

Amphibians

The World of Frogs, Toads, Salamanders and Newts

Robert Hofrichter, Editor





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Cover (back): Red-eyed (tree) frog (*Agalychnis callydrias*, Hylidae) from Central America, fire salamander (*Salamandra salamandra*, Salamandridae) and two juvenile emerald-green tree frogs (*Pelodytes caerulea*, Hylidae).

Page 1: *Dendrobates azureus* (Dendrobatidae)

(Photo: Photo Press / Möhn)

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Page 5: *Gastrotheca walkeri* (Hylidae)

(Photo: K.- H. Jungfer)

Page 6/7: *Pachymedusa dacnicolor* (Hylidae) from Mexico on a leaf, photograph taken against the light.

(Photo: R. Hofrichter)

Page 8: Hybrid edible frog (*Rana kl esculenta*) (Photo: N. Wimmer).

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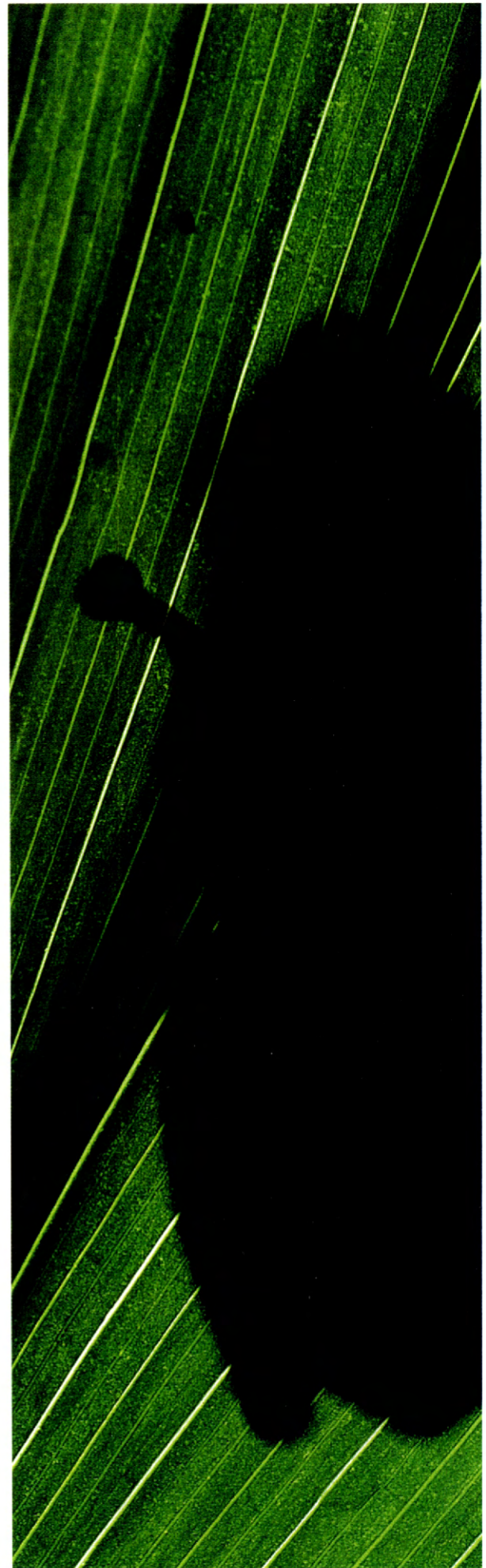
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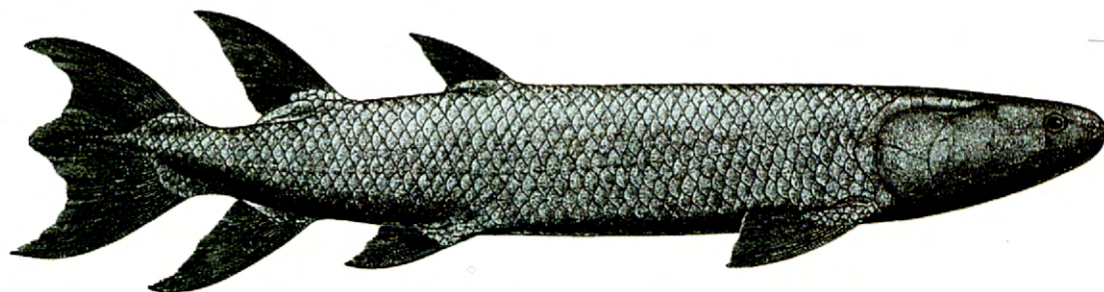
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Phylogeny and Evolution

Paleontological findings dating back to the Devonian period (350 to 370 million years ago) prove that amphibian ancestors were fish-like vertebrates with elongated body and a tail fin that allowed them to move forward, much as newts still do today. They also had a number of ventral and dorsal fins; the unpaired of these fins are of no interest in this context. What does interest us, however, are two pairs of fins on the ventral side of the body, the pectoral and abdominal fins, which represent the raw material for a great evolutionary future. These fins, originally used as balancing organs (to maintain the body in a vertical position), evolved into the extremities of terrestrial vertebrates.

The search for amphibian ancestors leads to Crossopterygii (or lobe-fin fishes), more specifically to Osteoleptidae or Panderichthyidae, both families of Rhipidistae. Right: Devonian Eusthenopteron (after Jarvik, 1980).



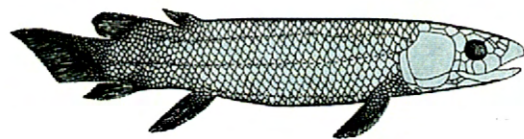
Amphibian Ancestors

In the Devonian, that is, in the period of time when vertebrates began to colonize dry land, oceans abounded with various groups of aquatic vertebrates. Leaving so-called jaw-less fishes (Agnatha) aside (excluded from the list of potential amphibian ancestors because they did not have jaws), the following groups remain as potential forerunners: acanthodians, placoderms, Chondrichthyes (sharks and their relatives), bony fishes (Osteichthyes), lungfishes (Dipnoi), and lobe-fin fishes (Crossopterygii).

At first glance, the Dipnoi seem the most likely ancestors. In their living representatives—*Neoceratodus* in Australia, *Protopterus* in Africa, and *Lepidosiren* in South America—the swim-bladder performs the function of a primitive lung. The swim-bladder develops in the embryo as an evagination of the anterior section of the digestive tract. Since the connection between the digestive tract and swim-bladder is preserved in adults as the “ductus pneumaticus,” the air in the swim-bladder can permanently be replenished from the atmosphere by swallowing,

and oxygen can be absorbed into the blood through the walls of capillaries in the walls of the swim-bladder. This is a simple form of air breathing. Despite this fact, Dipnoi, too, do not meet all the criteria necessary to make them ancestors of land vertebrates.

The reasons are found in the anatomy of their Devonian representatives. Some of their structural features clearly separate them both from other fish-like vertebrates and amphibians. For instance, while the skull roof in the majority of vertebrates is formed from a pair of frontal bones and a pair of parietal bones, there is only an asymmetric mosaic of bones in lungfishes. Besides, Devonian “lungfishes” did not breathe atmospheric air; this is an ability they reached only in the Tertiary. Only then did Dipnoi have underdeveloped branchial arches, like in modern Dipnoi, indicating that besides vestigial gill respiration there was some sort of additional (i.e., lung) respiration. Devonian dipnoans, that is, dipnoans contemporary with amphibian evolution, all had fully developed branchial arches and no trace of reduction. This means that they still relied on gill respiration and depended fully on being in an aquatic environment.



Dipterus, a lungfish (Dipnoi), can be excluded from the possible circle of amphibian ancestors. Dipnoi lack the teeth-carrying premaxilla, maxilla and dentary found in the majority of vertebrates where they form the characteristic tooth-bearing jaws. Instead, Dipnoi have so-called dental plates (after Forster-Cooper, 1937).

