The Origin of Land Vertebrates.[1]

By Prof. E. S. GOODRICH, F.R.S.

WE are all agreed that the four-footed terrestrial vertebrates or Tetrapoda have arisen from some fish-like aquatic ancestor. Two chief changes must have occurred in the passage from water to land—one connected with respiration, the other with locomotion. Moreover, the land animal must have acquired a resistent skin. The fish breathes oxygen dissolved in water, which it takes in by its mouth and expels through its gill-slits, the gills on its gill-arches being organs of respiration.

In the tetrapod, the respiratory organ is a ventral bilobed diverticulum of the pharynx ; air is taken in at the external nostrils, passes by the internal nostrils into the buccal cavity, and is thence forced or sucked through the median ventral glottis into the trachea and so to the distensible lungs.

The fish, also, swims by undulations of its body and tail and with the help of paired fins, stiff outstanding folds of the body-wall, each with an internal skeleton movably articulated at its base to the supporting limb-girdle. The walking limbs of the tetrapod, on the other hand, consist of paired pectoral and pelvic projecting limbs built on essentially the same plan, and each subdivided by movable articulations into three regions, the outermost bearing typically five digits. Hence it is called the pentadactyle limb.

The problem before us is, then, to explain how the walking tetrapod evolved from the swimming fish without any sudden alteration of the structure and function of its parts, by a series of gradual steps each of advantage in the struggle for existence.

Before considering the possible claims of any known fish to be considered as ancestral to the land vertebrates, we must first attempt to determine, without going into detail, what must have been the fundamental structure of the common ancestor of all the Tetrapoda. Since the Amphibia still lay their eggs in water and pass through a larval stage provided with gills, it is agreed that they represent the most primitive group of tetrapods living at the present day. The problem is thus narrowed to that of the origin of the class Amphibia. But all the modern forms of the class are highly specialised remnants of a much more ancient and primitive group known as the Stegocephalia (or Labyrinthodontia), which flourished in Carboniferous and Permian times—many of them far larger and more formidable animals than their degenerate modern descendants.

Briefly, we may conclude from a study of extinct and living Amphibia that the primitive ancestral tetrapod had the following chief characters in addition to the lungs and pentadactyle limb already mentioned. It was a heavily built animal, shaped somewhat like a salamander or newt, with a large head, a complete covering of bony plates and scales underlying a soft skin protected by a renewable outer cornified layer and provided with abundant glands to keep it moist when out of the water. The roofing of the skull was pierced by two orbits, two external nostrils, and a median pineal foramen. Internal nostrils opened on the palate. The Eustachian tubes led to a tympanic cavity closed by a tympanic membrane behind the quadrate. A columella auris extended between this membrane and the auditory capsule. Probably the lateral line system of sense organs, present in all fish and in the aquatic larvæ of Amphibia, persisted even in the adult. The brain had well-defined paired cerebral hemispheres. The heart was asymmetrically twisted and the atrium subdivided into left arterial and right venous auricles. The lung received venous blood from the sixth aortic arch and returned it aerated to the heart by pulmonary veins. A vena cava inferior made a short cut from the kidneys to the sinus venosus. The rectum and urinogenital ducts opened into a common cloaca.

Now we may ask from what known kind of fish could such a primitive tetrapod have evolved ? What group of the Pisces is sufficiently advanced and at the same time sufficiently primitive to give rise to such a form ?

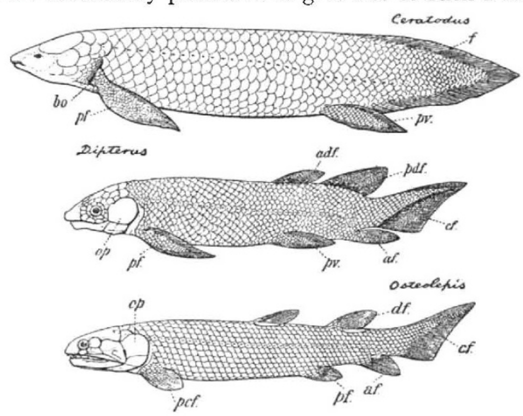

FIG. 1.—*Ceratodus forsteri*, the lung-fish of Australia ; *Dipterus valenciennesii*, a Devonian dipnoan (after Traquair); *Osteolepis macrolepidotus*, a Devonian teleostome (after Traquair). From "A Treatise on Zoology," Part IX., by kind permission of Messrs. A. and C. Black.

We divide the Pisces into Chondrichthyes (sharks and rays), with a purely cartilaginous skeleton, and Osteichthyes, in which bone is present. Clearly the Chondrichthyes, with neither true bone nor true scales and with no form of air-bladder or lung, are not eligible. The second group, the Osteichthyes, contains the Dipnoi and the Teleostomi. We shall see that of these the Dipnoi alone display a considerable assemblage of characters which the ancestor of the Tetrapoda must have possessed.

The teleostomes include Polypterus and the Actinopterygii (Acipenser, Amia, Lepidosteus, and the Teleostei and many fossil forms). Of these the Teleostei, which appear only in the Jurassic strata, may be dismissed at once as far too specialised and modern—for it is obvious that the common ancestor of the tetrapods must have diverged from the piscine stem in Carboniferous if not in Devonian times. But even the lower living Actinopterygii show specialisations in the skeleton, brain, and viscera which prove that they all belong to side branches not in the direct line of ancestry.

In the Devonian strata, however, are found certain very primitive teleostomes, such as Osteolepis, which much more closely resemble what we believe to have been the ancestral form.

[1] Substance of a paper opening a discussion in Section D (Zoology) of the British Association at Toronto on August 13.

