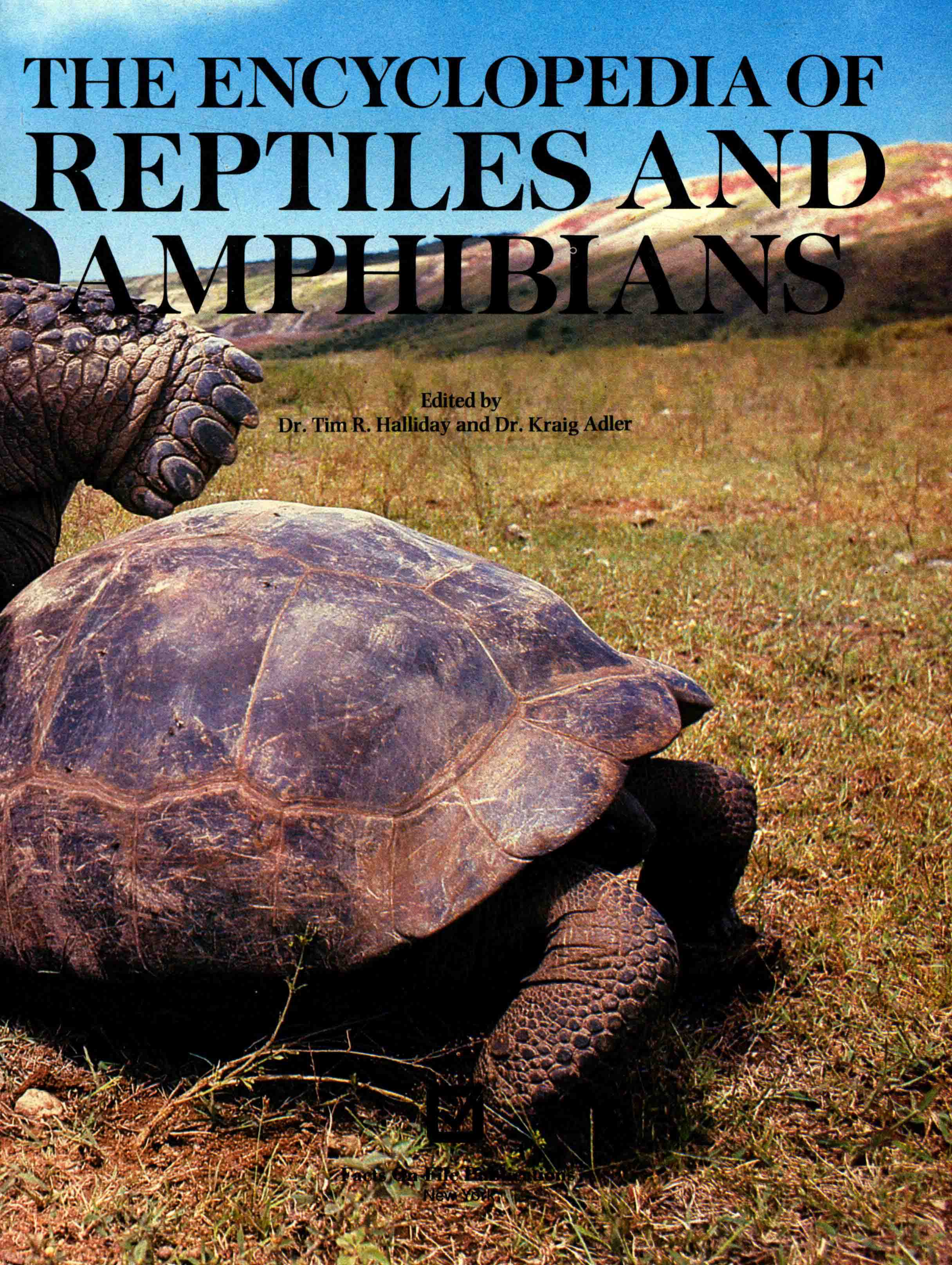
THE ENCYCLOPEDIA OF REPTILES AND AMPHIBIANS

Edited by
Dr. Tim Halliday and Dr. Kraig Adler



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Left: male Golden toads (Bufo periglenes) at mating pond (Michael Fogden); half-title: White's tree frog (Litoria caerulea) (Bruce Coleman); title page: Galapagos giant tortoises (Geochelone elephantopus) courting (Oxford Scientific Films).