In the first half of the nineteenth century, when only fossil Dipnoi were known, no one would have thought to consider them as amphibian ancestors. The view on relationships between

amphibians and Dipnoi was first expressed when living lungfishes were discovered in the middle of the last century. The discovery that they are capable of breathing atmospheric oxygen caused a sensation. However, a trivial mistake caused made in comparing living, instead of Devonian, dipnoans with amphibians. Therefore, Dipnoi can be eliminated from the list of potential amphibian ancestors.

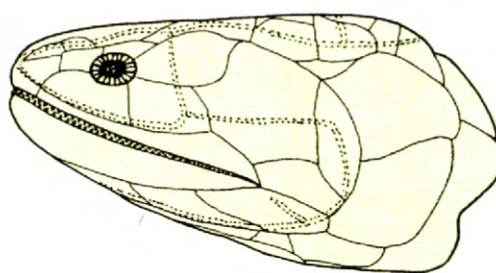
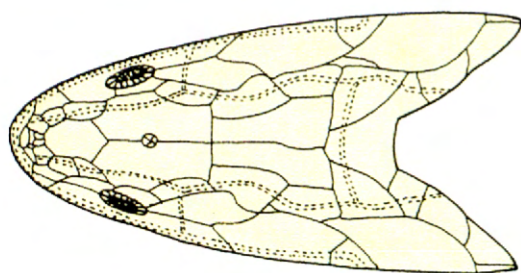
➤ The Lobe-Fin Fish Eusthenopteron

In the 1920s the paleontological excavations in Escouminac Bay, Canada, also known by its Native name, Miguasha, yielded a series of well-preserved three-dimensional fish-like vertebrate fossils, among them several specimens of the lobe-fin fish *Eusthenopteron* from the family Osteolepidae. One of these fossils was acquired

mammals. Stensiö's sensational discovery was this: *Eusthenopteron* had been almost "amphibian" but still in the "mantle" of a fish. Since then, a number of osteological matches have proven that crossopterygians were indeed amphibian ancestors. Although *Eusthenopteron* cannot be counted as a direct ancestor, it helped to document the anatomical characteristics that stood at the beginning of the evolutionary changes that led to the birth of amphibians. *Eusthenopteron* cannot be a direct ancestor because it was found in Greenland in the same geological layers as another vertebrate, called *Ichthyostega*; the latter already had the ability to move on land and must therefore be regarded as a creature halfway between fish and amphibian.

The anatomy of Devonian lobe-fin fishes pro-

The skull of Crossopterygian fish Eusthenopteron with branches of the lateral line system. This superficial duct system contains groups of neuromasts, mechanical receptors that register movement in the water that penetrates into the duct via the pores. Ichthyostega and many other early amphibians have this lateral line organ in common and its structure strongly resembles that found in Crossopterygii. It is also present in amphibian larvae and in some aquatic amphibians (after Jarvik, 1980).



by Swedish paleontologist Erik Stensiö, whose studies at that time concentrated on the inner structure of the skull in primitive jaw-less fishes Agnatha. Stensiö realized that the outer appearance of the fish-like vertebrates was a result of their permanent life in water, and that the answer to the question whether lobe-fin fishes (Crossopterygii) were somehow related to amphibians lay in their internal anatomy. To this end, he decided to make the grinding sections of one of the valuable skulls of the *Eusthenopteron* specimens mentioned above, using Sollas' method to completely reconstruct the internal skull structure even if this process meant the destruction of the specimen. The method requires that an object be cut into extremely thin sections, much like slicing salami. The skull, approximately 5 inches (12 cm) long, was cut in 200 sections, each 60 micrometers thick, and each cut surface was photographed and enlarged. Then, discernible cranial structures were reconstructed as a model in wax. The entire process took 25 years and was completed in 1952.

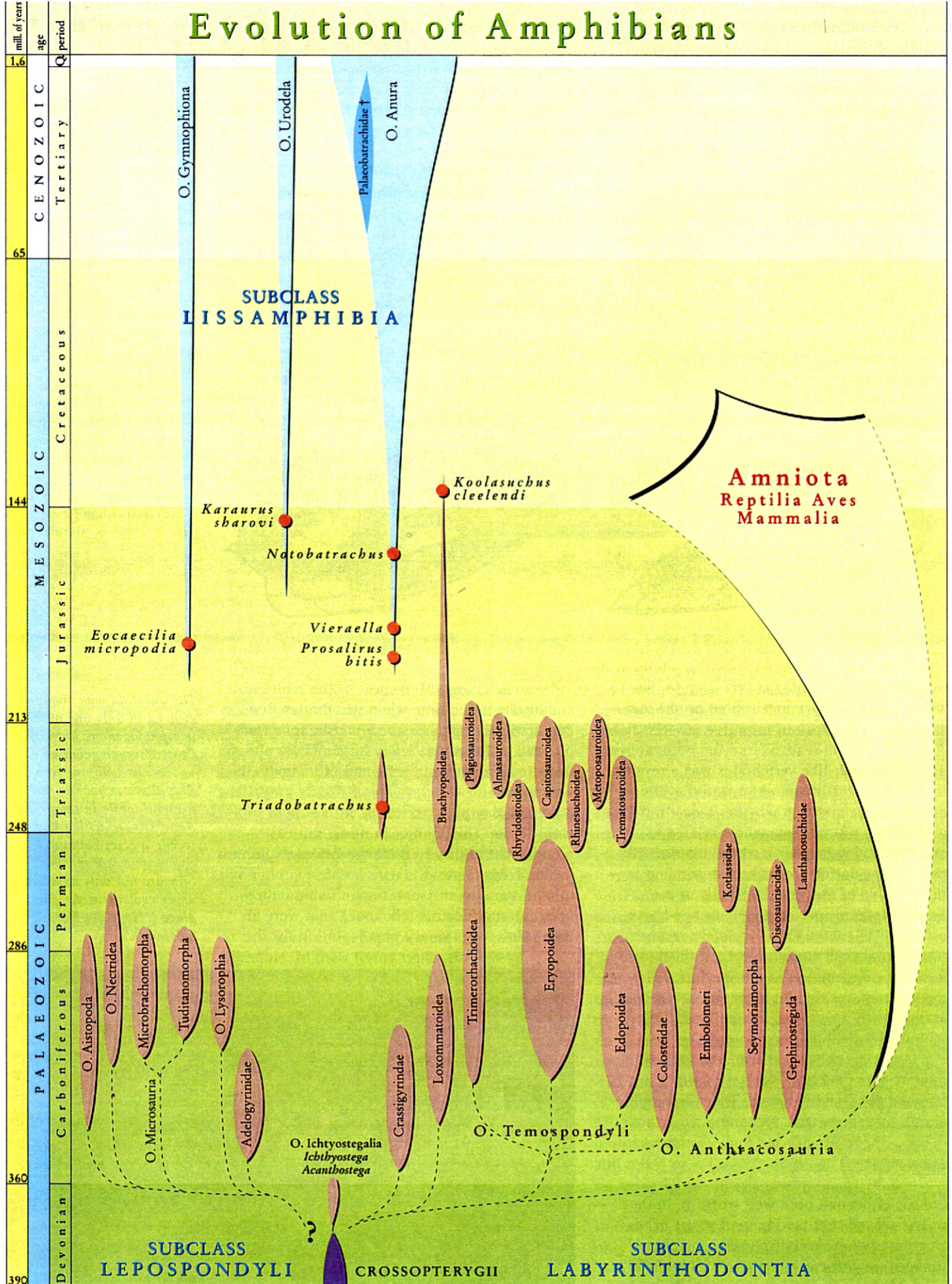
But the effort had been well worth it. In the end, it proved that the inner structure of the crossopterygian skull displayed a number of similarities with corresponding structures in amphibians and higher vertebrates, including

vides some clues with respect to the ecological conditions in the time when vertebrates first colonized dry land. *Eusthenopteron*, for example, had a characteristically large tail fin and unpaired fins shifted to the end of its body. It was a predator who lay in wait for its prey, like a present-day pike, attacking with a rapid forward thrust. This kind of hunting strategy required the ability to remain motionless in one position. Maybe that is why *Eusthenopteron* and other Devonian crossopterygian fishes developed internal nostrils (choanae), that were an important evolutionary preadaptation for the

The question why choanae evolved in only one of the two phylogenetic lines of Crossopterygii remains unanswered. In one line, Rhipidistia, choanae are present, while in the other, Actinistia, of which the recent species Latimeria chalumnae is a member, they are not only absent but never evolved in the first place ("Haus der Natur," Salzburg).



