Bioblog 26

Let’s hear it 4 legs!

Carboniferous

The Carboniferous Period was characterised by expansion of the Tethys Ocean and collision of the future North America with Greenland, Britain and Northern Europe forming land masses which housed several inland seas. For much of the period the Tropical areas were covered by hot and humid rain forest. It is the incomplete biodeterioration of largely plant debris that today has yielded the coal measures which triggered the Industrial Revolution in Britain followed by many countries across the world.

Credit: *Massimo at MI LABORATORIO DE IDEAS* Public Domain.

The map shows the outline of modern countries projected onto an approximate image of the landmass, today called Pangaea, towards the end of the Carboniferous period. It is heavily interpreted and you should regard it as speculative and since it is spherical, visual distortion of apparent size of countries will occur.

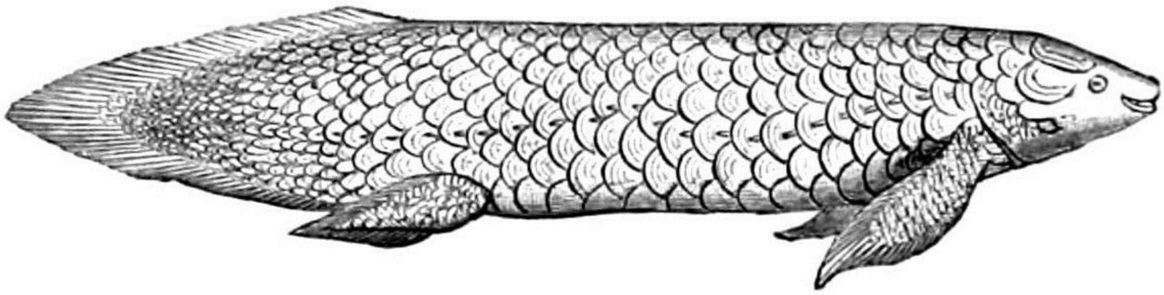
Shallow lakes and inland sea margins with copious plant cover were ideal for the next major biological transformation, water to land. The transfer of vertebrate life to land was also favoured by high oxygen levels, reaching over 30% during the Carboniferous Period, very probably a result of plant growth and consequent photosynthesis.

Advantages of the land environment

- Reduced predation, although over time formidable amphibian predators evolved.
- Increase in niches for use by newly arrived land dwellers. A “niche” is a term combining where an animal lives and what it does there, so occupying a hole left by a partially decayed tree trunk would be a Niche because it offers both a home and also a concealed base from which the animal is able to prey on other passersby.

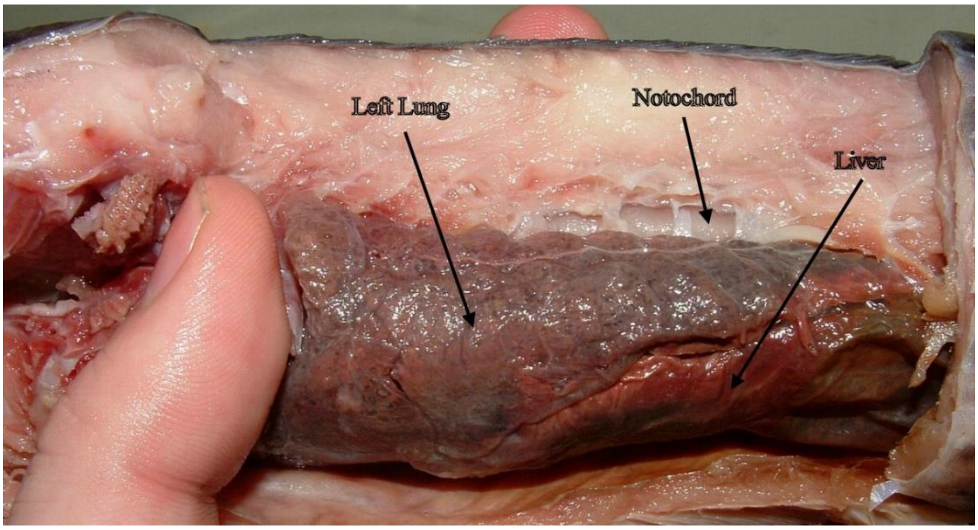
The problems to be solved in order for animals to transfer to the land are formidable. However, even today, a remarkable surviving relative of those times, the lung fish, is able to make the transfer to land to seek a more favourable accommodation when its pond dries out, see drawing below of a rather beguiling Australian **Lungfish, *Neoceratodus forsteri***. These animals are thought to have little changed since they evolved in the Carboniferous Period, around 300Ma ago and represent a "Living Fossil". Of the 5 species of modern lungfish, these are regarded to be the most primitive, with only one lung, others have two. The fins are thought to be **homologous** (see below re homologous lungs) to tetrapod legs.