PREFACE

"These foul and loathsome animals" . . . "their Creator has not exerted his powers (to make) many of them." These remarks about amphibians and reptiles are attributed to the famous Swedish scientist Carolus Linnaeus who, in the mid 1700s, established the system for naming species that is still in use today. Even before this time these "lower forms" of life were regarded as less worthy of study and interest than the "higher" mammals and birds. Such is the historical burden which amphibians and reptiles have borne for many centuries. Today their joint study continues under the name of a single discipline (herpetology: from the Greek *herpeton*, meaning "crawling things"). This also owes more to tradition and to the fact that methods of collecting and keeping amphibians and reptiles have always been very similar, than it does to any great degree of similarity between them. Herpetologists have found that in many ways the differences between the two groups are more marked than their similarities. They have also found that there is much in particular about these animals to arouse fascination, and much to learn from them about animal life in general. An upsurge of interest in these animals has been one of the results.

Apart from the way in which they maintain body temperature and some other similarities, such as having a single ventricle in the heart (birds and mammals have two), amphibians and reptiles differ markedly. Amphibians have a soft, smooth skin that is permeable to water; reptiles are covered in coarse, dry scales that are impervious to water. The eggs of amphibians lack a waterproof outer covering and are always laid in water or in damp places, whereas the reptilian egg has a thick parchment-like or hard shell that holds moisture in, enabling the young to develop within it even on dry land.

These differences reflect the significant position that each group occupies in the evolutionary history of the vertebrates. The amphibians made the transition from the totally aquatic life of fishes and evolved the ability to move about freely on the land. This involved a radical reorganization of the skeleton, particularly of the bones in the limb, in comparison to that in the fins of fishes. It also involved an elaboration of the ability to breathe air, rather than dissolved oxygen, that had already evolved in their lungfish ancestors. The reptiles took the conquest of the land a stage further and, by acquiring an impermeable skin and an impermeable covering for the egg, became completely emancipated from standing water. In different ages, nature has, in fact, exerted its powers to make a great many of these creatures, for early in their history, both groups were a much more prominent feature of the Earth's fauna than they are today. The reptiles were, for many millions of years, the dominant form of life. Each, however, has become much less important in terms of numbers of species so that today the amphibians, with about 3,000 species, are the smallest vertebrate group, while the reptiles, at around 6,000 species, are less numerous than either fishes or birds.

In the present upsurge of interest in amphibians and reptiles among professional biologists, the science of herpetology is making significant contributions to zoological knowledge that compare favorably with those made in ornithology and mammalogy. Partly this is due to the realization that the traditional distinction between "higher" and "lower" vertebrates is no longer valid. Amphibians and reptiles have been thought inferior on account of being "cold-blooded" in contrast to the "warm-blooded" birds and mammals. These terms are now thought misleading and are no longer used by biologists (see p70–71).

Amphibians and reptiles are not degenerate or inferior in comparison to birds and mammals; they simply go about things in different ways and are, in many respects, just as successful. They are, for example, much more efficient in their use of energy and, because of various special features that they possess, are able to live in environments that are inaccessible to other groups. Most notably, reptiles are able to thrive in the driest deserts where birds and mammals cannot.

Another factor in the enhanced status of amphibians and reptiles has been the recognition that they are much more diverse than was previously realized. Modern biology has its foundations in Europe, a continent that is relatively impoverished in terms of numbers of amphibian and reptile species compared with the Americas and, especially, the tropics, where new species are still being discovered. Finally, biologists have discovered that amphibians and reptiles are ideal subjects for study within a variety of different zoological disciplines.

The science of zoology is like a tapestry, with numerous interwoven threads. In one direction run several distinct disciplines, such as anatomy, physiology, ecology and behavior, which consider similar processes in a variety of animal types. In the other direction are those branches of zoology that each consider just one kind of animal, such as insects, fishes or birds. This book reflects the complex, integrated nature of zoology inasmuch as, while it is concerned with only two classes of animals, it also considers phenomena, in physiology and behavior for example, that are found in a wide variety of animals.