Evolution of Amphibians



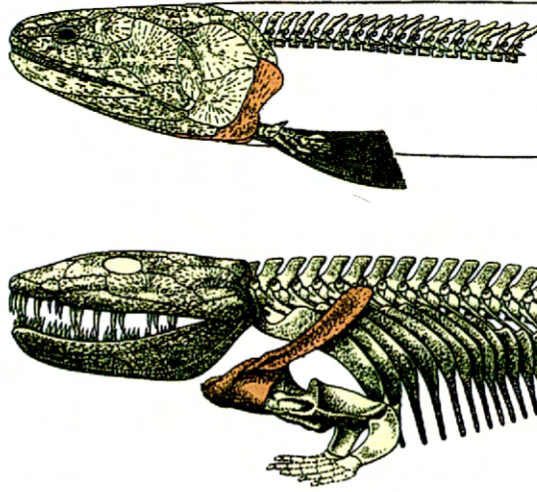
transition to life on land. Most fishes have two pairs of external nostrils, with no communication between the nasal cavity and the mouth cavity. Water enters into the anterior pair of them, flows along the olfactory epithelium of the nasal sac and then exits again through the posterior pair. But in Devonian crossopterygians the anterior opening of each side lies close to the edge of the upper jaw, and the posterior opening is connected to the mouth cavity. The alternating motion of the jaws and gill slits generates a flow of water that supplies oxygen to the gills; as a by-product in the choanate fishes, the same motion also forces a stream of water through the channel connecting the external nostrils with the internal nostrils (choanae) in the mouth palate. These internal nostrils or choanae are the basic prerequisite for subsequent “nose breathing” in dry-land vertebrates and thus for vertebrate land colonization.

But we should also ask whether internal nostrils—as seen in *Eusthenopteron* and in other Devonian Crossopterygii—are homologous to the external rear nostrils in fishes. There is neither paleontological nor embryological proof for an evolutionary shift of these nostrils from the outside of the skull to the internal roof of the mouth cavity. The argument has been made, however, that this shift not only is possible in theory, but did in fact occur, because the choanae in the oral cavity of the Devonian crossopterygian fishes are directly adjacent to the suture between the maxilla and praemaxilla (two bones of the upper jaw); this is the only position where such a shift could possibly take place. The search for amphibian ancestors should therefore concentrate on the group of Devonian crossopterygian fishes that possessed the choanae, the Rhipidistia.

Devonian crossopterygian fishes included some forms that had adapted to life in extremely shallow water. *Panderichthys*, found in the Devonian strata of Lithuania and Canada, was one. Similar to *Eusthenopteron*, this, too, was a cosmopolite, a fact that is of great importance for early amphibian evolution. *Panderichthys* had a dorsoventrally flattened head, with only the eyes peaking above its dorsal surface. This might be a clue that it lived in very shallow water with fluctuating water levels. One cannot fully exclude that it may already have been able to leave water for short periods of time.

Between Fish and Amphibian

Among those forms that can be considered transitional between lobe-fin fishes and amphibians, *Ichthyostega* has been studied in more detail than any other. The story of its discovery is a fascinating one and represents one of the most significant discoveries in paleontol-



The separation of the pectoral girdle from the skull in the evolution of amphibians: the development of a neck region was an important step in the evolution of tetrapods.

Top: *Eusthenopteron* (after Jarvik, 1980);
Bottom: *Ichthyostega* (after Jarvik, 1996).

ogy and evolutionary research. From the early twentieth century onwards, numerous geological expeditions were undertaken to Greenland with the goal of charting the region and evaluating its mineral resources. At the beginning of the 1930s, Danish expeditions were led to the same area by young Swedish paleontologist Gunnar Säve-Söderbergh.

In 1931 a section of vertebrate tail was discovered: it was fish-like in character with scales and fin rays, but also exhibited some traits of a land-dweller—the lower fin rays were mechanically worn. Professor Stensiö, to whom this specimen was given, identified it as the “fragment of a fish-like vertebrate covered with scales.” Further specimens, discovered at the same site the following summer, would turn out to be one of the greatest paleontological sensations of the century.

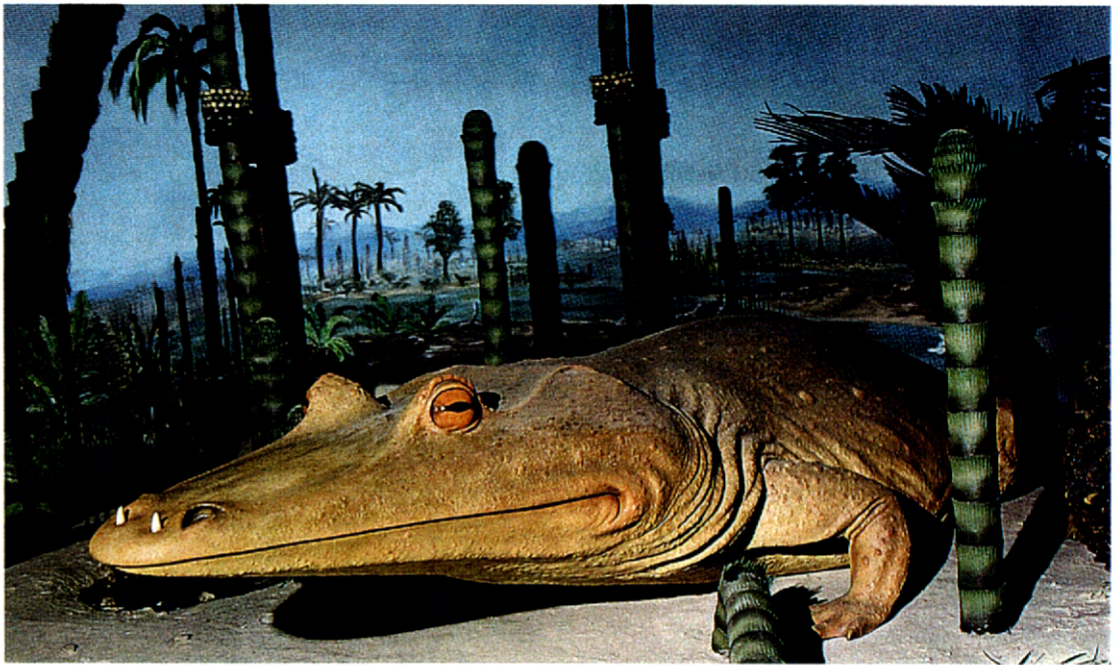
One should remember that in the 1930s the oldest amphibians known were all from the Lower Carboniferous. Hence it was a true sensation when a similar but far more complete finding surfaced the following year: a seven-toed hind extremity with pelvic girdle. It was soon evident that this animal had moved on land, which explained the worn lower part of the tail fin. As more findings followed, the entire body of the sensational animal was gradually assembled and reconstructed, with the exception of the fore legs. Säve-Söderbergh published his finding as soon as he was able to and named it *Ichthyostega*. The name translates loosely as “fish roof,” because the roof of the skull was strongly reminiscent of that found in fossil fishes.