Credit: W H Flower - Guide to the galleries of reptiles and fishes of the British Museum, Public Domain



Credit: Mokele at English Wikipedia

Dissection to show Left Lung of Australian Lungfish



The lungs are **Homologous** structures to the lungs of Tetrapods and contain air sacs which greatly increase the surface area for gas exchange.

The fact that we use the term "**Homologous**" is highly significant because it means that the structure of the lung is directly the ancestral to the lung of modern tetrapods. The Notochord shown in the dissection is a primitive forerunner of the vertebral column, another ancient vertebrate feature of the Lung Fish.

Disadvantages of migration to the land

- **Gas exchange**. Gills would be unsuited to life on land because their delicate membranes will dry out. Once a surface film of water had evaporated off, the gill would become highly inefficient. They would also lose large amounts of water although the atmosphere of the Carboniferous swamps probably had very high humidity.
- **Loss of water.** Changes would be needed to gas exchange as mentioned above to reduce water loss and also to the body covering: the skin would need waterproofing. For the early Tetrapods this is a work in progress, waterproofing was only solved by the reptiles (see my later article on reptiles). Although not a totally waterproof barrier to prevent dehydration, the skin of amphibians has additional functions: protection and gaseous exchange. Many amphibians produce toxins, released from glands in their skin. Some of such toxins are remarkably effective, for example the neurotoxin Bufotoxin produced by several tropical amphibians.

These examples of the "**Poison dart Frog**" are members of the genus ***Dendrobates*** and famous for their use by indigenous tribes of South America to gather food by lethally tipping their blow pipe darts with venom from glands in their skin. The poison contains digitalis like alkaloids which cause cardiac arrhythmia, (see my article "Electrical Control of the Heart: Problems ").

In practise the poison of choice is **Curare** which is more easily resourced from a variety of Rain Forest plans, notably of the genus *Chondrodendron*. Curare binds to acetyl choline receptors of skeletal muscle thus preventing nervous enervation and causing muscle relaxation. Death follows from asphyxiation because of inaction of the breathing muscles. Such poisoned animals are remarkably limp, a characteristic which is used in moderation by anaesthetists to aid surgery.

Some modern amphibians are totally reliant on the skin as a means of excretion of CO_2 and absorption of O_2, notably the group ***Plethodontidae***, salamanders that lack lungs.

Credit: Kaldari, Wikipedia Commons

This is ***Batrachoseps attenuatus***, the **Californian Slender Salamander**. This is a member of a very successful group of amphibians with wide distribution and a fossil history stretching back to the **Miocene** (23 to 5 Ma ago). The animal uses its skin and the lining of its mouth as respiratory surfaces.

- **Excretion:** Changes would be necessary over time to the renal system inherited from fish ancestors so that excretion minimised water loss. It is possible that this problem had already been tackled by fish: modern trout and salmon migrate from the open sea to spawn in fresh water; this requires changes to kidney function because of the differing osmotic potential between sea water and fresh water.
- **Reproduction**. Without water sperm cannot be transferred to the egg. Amphibians could not solve this problem and still today have to return to water in order to allow sperm to fertilise eggs. This restricts the range that amphibians can monopolise land and also means that large number of eggs and sperm are lost by inefficient transference of sperm between the sexes and also by predation of eggs. Some modern amphibians have developed various methods to reduce losses of young by predation, for example the **Back-carrying Toad** and the **Male Mouth-brooding Toad**.