The formal plan of the book follows the tapestry's threads in the direction of classification. A major article introduces class Amphibia and another introduces class Reptilia, detailing their evolutionary history and outstanding aspects of physiology, life history and behavior.

A separate main entry is devoted to each of the three orders of amphibians and to each of the six orders and suborders of reptiles. Each entry is introduced by an opening panel giving the number of its species, genera and families, its distribution and a summary of habitat, size, color, reproduction and longevity. The scale drawings indicate the ranges of sizes to be found in the group compared to a whole or part 6-foot (1.8m) man. The main text deals in general with the order's characteristic physiological forms and the varieties of the niches which it has occupied. A major portion at the end of the main text gives a separate description of each of the group's families, highlighting important genera and species.

The pages following the articles on five of these main entries collect fact-box summaries of the families within the groups in question. Each fact box gives the numbers of species and genera in the family, their general distribution, the range of sizes, colors and body forms and, where applicable, the distinctive points of life history. The fact box lists species or genera referred to in the text, together with their scientific names.

At several points, we follow threads running in the other direction, highlighting aspects of the study of amphibians and reptiles which have made it an increasingly important discipline

African chameleon (*Chamaeleo chamaeleon*) (NHPA).

within zoology as a whole. Articles of this kind appear as double-page special features following the two introductions and certain of the main entries, and they also appear within the main entries as shorter boxed features. Here we have allowed authors to report in greater depth on the most up-to-date understanding of fascinating aspects of amphibian and reptile life.

The authors often emphasise the need to conserve species threatened with extinction and by mismanagement. Many species and subspecies described in these pages are listed in the Appendices I to III of the Convention on International Trade in Endangered Species of Wild Flora and Fauna (CITES). The Red Data Book of the International Union for the Conservation of Nature and Natural Resources (IUCN) also lists numerous species as at risk. In this book the following symbols are used to show the status accorded to species by the IUCN at the time of going to press: [E] = Endangered—in danger of extinction unless causal factors are modified (these may include habitat destruction and direct exploitation by man). [V] = Vulnerable—likely to become endangered in the near future. [R] = Rare, but neither endangered nor vulnerable at present. [I] = Threatened but status indeterminate. [K] = Threat suspected but status unknown. We are indebted to the IUCN Monitoring Centre, Cambridge, England, for giving us the very latest information on status. The symbol [•] indicates entire species, genera or families, in addition to those listed in the Red Data Book, that are listed in CITES.

This book is the fruit of labors by an international team of expert authors, all actively engaged in disciplined research into the lives of amphibians and reptiles, some reporting directly from far corners of the globe where their work has taken them. To their efforts have been added those of the photographers and illustrators (particularly David Dennis) whose work has so skillfully brought these pages to life. Acknowledgements are due to all of them and especially my coeditor Dr Kraig Adler, for his painstaking and tireless attention to the accuracy and consistency of all of the information that we have included, and to Dr Graham Bateman and his team of editors, designers and researchers at Equinox (Oxford) Limited who made this information into a book. Finally it is for the reader to decide whether Linnaeus' "foul and loathsome" creatures are in fact some of the most exciting and interesting animals alive today.