It is remarkable that the same region yielded further fossil vertebrates of approximately the same age, which were no longer fish nor yet typical land tetrapods. Erik Jarvik, another participant in the Greenland expeditions, described this form in 1952 under the name *Acanthostega*.



Fossil skull of *Mastodonsaurus giganteus*, the heaviest and longest (13 feet/4 m) amphibian of all time (original specimen, Kupferzell, Baden-Württemberg, Upper Triassic, approx. 235 million years).

Right: Reconstructed *Mastodonsaurus*. Its huge mouth could open up to a 90 degree angle. The two fangs in the lower jaw projected upward through two openings located in front of the nostrils in the upper jaw ("Haus der Natur," Salzburg).



Recently, English paleontologist Jennifer Clack studied extensive material all gathered on British expeditions to the same region of Greenland. She was able to fully reconstruct *Acanthostega*. *Ichthyostega* and *Acanthostega* are now the best-studied Devonian vertebrates and point the way to amphibians along a path whose evolutionary beginnings were already characterized by a surprisingly high degree of taxonomic diversification. Further Devonian findings in other regions have documented this clearly.

At the beginning of the 1980s fossil vertebrates were discovered in the Devonian strata near the town of Tula, approximately 180 miles (300 km) south of Moscow. The extremities of these vertebrates showed distinct digits, six on both anterior and posterior legs. The animal was named *Tulerpeton* after the site, but was too fragmentary for a full reconstruction. The evolutionary status of this species is therefore not fully understood; the same is the case for *Elginerpeton* from Scotland (Upper Devonian, near Scat Craig), which is documented mostly by the jaw-bones. Details of dentition indicate, however, that this animal had some fish-like features. Another form, described as *Obruchevichthys*, was discovered near Velna-Ala in Lithuania, as was yet another specimen near Novgorod, Russia, and originally classified into the family Panderichthyidae.

But the existence of fish–amphibian transitional forms is not only based on fossil skeletons. There are also fossil trackways preserved in Devonian deposits, which do not resemble the type of imprint one might expect from a fin, for example, footprints and small bone fragments in southern Australia (*Metaxygnathus*). Judging by these findings, there was a range of animal

forms worldwide in the Middle and Late Devonian (370 to 350 million years ago) with characteristics of both fish and amphibians. In any further consideration of the origin and early evolution of amphibians, the astonishingly high diversity of these forms and their widespread geographic distribution from Australia to Greenland are of utmost importance.

✦ The Transition from Water to Dry Land

Which changes were necessary in the anatomy of fish to transform them into amphibians? Some of them emerge from comparative anatomy, such as respiration (gill to pulmonary respiration) and features linked to circulation. Others are proven through paleontological findings. On the basis of data now available, we are able to reconstruct quite precisely a sequence of anatomical changes that led from fish to amphibian, and see how these changes influenced their physiology, ecology and ethology. We are dealing with so-called mosaic evolution, where characteristics evolve at a different rate, some faster, others slower. This results in a pattern or "mosaic" of characters at different stages of evolution.

One of the primary changes is undoubtedly the transition from gill to pulmonary respiration. Surely this was not a sudden but a gradual change; present-day Dipnoi provide a quasi model view of this change even though, as we have noted, they are not linked to amphibian evolution. The lungs evolved from the swim-bladder, which originally performed a hydrostatic function. Since the walls of the swim-bladder are heavily vascularized with small capillaries and since the air in it is separated from the bloodstream only by an extremely thin cellular layer, the blood was

enriched with oxygen and this led to respiration. In these early phases, air was swallowed and reached the swim-bladder via the intestine-swim-bladder tract (ductus pneumaticus). Air reached the oral cavity mostly through the external nares and internal choanae. Gradually changes followed in the circulatory system—namely, the separation of body and pulmonary circuits, and subdivision of the heart.

Numerous changes occurred in the skeleton. For instance, *Ichthyostega's* ribcage was solid, in contrast to fish, whose ribs are thin. This was caused by the fact that the body of *Ichthyostega* was subject to gravity, whereas the body weight of fish is supported by the buoyancy of water and pressure is distributed evenly across the body's surface.

The transformation of the extremities is an excellent example of gradual evolution. Paired fins can be regarded as a polydactyl extremity in which the number of digits gradually diminished. *Ichthyostega* still featured seven toes on the hind limb, *Tulerpeton* six, and only true amphibians had the pentadactyl, a five-toe extremity typical of land tetrapods, diminished even further to four in the fore extremities of frogs. Upon looking at the timeline of this evolution, we find that the transformation of the fish fin into the extremity of a land tetrapod required approximately 9 million years. The weight-bearing and locomotory function of the extremities was made possible by the fact that they were joined to the axial skeleton (i.e., the spine), with fundamental differences between fore and hind limbs.

In the lobe-fin fishes the anterior extremities are still directly attached to the skull, more specifically to the rear margin of its dermal part (dermocranium). The joint is formed through a bone called the scapulocoracoid (which ossifies from the cartilage) fused to the inner surface of the dermal bone, called the cleithrum; the articular fossa that accommodates the head of the short and robust humerus is on the posterior surface of the scapulocoracoid. The pectoral fin projects from the ventral section of the posterior margin of the skull, as it does in other fish. This fin position would have been impractical for movement on land, for which the mobility of the head also needed to increase. For these two reasons the complex that included anterior extremities (pectoral fins) separated from the skull and gradually shifted along the spine to the rear. This resulted in the development of the pectoral girdle and of the anterior movable section of the vertebral column, the neck. During the first phase of adaptation to life on land, the supracleithra gradually diminished as well; one need only look at *Ichthyostega* and *Acanthostega*, although both still featured a



cleithrum. The most important dermal elements of the pectoral girdle in amphibians are the clavicle and the cleithrum, but the entire pectoral girdle is now—in contrast to fish—connected to the skull and the axial skeleton only by muscles.

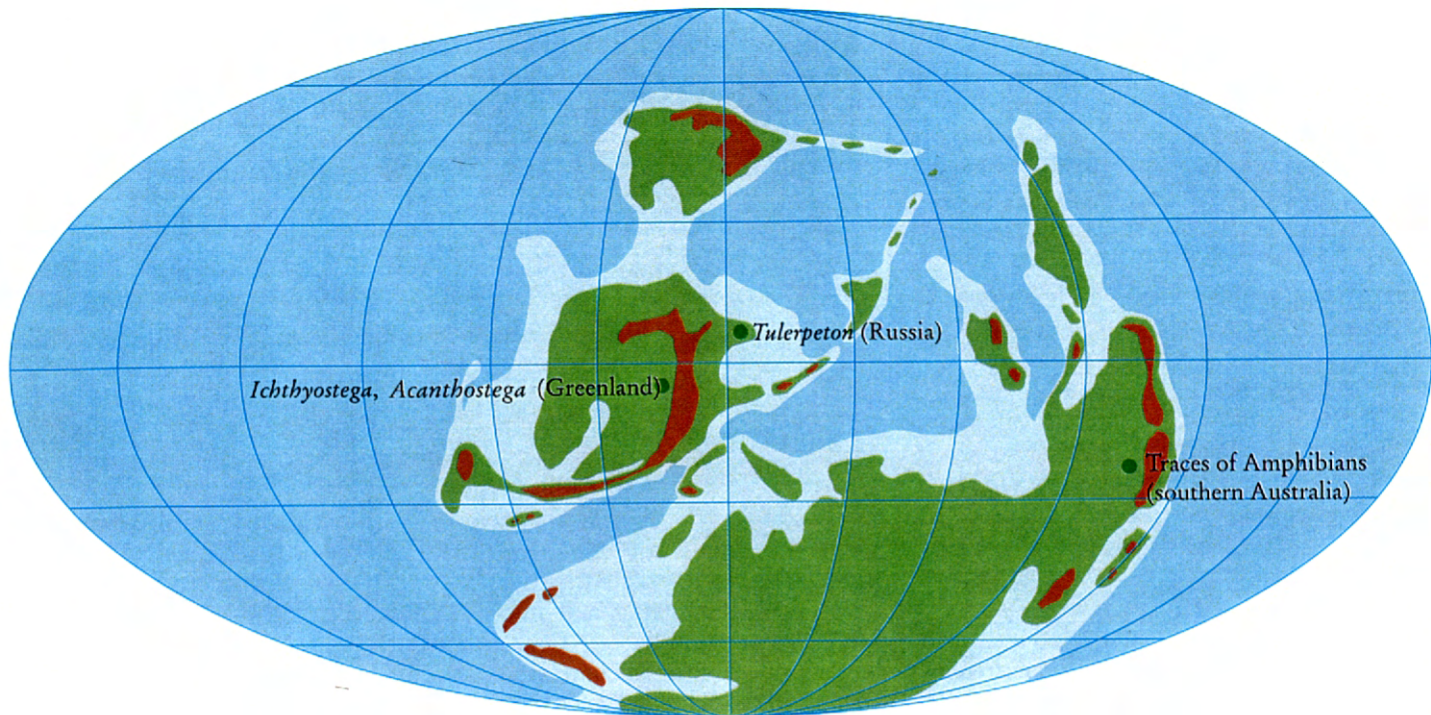
Upper jaw (middle) and lower jaw of Mastodonsaurus giganteus ("Haus der Natur," Salzburg).

