallow waters and wetland habitats along the margins would have provided an important source of organic matter to aquatic animals in streams and estuaries.