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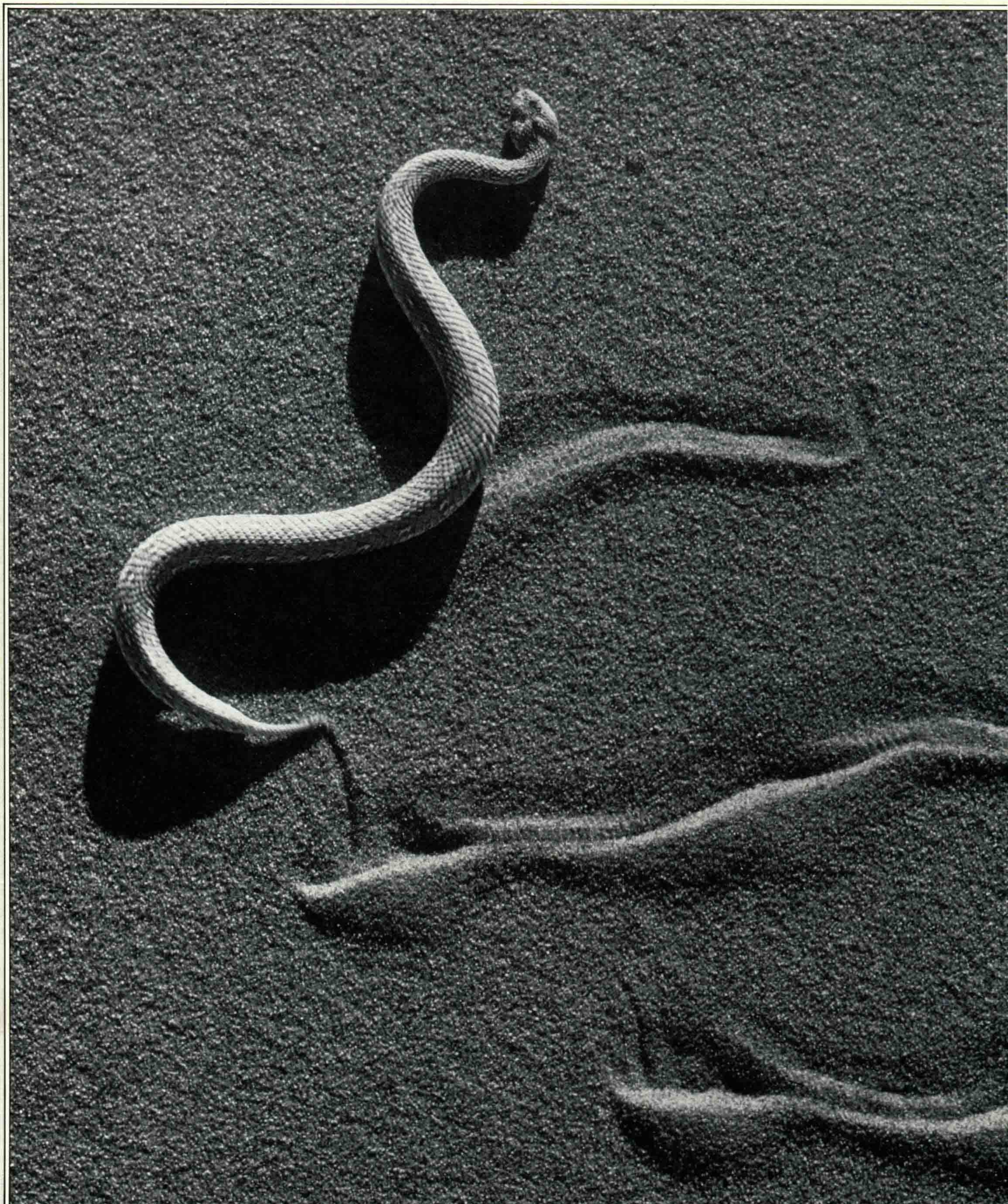
CONTENTS



Sidewinding adder (Bitis peringueyi) in desert (Anthony Bannister).

THE ENCYCLOPEDIA OF REPTILES AND AMPHIBIANS

AMPHIBIANS

CLASS: AMPHIBIA
Three orders: 34 families; 398 genera; 4,015 species.

Caecilians
Order: Gymnophiona (Apoda)
One hundred and sixty-three species in 34 genera and 5 families.

Salamanders and Newts
Order: Urodela (Caudata)
Three hundred and fifty-eight species in 60 genera and 9 families.
Includes: **Alpine newt** (*Triturus alpestris*), **American mole salamanders** (genus *Ambystoma*), **amphiumas** (family Amphiumidae), **Asiatic salamanders** (family Hynobiidae), **axolotl** (*Ambystoma mexicanum*), **Fire salamander** (*Salamandra salamandra*), **giant salamanders** (family Cryptobranchidae), **lungless salamanders** (family Plethodontidae), **mudpuppy** (*Necturus maculosus*), **olm** (*Proteus anguinus*), **Red salamander** (*Pseudotriton ruber*), **Red-spotted newt** (*Notophthalmus viridescens*), **sirens** (family Sirenidae).