Entirely different is the situation with the abdominal fins. In fish, they are anchored to a small pelvic girdle that is not connected to the spine, but instead imbedded in the trunk musculature. This has also been well documented in *Eusthenopteron*. *Ichthyostega* already had a well-formed triangular pelvic girdle with a fully formed articular fossa (acetabulum) to receive the head of the femur. Dorsally, this girdle was already syndesmotically joined to the ribs of the sacral vertebrae. In all tetrapods the pelvic girdle is readily divided into three sections: the dorsal bone fixed to the spine is called the ilium, the fore ventral bone is called the pubis and the rear ventral bone is called the ischium. The acetabulum is always between all these three bones. Thus the pelvis evolved into a horizontal, half-cylindric structure that is closed on the ventral side and whose dorsal ends are joined on the outside to the sacral vertebrae.

In contrast to modern amphibians, Ichthyostega had an impressive array of teeth. The sometimes long and pointed teeth were arranged in two rows (after Jarvik, 1996).

Noticeable changes occurred in the formation of the vertebrae. In fish, the intervertebral articula-





Map showing the estimated arrangement of continents in the Devonian Age, some 370 million years ago. Australian findings are especially important because they suggest that amphibians were able to colonize these far-flung regions quite rapidly. They may also indicate, however, that amphibians evolved simultaneously from different ancestral groups that were already distributed across all continents. The original taxonomic differentiation of amphibians was therefore a rapid process (after Scotese and Golonka, 1993).

tion is very simply constructed because the neighboring vertebrae are in contact with one another by the entire surface of the vertebral body. While this structure limits the mobility and flexibility of the skeleton, it is fully sufficient for fish. For life on land, however, away from water's buoyancy, the spine must cope with completely different stresses and loads. Two powerful articular surfaces developed between the neural arches (which enclose the spinal cord) of neighboring vertebrae; those pointing anteriorly are called the praezygapophyses, whereas those on the hind surface of vertebra are the postzygapophyses. These joints improved mobility in the spine.

Other Changes Associated with Land Colonization

The origin of pulmonary respiration was accompanied by a transformation or reduction of the branchial arches, also noticeable in the simplification of the pattern of the dermal bones of the skull. Clearly the bones of the gill cover—the opercular, praeopercular and subopercular—became less important and receded over time. *Ichthyostega* still featured tiny vestigial praeoperculars and suboperculars while, in *Acanthostega*, they had already disappeared completely. The skull remained otherwise unchanged, at least as far as its roof was concerned.

Considerable changes took place, however, in the inner parts of the skull, that is, in the parts that are formed from cartilage (chondrocranium). As we have already mentioned, the first major change to take place was in the branchial or gill arch elements. As in all fish, Crossoptery-

gii, too, had a hyoid arch behind the jaws. Its robust dorsal element, the hyomandibular, was located near the capsule of the inner ear. Ventrally, the hyoid arch continued in the large ceratohyal and small hypohyal, which were originally located on the ventral side of the gill basket. From the amphibian onwards, the hyomandibular is no longer connected to the ventral elements of the hyoid arch. In *Ichthyostega*, and even in amphibians from the Carboniferous, the hyomandibular had approximately the same size and shape as in crossopterygian fishes. As tetrapods evolved, it changed gradually into a small rod-like element, called the columella auris, which is capable of transmitting sound from the outer environment to the inner ear. It is the single element in amphibians, reptiles and birds, while mammals have two additional auditory ossicles.

From the ceratohyal, that is, from the element of the lower section of the hyoid arch to which remnants of the subsequent branchial arch were joined, the main part of the hyoid (i.e., the skeleton that supports muscles of the tongue) evolved in tetrapods. The movable tongue is an organ that appeared for the first time in amphibians, playing an important role in feeding. When land vertebrates take in food, it rests on the floor of the mouth cavity because of the earth's gravity. The food must somehow be transported from the mouth down the gullet and this function is performed by the tongue, a mobile muscular organ attached to the hyoid and in part to the inner surfaces of the lower jaw. The development of the lingual skeleton and the mobile tongue are yet another illustration of the changes necessary as vertebrates shifted from aquatic life to life on land.

Another important change occurred in the internal anatomy of vertebrates. This process is called the blockage of ossification and is best demonstrated by comparing the skull of a fish to the skull of an amphibian. The inner parts of a fish skull are formed by bone that arises from cartilage, and this, in turn, arises from soft connective tissue. In amphibians the sequence tissue → cartilage → bone tends to arrest at the stage of cartilage. Only few sections of this inner part of the skull (called the chondrocranium or endocranium) actually ossify, for example, the sphenethmoid, prooticum and the occipital. The other structures, including a major part of the palatoquadrate, remain in the cartilaginous stage.

Surprisingly, no changes touched vertebrae. There are many similarities in the structure of vertebrae in Devonian amphibians and lobe-fin fishes. A well-developed notochord is present in both; it is surrounded ventrally by the intercentrum and dorsally by a pair of the pleurocentra. Hence each body of vertebra is composed of several elements.

Ecological Aspects of Amphibian Origin

Let's look at the transition of vertebrates onto dry land in terms of the environment in which it took place. One important event was the appearance of the first terrestrial plants at the end of the Silurian more or less concurrently with the time when the first invertebrates colonized land (end of the Silurian/beginning of the Devonian). The plants, which soon covered the land surfaces during that age, enriched the earth's atmosphere with oxygen. Geochemical investigations have shown that the oxygen content in the Devonian was as high as 35 percent, much higher than today's 21 percent. This was probably why the Early Devonian was marked by unusual incidents of adaptive radiation. Within nearly all animal groups new lineages emerged—including Crossopterygii and Dipnoi. Adaptive radiation was therefore not limited to the terrestrial environment.