It's worth mentioning the modern pressures that many of these species are subject to. Having existed from the Carboniferous Period, for around 300Ma, many amphibians are recently under intense environmental pressure, an example is the **Mouth Brooding Toad (*Rhinoderma rufum*)** often referred to as "**Darwin's frog**". The male gobbles up the fertilized eggs and tadpoles develop and metamorphose within his vocal sacs, later to be released as miniature adults from his mouth. These animals existed as two related species in the temperate forests of **Southern Chile**. Replanting of the native forest with pine trees has dried out the forest floor and the northern species has not been seen for 30 years and is considered to be extinct, the other, related species seems to be hanging on, just about. Another casualty of unfettered expansion of human numbers and resource exploitation: we should not duck our responsibility. The problem is not change itself which species can often adapt to accommodate, but rapid change for which genetic selection of an environmental favoured genome is too slow.

Credit: Dein Freund der Baum – Wikimedia Commons.

This is ***Pipa pipa*** otherwise "**The Suriname Toad**". Adults live on the floor of the rain forest and resemble fallen leaves. They are particularly of interest for their sexual adventures and strange way of bringing up their young! When they couple (amplexus is a polite scientific name) they together rise out of the pond and flip over as a sort of amphibian swimmers' pas de deux. As they arc through their back flip, the female releases 3 to 10 eggs which become fertilised by sperm from the male and pushed into the skin of her back by movements of the male. You can see the result in the picture. Once in her skin, the eggs sink further and form pockets where they develop into tadpoles and eventually metamorphose into miniature adults which emerge from the mother toad's back to start another cycle of largely solitary life in the forest.

Credit: Wikipedia

This is one of the very few photos of ***Rheobatrachus silus***, the "**Gastric Brooding Frog**" of Eastern Queensland, Australia. There were two species of Gastric Brooding Frog which were discovered in the early 1970's and concluded as extinct 10 years later. They were notable experiments in avoiding predation of their fertilised eggs and did this by the female swallowing them, subsequently incubating the resulting tadpoles in her stomach. Metamorphosis occurred in the mother's stomach and froglets were later regurgitated and released into pools. To preserve their life within the mother frog's stomach, the tadpoles produced **prostaglandin E2**, a hormone like chemical produced by commonly in most animals and their tissues and currently used to hasten birth in human medical care. In this case Prostaglandin E2 turns off Hydrochloric Acid production in the mother frog's stomach.

The frogs lived in a very small area (less than 540 square miles) of pristine forest where the only traces of humans were occasional indistinct tracks. The certain agent for their demise is not known and could be several factors combining together, although degradation of the forest and introduction of the fatal Chitryd fungus seem likely major players. Recent attempts have been made to clone, and therefore re-create the extinct species, by transferring nuclei from preserved body (somatic) cells of the extinct frog into de-nucleated eggs of another species, see:

https://newsroom.unsw.edu.au/news/science-tech/de-extinction-research-feature-abc-tv

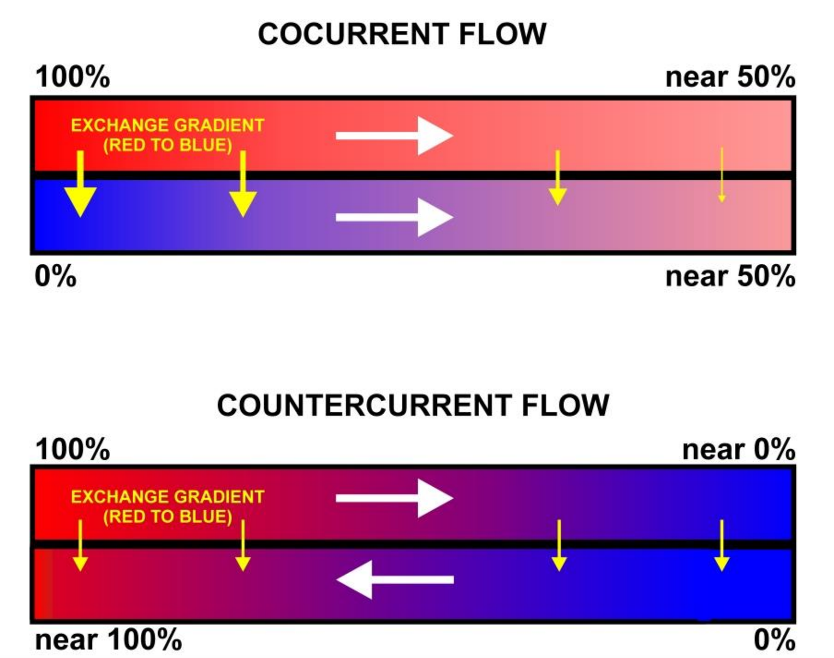
It’s worth considering some of these difficulties faced by the newly arrived land animals in the Carboniferous Period in some detail, to look at the solutions which were adopted and, since we have that luxury, think of better ways of going about it!