Frogs and Toads
Order: Anura (Salientia)
Three thousand four hundred and ninety-four species in 303 genera and 20 families.
Includes: **fire-bellied toads** (genus *Bombina*), **Gastric-brooding frog** (*Rheobatrachus silus*), **Hamilton's frog** (*Leiopelma hamiltoni*), **Pouched frog** (*Assa darlingtoni*), **midwife toads** (*Alytes cisternasii*, *A. obstetricans*), **poison-arrow frogs** (family Dendrobatidae), **Seychelles frog** (*Sooglossus sechellensis*), **Surinam toad** (*Pipa pipa*), **Tailed frog** (*Ascaphus trueii*), **true tree frogs** (family Hylidae).

THE amphibians—frogs, salamanders and caecilians—display a stunning variety: some animals with tails and others without, some looking like snakes or lizards, others hopping on long hind legs, and with colors ranging from drab browns to iridescent blues, greens and reds.

Yet of 40,000 known species of vertebrates (animals with backbones), only about 4,000 are amphibians. They are the smallest class of living vertebrates, all that remain of a once dominant class of animals, some the length of a moderate-sized crocodile, that flourished several hundred million years ago.

Amphibians are an important group for study because they were the first vertebrates to conquer land and also the group which later gave rise to reptiles (and they, in turn, to mammals and birds). Living amphibians are divided into three orders: Urodela (the salamanders, including newts and sirens), Anura (the frogs, including toads) and Gymnophiona (the legless caecilians).

The word "amphibian," from the Greek *amphibios*, means a being with a double life; specifically, one that lives alternately on land and in water. Such a double life is the rule for Amphibia, but there are exceptions; some species are permanently aquatic and others completely terrestrial. All are ectotherms, using environmental temperature to regulate body temperature.

No structure uniquely defines all amphibians—as feathers do birds—so one must resort to a combination of characteristics. Further complicating any definition is the fact that living forms have diverged significantly from the primitive fossil ones and there is no information at all on certain key features in the fossil forms.

Evolution and Fossil History

Some of the oldest known amphibians are *Metaxygnathus*, found in the freshwater beds of late Devonian deposits in Australia, and *Ichthyostega* and *Acanthostega*, found in similar beds in Greenland. All date from about 360 million years ago. Greenland may seem an unlikely place for any amphibian to have lived but its location and climate were very different during the Devonian period (410–345 million years ago), when it straddled the equator and lay within a moist and warm tropical region extending from present-day Australia through Asia to northeastern North America. Very recently, a single amphibian footprint was reported from still older, mid-Devonian deposits in southern Brazil, which was nontropical at the time.

Until the early Jurassic (about 190 million years ago), all of the earth's land mass was united into a single supercontinent called Pangaea. Thus, it is not surprising to find evidence that the earliest amphibians rapidly spread to now distant lands including Europe and eastern North America and, by the early Triassic (about 230 million years ago), even to Antarctica.