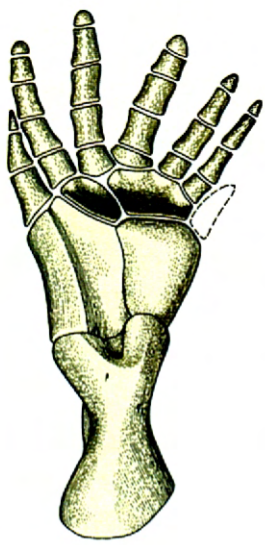
Today, we can only guess at what prompted fishes to move onto land. Was it the abundance of invertebrates (the main diet of present-day amphibians) who covered the land in the wake of the adaptive radiation mentioned above? This hypothesis fails to convince because *Ichthyostega* and *Acanthostega* were mostly fish eaters. American paleontologist Romer convincingly presented another hypothesis on why vertebrates colonized land. He argued that frequent droughts forced the crossopterygians to abandon desiccated ponds in search of other water sources. This led—at least according to Romer's hypothesis—to an evolutionary paradox: lobe-fin fishes adapted to life on land as a result of

their efforts to remain in water. The interpretation is also supported by current observations of fish behavior (not only recent lungfishes) in bodies of water that are drying out. There is an evidence that a long period of aridity occurred in the Devonian. Still, one shouldn't imagine heavy, one-meter-long fish trying to move on land. This behavior probably evolved first in juveniles, who are more adaptable than the adults. Paedomorphosis may have been another factor in land colonization. It is generally understood as a shift of capability to reproduce into the earlier stages of ontogeny (individual development). This phenomenon is well documented, for example, in recent salamanders.

Lessons from Paleogeography

It is very interesting to look at the origin of amphibians in context of paleogeography. For a long time, it was assumed that amphibians evolved in the Northern Hemisphere, or Laurasia, the northern *Ur*-continent, which has been the most prolific region for paleontological discoveries: the crossopterygian fishes *Eusthenopteron* and *Panderichthys*, the so-called transitional forms *Ichthyostega* and *Acanthostega*, and the findings of primitive amphibians from the Early Carboniferous were all found in this region. This, in combination with knowledge gained from comparative anatomy and developmental biology, led scientists to the conclusion that amphibians evolved from a single group of crossopterygian fishes. However, subsequent discoveries have modified this assumption because amphibian trackways from the Middle and Late Devonian were found in Australia, which was then part of the southern supercontinent called Gondwanaland, separated from Laurasia by sea. More recently still, new findings point to an unexpectedly diversified amphibian fauna from the Lower Carboniferous of Australia. This means that the process of anatomical transformation of fish to amphibians took place across a huge area of the entire tropic circle of that age, which stretched from present-day Greenland to eastern Europe, Southeast Asia, Australia, and back to the Northern Hemisphere. The position of this prehistoric tropic circle can be determined by reconstructing the position of the magnetic poles of that time with the help of geophysical methods; the results confirm what we already know from paleontological evidence on the distribution of early amphibians and their crossopterygian ancestors.

What conclusions can we draw from these observations, especially from the fact that transitional forms and early amphibians were so diversified in the geographically distant tropical zones of that age? They evolved from the freshwater crossopterygian fishes whose vast range



The Devonian tetrapod *Ichthyostega* combined fish and amphibian characteristics. It has been one of the most important palaeontological discoveries. *Ichthyostega's* extremities were already differentiated and corresponded to the basic structure found in tetrapod extremities (from Benton, 1990, after Jarvik).

of distribution, from present-day Greenland to Australia, separated by sea at that time, suggest that they could hardly have been taxonomically identical everywhere. Therefore it seems reasonable to assume that amphibians evolved from several phylogenetically different groups of crossopterygian fishes living in distant geographical regions.

In fossils the precise boundary between fish and amphibian is extremely vague and it is difficult to say whether *Ichthyostega* was "more amphibian" than its contemporary *Acanthostega*. What is probable is that the evolution of early amphibians was a product of diversity in their ancestors—the crossopterygian fishes of the subgroup Rhipidistia—preceding the actual evolution of amphibians *per se*.

Early Amphibians

As has been noted, it is difficult to draw a clear line between fish and amphibians in the Devonian. The situation changes drastically, however, when we compare fish with the amphibians of the Carboniferous. The latter already had unique adaptations which enabled them to live on land, and reached a high degree of morphological diversity. These early amphibians already included the group that later evolved into reptiles.

The fact remains, however, that there is a considerable time gap between the Devonian transitional forms and Early Carboniferous definitive amphibians with no paleontological record. At the end of this period the amphibians emerged in an evolutionary stage in which they existed for a staggering 200 million years, until the Early Cretaceous.

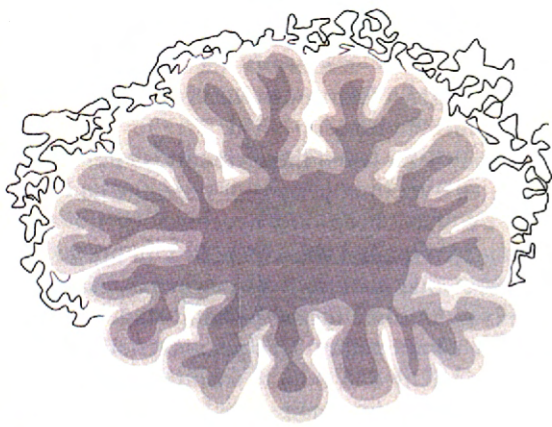
In the Northern Hemisphere, numerous sites with amphibian fossils have been discovered in Euramerica, a large continent in which present-day Europe and North America were united at that time. Especially well documented are amphibians from the Early Carboniferous. Even then, amphibians had splintered into two distinct phylogenetic lineages: Labyrinthodontia and Lepospondyli. Labyrinthodontia—as their name indicates—have specially formed teeth (a superficial layer of tooth, dentin, is folded like a labyrinth) and include a distinct group called Temnospondyli ("with divided body of vertebra"). In the region of present-day Europe, the Temnospondyli were represented by the genus *Pholidogaster* and in North America by *Greerpeton*. *Caerorhachis*, too, belonged to the Temnospondyli, although its exact taxonomic position within this group is still not quite clear. In addition to Temnospondyli, Labyrinthodontia in the Early Carboniferous included also other forms whose distinguishing feature were orbits

strangely shaped like keyholes; these amphibians are classified into the family Loxommatidae.

In addition to these readily classifiable forms, there were others with unusual features, which made them more difficult to classify. One of them is *Crassigyrinus*, with tiny legs and a snakelike body elongated to 50 inches (130 cm). The head—especially the preorbital section of the skull—was noticeably shortened. This amphibian was a permanent water dweller and a predator that fed exclusively on fish. Its phylogenetic position and relations to other amphibians are still hotly debated. Some argue that this was an advanced amphibian that returned to permanent life in water, while others maintain that it represents a primitive form that had not yet reached the evolutionary stage of life on land. As to its phylogenetic relations to other amphibians, it is generally regarded as a phylogenetic lineage that died out without descendants.

Besides labyrinthodont amphibians classified as Temnospondyli and Loxommatidae, another well-defined amphibian group existed in the Early Carboniferous, the Anthracosauria. Later, by the end of the Carboniferous, reptiles evolved from this group of amphibians; that is, the vertebrates completely independent on water. The main representatives of the Anthracosauria were *Eoherpeton*, *Westlothiana*, *Whatcheeria* and *Proterogyrinus* from Scotland, Iowa and West Virginia. *Westlothiana* shared so many features with reptiles that it was even classified among the reptiles for a certain time. Lepospondyli—after Labyrinthodontia the second largest group of Carboniferous amphibians described so far—displayed an evolutionary innovation in the form of a compact, undivided body of vertebra. The Early Carboniferous Lepospondyli are represented by the genera *Lethiscus*, *Adelogyrinus*, *Adelospondylus*, *Dolychopareias*, *Palaeomorgophys* and *Acherontiscus*.

All fossils mentioned up to this point were found in the Northern Hemisphere. This was a decisive factor to the wide-spread view that early amphibian evolution was limited to this hemisphere. However, Early Carboniferous amphibians recently discovered in northeast Australia point to the existence of highly diversified amphibian assemblages in geographically remote areas of the Southern Hemisphere; they are classified into the temnospondyl (i.e., labyrinthodont) family Colosteidae and the Anthracosauria.