Gills v Lungs

There is less Oxygen in water than in air. Air at sea level and at 20°C contains 94×10^{-4} moles of oxygen per litre whereas water at 20°C contains a solution of diatomic oxygen with a molarity of about 2.8×10^{-4} mol per litre. However, gills are very efficient structures for removing oxygen from water. Not only are their membranes very thin, but also blood flows close to the membrane and in the **opposite direction** to that of water, that is using **Countercurrent Flow**. Lungs have a much less efficient system of extracting Oxygen since blood flow is **Cocurrent**, not countercurrent, i.e. in the **same direction** as does the air (top diagram).

Here’s a diagram showing how it works and comparing the two systems:

Credit: Cruithne9, Wikipedia Commons



This is a comparison between the effectivity of a cocurrent and a countercurrent flow exchange systems. In both diagrams red has a higher value, in this case of either CO2 or O2. Diffusion of gases across the separating membrane will be from High to Low concentration of O2 and CO2. For this to work efficiently in either case there must be minimal separation between blood flows in each channel and the rate of flow must allow for near equilibrium to form, i.e. not too fast to allow time for the gases to diffuse across the membrane. The conclusion to draw is that lungs, whilst not as efficient as gills since they lack the efficient Countercurrent flow between blood and air, are as good as is possible given the structures available for evolutionary change, time and the genome of those Carboniferous amphibians making the hop to living on land. Things ain’t going to change any time soon.

Then there are probably many things that we have not thought of. An example of this occurred the other day when reading: the author made the point that moving around in a slimy swamp would be impossible without the development of claws. Well… of course, a light bulb flashed on in a darkened room!

Final Thoughts

What are these articles for? You will be hard pressed to find much in any of the A Level specifications which relate to an extensive knowledge about Tetrapod evolution! There are other considerations however. This series of articles introduces material which certainly is within the A level cannon and in a context which I hope is interesting to you. I say this about my own experience of A level, but I suspect this also is true for you: there is no point in keeping on reading the same material over and over again. A new view is often helpful in widening our understanding and, my central purpose, to deepen our gratitude to be a human in this wonderful world.

Here's the table:

Here is a list of topics which have had a shake-out in the series:

Bioblog	Title	Topics Covered
19	To Begin at the Beginning	• Evolution: Protocells and reliance on RNA • Cell Structure • Structure and Function of RNA(s) and DNA
20	None	• Evolution: the Eukaryotic Cell • Classification • Relationships between structure and function of major life groups • Cell membrane structure
21	The Eukaryotic Cell Cook Book	• Cell structure • The origin of cell organelles • Membranes
22	Legs: origins	• Cladistic Taxonomy • Use of Cladograms • Vertebrate structure
23	Something Fishy	• Evolution • Ancestral vertebrate structure
24	When Fish Wore Armour: enter the Placoderms	• Cladograms • Predation • Evolution, convergent evolution • Vertebrate structure • Genetics
26	Let's Hear It For Legs!	• Predator-Prey relationships • Methods of Gaseous Exchange • Effect of Habitat Loss/Degradation • Countercurrent Flow

Until next time,

Sphenodon.