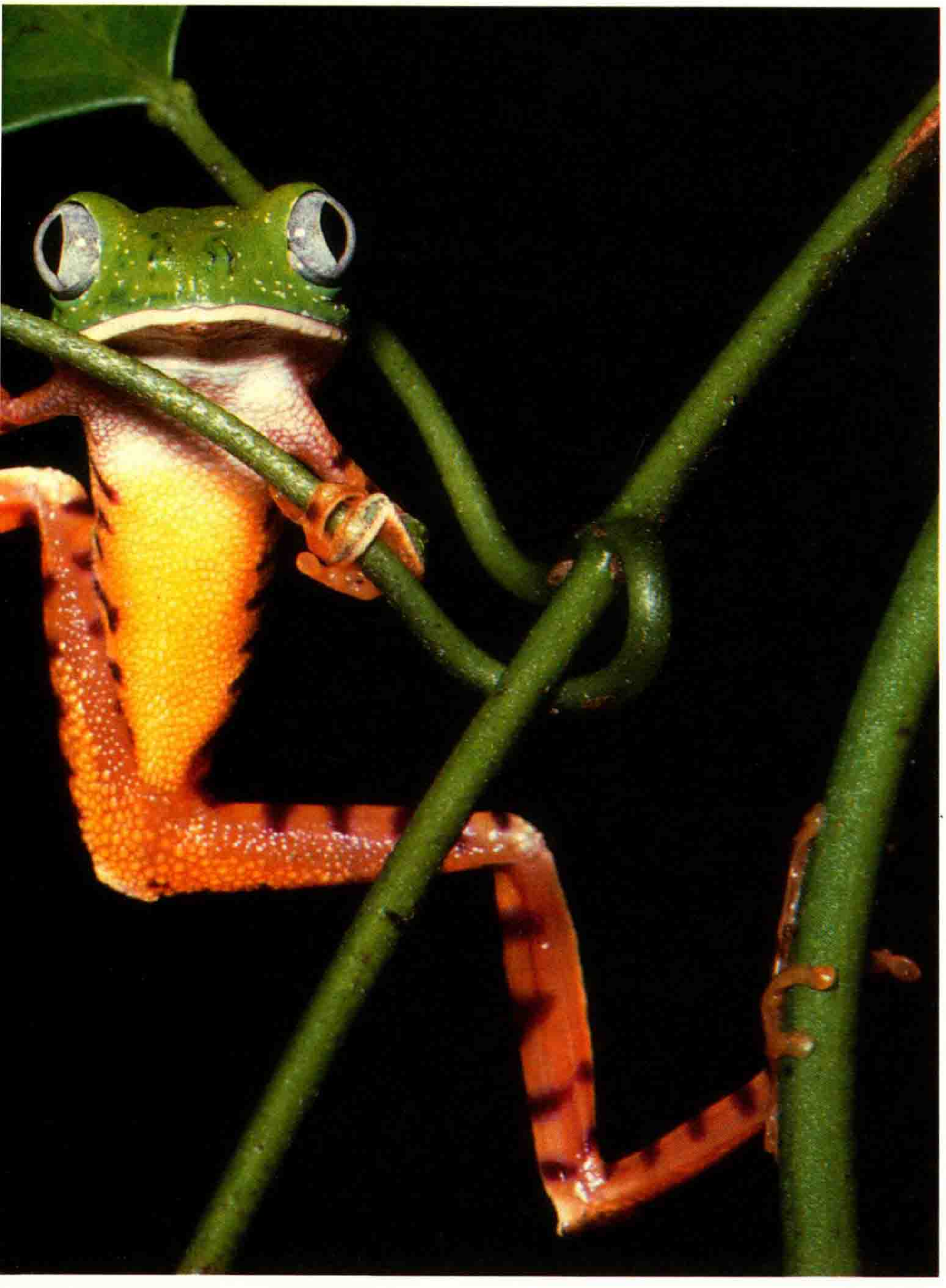
The most likely ancestors of these early Amphibia were lobe-finned fishes of the order Crossopterygii. Unlike other members of the class Osteichthyes, which had fins supported by cartilaginous rays, the fins of crossopterygians had bony elements comparable to those of the limbs of land vertebrates (tetrapods).

Furthermore, the crossopterygians had lungs and some had internal nostril openings (nares), so air could be taken into the lungs when the mouth was closed or when only the external nares were above water. Internal nares are characteristic of land vertebrates. In most fish the external nares serve only a sensory function; they lead to blind pockets not connected to the mouth cavity.

Ichthyostega was similar to the extinct crossopterygian fish *Eusthenopteron*, found in Devonian deposits in Europe and North America. Both had lungs and internal nares

► **Slender amphibian.** The Many-ribbed salamander (*Eurycea multiplicata*), a North American lungless salamander, displays the elongated body, long tail, small limbs and smooth, moist skin typical of salamanders. This is one of many species with vertical rib grooves along its body.

▼ **Agile climber.** Like all frogs, the Barred leaf frog (*Phyllomedusa tomopterna*), a tree frog of the Amazon rain forest, has hind limbs much longer than its forelimbs. The very large eyes of frogs reflect the importance of vision, in particular for locating prey.



and shared two traits found only in some other crossopterygians and in the earliest amphibians: a brain case divided transversely into anterior and posterior portions and, secondly, an infolding of the enameled surface of the teeth that creates, in cross section, a complex labyrinthine pattern.