Extinction of Lepospondyli

The first major crisis to hit amphibians occurred in the Early Permian. This was the extinction of the Lepospondyli—one of the major lineages in amphibian evolution. They included bizarre forms, and some authors believe that they stood in no phylogenetic relation to the lobe-fin fishes grouped in the Rhipidistia. Many of them had an extremely elongated, snakelike body with up to 230 vertebrae and vestigial extremities. Others had no legs whatsoever. Many features indicate that most of them were permanent water dwellers. Lepospondyli seem to have evolved into a highly specialized group of amphibians within a very short span of time, only to become extinct soon after. Some paleoherpetologists argue that they survive in present-day limbless caecilians. However, this argument cannot be proven since the period between the Early Permian and the Early Jurassic (to which the earliest caecilian fossils have been dated) was a long stretch for which no fossils have been found that might document such a relationship.

Successful Labyrinthodontia

Labyrinthodontia, on the other hand, survived the mass extinction at the end of the Permian, brought on by deterioration of climate in terrestrial ecosystems, without any visible damage. During this crisis, the most severe in the history of vertebrates, numerous invertebrates and

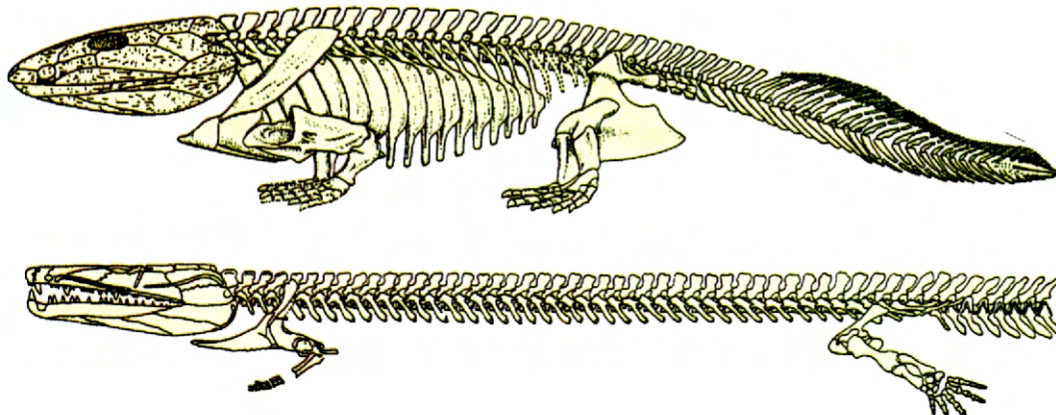
vertebrates died out, including groups that were widely distributed and very successful during the Paleozoic.

Labyrinthodont amphibians of the group Temnospondyli were among successful survivors. As early as the Carboniferous, some temnospondyl phylogenetic lineages became dominant, for example, those represented by the genera *Edops* and *Eryops* with a body length of up to 59 inches (150 cm). These were primitive forms, which is proven by their large columella, the only auditory ossicle in amphibians. On the other hand, another group of temnospondyls, previously called Rhachitomi, produced several progressive forms, many of them described from the Late Carboniferous and Early Permian deposits of the Czech Republic (e.g., *Cochleosaurus*, *Chelyderpeton*).

Rhachitomi, like other Triassic temnospondyls, inclined to paedomorphosis (abbreviated development), probably caused by climate deterioration toward the end of the Permian. Their larvae did not mature into fully developed adults, and in some the adult stage was eliminated altogether if their larvae became capable of reproduction (a phenomenon called neoteny). This has been proven in many findings of larval but fully ossified skeletons. A completely ossified skeleton is a sign of sexual maturity. Among these findings are *Doleserpeton* from North America, and European forms gathered under the name *Branchiosaurus*, as well as the Triassic amphibians *Capitosaurus* and *Dvinosaurus*. All have short skull, large orbits (eyeholes), and reduced mouth palate that are characteristic for temnospondyl larvae. Recent Anura exhibit a similar skull structure, which has led some to argue that they evolved from Permian and Early Triassic paedomorphic Temnospondyli.

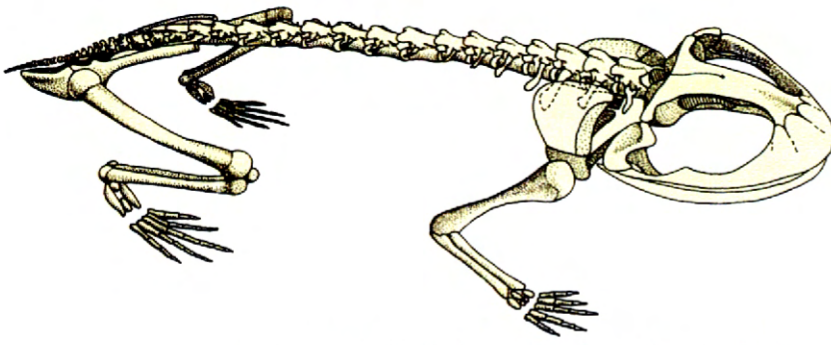
A special group among Paleozoic temnospondyl amphibians are Plagiosauria. Although their vertebrae consisted of two parts as in other Labyrinthodontia, they are different in the position of the boundary between them. Plagiosaurs had a short, wide skull, and impressions of their

One important factor in the argument for Crossopterygii as ancestors of early amphibians is their internal tooth structure. In Rhipidistia, as well as in all known Labyrinthodontia (but not in Lepospondyli), teeth display a characteristic plication in the wall. This is called a "labyrinthodontine" structure. To the left, section of an Eusthenopteron tooth (after Benton, 1990).



The massive ribs of *Ichthyostega* indicate the need for protecting the thoracic cage or chest and the body cavity against the compression that results from crawling across land. The largest ribs were located immediately behind the heavy skull, decreasing in size until they terminated just in front of the pelvic girdle.

Below: *Greerpeton* from the North American Carboniferous is a representative of the Colosteidae. It had a well-developed lateral line organ and was aquatic (after Carroll, 1988, from Jarvik, 1975, and Godfrey, 1986).



Triadobatrachus massinoti from the Triassic is the oldest finding of a frog-like amphibian. It probably belonged to an extinct sister group of recent Anura (after RAGE & ROCEK, 1989).

external gills have often been found, which indicates their neoteny.

Besides Temnospondyli, Anthracosauria were also successful amphibians from the Early Carboniferous onwards, and in the Late Carboniferous they gave rise to reptiles. Embolomeri were among the dominant anthracosaur groups. Their intercentrum surrounded the chorda like a ring, and both pleurocentra fused into the ring. These were predominantly aquatic predators (e.g., *Diplovertebron*), while others were adapted to life on land and resembled lizards. One of the latter, *Gephyrostegus*, corresponds to reptile ancestors.

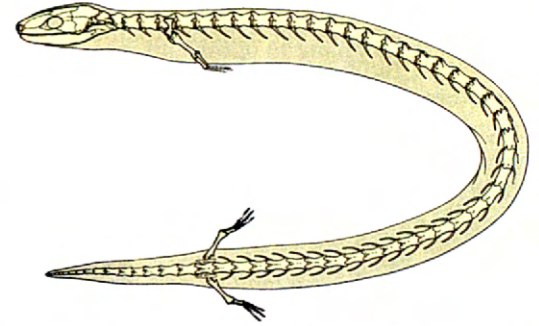
Seymouriamorpha, too, were advanced labyrinthodonts—their skeleton was so similar to a reptile skeleton that they were thought of as primitive reptiles for a long time. Only discoveries of their larvae with well-developed external gills proved that they had been amphibians. Numerous representatives of the anthracosaur family Discosauriscidae are known from the Late Carboniferous and Early Permian deposits of Central Europe.