Indeed, as we pass downwards, we find a gradual convergence in structure between Teleostomi and Dipnoi, and between these and the Stegocephalia, which seems unmistakably to point to a common undifferentiated form from which all three could have evolved. It is just this sort of convergence as we pass to earlier and earlier fossils which makes the study of palæontology so fascinating—affording evidence not only that evolution has taken place, but also enabling us to trace out the course it has actually followed.

Following, then, the teleostomes down into the Devonian, we find that the osteolepids acquire a complete covering of thick scales of the peculiar structure I have named cosmoid, a complete set of roofing bones to the skull which may be compared almost bone for bone with those of the Stegocephalia (a comparison further borne out by the very similar disposition of the lateral line canals and the pineal foramen). Not only were there ventral external nostrils but also internal nostrils on the palate, as Prof. Watson has shown. Both the pectoral and the pelvic fins had outstanding scale-covered lobes.

Allied to Osteolepis, but, it would seem, somewhat off the main line of descent, are the Rhizodontidæ, represented, for example, by Eusthenopteron from the Upper Devonian of Canada and so well described by Whiteaves and Bryant. Primitive as they are, even these Devonian teleostomes are probably already too specialised in their jaw apparatus, large opercular bones, and fin skeleton to be the actual ancestors of the Tetrapoda.

There remains to be considered the very isolated fish Polypterus, surviving at the present day, with a closely allied genus, only in the rivers of tropical Africa. It has a strong superficial resemblance to the osteolepids and was long ago placed with them by Huxley in the group Crossopterygii.

Pollard and others since, relying chiefly on similarities in the roofing bones of the skull, have claimed that Polypterus is, of all living fish, that most closely allied to the tetrapods. The resemblance is, I think, to a great extent deceptive, and only such as might be expected in any fairly primitive fish. It is true that it has a ventral lung-like air bladder supplied from the sixth aortic arch. Nevertheless the structure of its scales, the jaw apparatus, the position of its double nostrils on the outer surface of the snout, the absence of a cloaca, the skeleton of the pelvic fin and girdle, and its specialised brain show that Polypterus is well on the actinopterygian line of specialisation, as I endeavoured to show in a paper on the subject before the British Association in 1907. Indeed there is some reason to believe that it may be the living representative of the ancient group of Palanoniscidæ.

Finally we come to the Dipnoi, that ancient branch of the Osteichthyes dating from Devonian times, but still surviving to-day in isolated remnants, of which the Australian lung-fish Ceratodus is the most primitive genus. Although the modern forms have a highly specialised dentition and have lost many of the dermal roofing-bones of the skull and marginal bones of the jaws, yet they retain several important characters indicating affinity with the Tetrapoda. They have internal as well as external nostrils, and a lung sac opening ventrally, receiving venous blood from the sixth aortic arch and returning aerated blood directly to the heart. The heart itself is remarkably amphibian in the structure of the truncus arteriosus, in the tendency of the valves of the conus to fuse to a spiral longitudinal septum; and even the atrium is beginning to become subdivided, so that the venous and arterial bloodstreams pass separately to the right and left sides of the ventricle. The vena cava inferior and the anterior abdominal vein are well established. A cloaca is present, and the urino-genital organs conform to the amphibian plan, as do also the eggs and the larval forms. But more important still is the structure of the brain, which possesses distinct paired cerebral hemispheres. Even the skin resembles that of the Amphibia, being provided with abundant multicellular glands. All these resemblances, both conservative and progressive, can scarcely be due to convergence.

Two important points remain to be mentioned. In all the primitive tetrapods, the hinder region of the palato-quadrate bar (the upper division of the mandibular arch) is not only firmly attached to the skull by basal and otic processes, but also bears an ascending process separating the profundus from the maxillary branch of the trigeminal nerve. Among all the fishes, the Dipnoi alone are known to show this typical disposition.

The second point is that they alone among known fishes, with the possible exception of the more primitive osteolepids, have pectoral and pelvic fins of the same structure—thus sufficiently alike to have given rise to paired walking limbs. In other fishes the pelvic fins are too much reduced or specialised, too unlike the pectorals, to have developed into the tetrapod hind limb. The early Devonian dipnoan Dipterus approaches so closely to the osteolepids (in the structure of the skull, scales, fins, etc.), that we may be sure these forms cannot have moved very far from the common starting-point.

We may conclude that the earliest Osteichthyes diverged into teleostome and dipnoan branches and that the tetrapods arose from the base of the latter branch before the Dipnoi had acquired their characteristic specialisation in palate and dentition. The Devonian Osteolepidæ and Dipnoi seem to have been fresh-water forms, and it is probable that the transition from aquatic to terrestrial life took place in streams and pools, whence access to land was easy.

What exactly were the transitional steps from fin to walking limb we do not yet know. The fin skeleton of the osteolepids is scarcely known, and that of the rhizodonts is probably already too specialised. The living Dipnoi, on the other hand, help us to understand how aerial was substituted for aquatic respiration. For, while retaining gills and open gill-slits, they have become adapted to survival in rivers liable to be dried up or become foul in dry weather by acquiring a nasal passage from external to internal nostril (by closure of the nasal groove) and a lung for breathing air taken in at the surface. The lung had no sudden origin; but, as suggested by A. Goette and Spengel, was probably derived from a posterior pair of gill pouches which failed to open to the exterior, retained an ample blood-supply, and joined together ventrally. To this day the lung first appears in tetrapods as a pair of diverticula of the pharynx.

Thus without break or sudden violent change of habit or structure could an aquatic ancestor have evolved into an animal living on dry land.