Labyrinthodontia survived the crisis at the end of the Triassic and are documented in Jurassic sediments of Asia and Australia. They survived into the Cretaceous, which is evidenced by findings in Australia. The last survivor was described as *Koolasuchus cleelandi* (Brachiopoda, Temnospondyli). In summary, Labyrinthodontia can be regarded as an unusually successful group: they lived from the Late Devonian (if we include *Ichthyostega* and *Acanthostega*) until the Early Cretaceous, that is, altogether 230 million years. All present-day amphibians and reptiles evolved from them.

➤ The Origin of Modern Amphibians

At the end of the Permian, a worldwide climate shift occurred in whose wake 75 percent of existing amphibian families and 80 percent of reptile families became extinct. The climate shift had its greatest impact on ectotherms because it involved dramatic drops in temperatures. These resulted in greater seasonal differences, which meant shortened periods of activity and prolonged periods of hibernation for amphibians. The shortening of the breeding season

influenced larval development, because lower temperatures—possibly accompanied by frequent dry spells—meant that the larval phase lasted longer. When cooler weather began before metamorphosis, larvae were forced to hibernate. And when these climatic conditions persisted over long periods of time, the gonads may well have been fully developed even before the metamorphosis was completed. In other words, sexual maturity was reached as early as in larvae. In some forms the adult stage was eliminated altogether. This phenomenon is called neoteny and is quite frequent in various groups, especially among amphibians. As we have already mentioned, these mechanisms played a very important role, especially in the origin of Anura. That Anura evolved from labyrinthodont ancestors is easily proven in a comparison with larval Labyrinthodontia. One of the diagnostic features of frogs and other modern amphibian groups is noticeable underdevelopment of the skeleton. Such reductions are evident in the temnospondyl larvae. We can readily imagine how the skull of a temnospondyl larva transformed into the skull of a frog, as a number of fossils offer paleontological proof of this process.



Right: Eoecilia micropodia from the Jurassic is the oldest fossil discovery of a Caecilian. These creatures still had tiny extremities; in recent Caecilians neither extremities nor pelvic girdles remain (after JENKINS & WALSH, 1993).

Anurans have yet another feature that distinguishes them from all other amphibians: their frontals and parietals are merged into one single element called the frontoparietal. This advanced stage in the evolution of the Anura is documented by *Triadobatrachus* from the Lower Triassic of Madagascar. Its skeleton represents an intermediate stage demonstrating the transition from the labyrinthodonts to anurans. Its skull is difficult to tell apart from a frog's or toad's skull; its postcranial skeleton, on the other hand, is reminiscent of labyrinthodont ancestors. As anurans evolved, the spine shortened and the number of presacral vertebrae decreased. At the same time, the ilium lengthened toward the posterior, which ensured a certain minimum distance between anterior and posterior extremities. There seems to exist some biomechanical reasons why this minimum distance must be maintained. The skeleton of *Triadobatrachus* shows that it was not yet capable of jumping; instead, it moved forward by means of crawling.

The South American tongueless frog (Pipa arrabali) is a member of the family Pipidae, of which many fossil findings exist. Many findings date from the Cretaceous.



After *Triadobatrachus* comes a gap of more than 30 million years for which we have no fossil evidence of the Anura, although this period was vitally important: it was during this time that the definitive shape and anatomy of Anura were established and they spread across the world. The oldest representative of a "true" anuran is *Prosalirus bitis* from the Early Jurassic. Its pelvis indicates that these frogs already performed saltatory movements. Other anurans from the Jurassic can be classified into the families Leiopelmatidae (*Vieraella*, *Notobatrachus*) and Discoglossidae (*Eodiscoglossus*); both families have survived up to the present time. The family Pipidae is also an ancient group of the Anura, although its contemporary representatives (*Pipa*, *Xenopus*) derive from the original anuran scheme.

When we assess the evolution of Anura, it is obvious that they were particularly successful amphibians despite their "conservative" nature. One needs only consider the fact that their definitive anatomy was established 200 million years ago, that is, or at the time the first dinosaurs appeared. Although Anura, and especially their larvae, are sensitive to environmental changes, they survived the mass extinction at the end of the Cretaceous. The only group of Anura to die out were the Palaeobatrachidae. The uniform anatomy and morphology of the anurans are rooted in their mode of life. Therefore, evolutionary diversification is expressed, above all, in their ecology and reproduction strategies.

Caudata ("tailed amphibians") have an underdeveloped skeleton too. However, their frontal and parietal have remained as independent bones, and they have a tail, which is also an original feature of their ancestors. Moreover, the larvae of Caudata have teeth (teeth are lacking in anuran tadpoles). Like in the Anura, in the tailed amphibians, too, neoteny was the most important mechanism of their evolution and, among their contemporary representatives, neoteny is still quite common. Neoteny, as an evolutionary factor, can be traced in the European Tertiary salamandrids, when from fully developed adult forms (e.g., *Chelotriton*) living in Eocene tropical climate evolved, as a result of the Oligocene drop of temperature, neotenic larvae (*Brachycormus*). From *Brachycormus* evolved the recent genus *Triturus*. Among well-known Oligocene neotenic larvae also belongs *Andrias* (hellbender), which has survived until the present. It is obvious that Caudata are a highly adaptable group that survived the extinction at the end of the Mesozoic, as did Anura. All representatives of recent and fossil Caudata originate in Laurasia and have amphicoelous and opisthocoelous vertebrae. Only a short time ago, a possible representative of Caudata (but with



procoelous vertebrae) was discovered from the Cretaceous of Gondwanaland, in Bolivia.

Caecilians (Gymnophiona) are the third group of present-day amphibians. Their recent representatives are limbless and do not have the shoulder and pelvic girdles, while fossil caecilians (e.g., *Eocaecilia micropodia*) still display tiny extremities. The aforementioned genus *Eocaecilia* from the Early Jurassic in Arizona is the earliest known caecilian and it is remarkable that the earliest known anuran *Prosalirus* was also found in the same site. Gymnophiona are therefore at least as old as are Anura. With their small legs, fossil caecilians resemble some salamanders, although they are readily distinguishable from them by their complete skull roof. Findings of fossil caecilians are extremely rare. A new, as yet unnamed, finding from the Lower Cretaceous of Bolivia has been reported, and fossil evidence also exists for the genus *Apodops* from the Paleocene of South America.

Left: The giant salamander *Andrias scheuchzeri*. In 1726, Swiss doctor and natural scientist Johann Jakob SCHEUCHZER (1672-1733) interpreted a fossil of this kind from the Öhningen quarries as a human remnant from the time before the Flood ("Homo diluvii testis: skeletal remains of human drowned in the Flood.")

Top right: Skeleton of giant frog *Latonia seyfriedi*. (Both reconstructions; "Haus der Natur," Salzburg. Öhningen in Baden-Württemberg, approx. 13 million years ago).

The oldest amphibian fossils

The oldest known amphibian fossils are *Ichthyostega stensioei* Säve-Söderbergh, 1932 and *Acanthostega gunnari* Jarvik, 1952. Both are from Greenland (Mount Celsius) and date back to the same age (Upper Famennian, Upper Devonian, circa 350 million years). *Ichthyostega* was approximately 1 yard (1 m) long and still had some fish characteristics (fishtail, remnants of opercular bones), but obviously moved on land. *Acanthostega* was somewhat smaller and lived in water.

The oldest known Anura is *Prosalirus bitis* Shubin and Jenkins, 1995 from the Lower Jurassic in North America (Pliensbachian, circa 180-185 million years), Gold Spring Quarry, Arizona, USA. Isolated skeleton fragments were discovered.

The oldest known Urodela is *Karaurus sharovi* Ivakhnenko, 1978 from the Upper Jurassic (circa 150 million years) in southern Kazakhstan.

The oldest known caecilian is *Eocaecilia micropodia* Jenkins and Walsh, 1993 from the Lower Jurassic (Pliensbachian, circa 180-185 million years) in North America, Gold Spring Quarry, Arizona, USA. The skull and parts of the post-cranial skeleton with rudimentary extremities were discovered.