Ichthyostega, although unquestionably amphibian, retained a number of fish-like characteristics, among them the opercular bones—remnants of bones that in fish connect the gill covering to the cheek—and a tail fin supported by bony rays. But the limb and girdle structure of ichthyostegids had already fully reached the early amphibian condition; thus, the earliest amphibians (and land vertebrates) remain undiscovered and must be sought in even older deposits.

How did the transition to land come about? The classic explanation has been that the Devonian was a period of severe droughts. Fish with sufficiently strong fins could avoid stranding and death by crawling to available pools. According to this idea, land vertebrates could have evolved as a by-product of selection originally for increased agility in finding water, not land! New evidence casts doubt upon the scenario of periodic droughts, however, and it seems likely that the Devonian was a time of relatively continuous moist environments, at least in tropical regions.

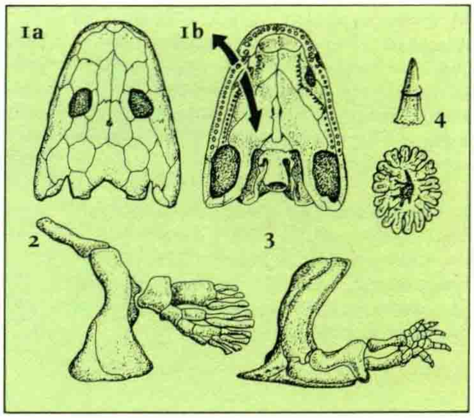
Possibly some of the features associated with the first amphibians actually developed in the aquatic environment. For example, the development of a functional neck and the separation of the skull from the pectoral girdle to accomplish this may have developed in protoamphibians, permitting sudden sideways movement of the head to capture prey in water. Perhaps this change was a preadaptation later facilitating the capture of prey on land.

One or more of the following factors are believed to have led to the evolution of land vertebrates. During Devonian times aquatic environments, with their enormous diversity of fish and other organisms, contained many more competitors and predators than did the land, and land also may have been a safer place to deposit eggs and for juveniles to survive. The water of the warm Devonian swamps in which amphibians arose was probably poor in oxygen, especially in the shallows, but the fish ancestors of amphibians must have had lungs, as all of their living descendants do. Possibly these fish congregated in shallow waters, and ventured occasionally onto land. It might have been the more agile juveniles that did so, in order to exploit insect and other invertebrate food. Although this transition doubtless occurred over a period of millions of years, there is no known fossil record of these stages. Some have even argued that the fish-to-amphibian transition occurred more than once, making amphibians, including modern forms, members not of a single line, but of several that evolved independently.

In becoming terrestrial, amphibians overcame numerous challenges, although some changes could have occurred even in a shallow water habitat. On land, gravity became a key factor molding the development of the skeleton. Without the buoyancy of water, the body was suspended from the vertebral column which, in turn, had to be supported by the limbs and limb girdles. When the animal rested on the ground, a well-developed rib cage, as was present in *Ichthyostega*, prevented injury to internal organs. The elongated neural arches and articulating surfaces of the vertebrae distributed the gravitational forces more evenly along the vertebral column.

The skin of living amphibians, which is moistened by the secretions of numerous mucus glands, is not a passive outer layer but plays a vital and very active role in water balance, respiration and protection. It is highly permeable to water, especially in terrestrial species. Aquatic forms have reduced permeability to offset the inflow of water by osmosis.

Although most amphibians are restricted to moist habitats, there are specializations that permit many species to live in otherwise inhospitable environments. For example, desert toads create an osmotic gradient across their skin by retaining urea in their urine, thus permitting water uptake from extremely dry soils. Most terrestrial frogs possess a patch of skin, rich in blood capillaries, in the pelvic region that allows uptake of water even from a thin surface



▲ **Anatomy of early amphibians.** (1) Skull of *Ichthyostega* from above (**a**) and below (**b**), showing internal nostril openings. (**2**) Shoulder girdles and fin of crossopterygian fish which had bony elements comparable to those of (**3**) primitive ichthyostegan amphibians. (**4**) Labyrinthodont tooth, whole and in cross section at base.

▼ **Giant amphibians of another age.** The Triassic (225–190 million years ago) saw crocodile-sized amphibians such as (**1**) *Mastodonsaurus*, 4m (13ft) from snout to tip of tail; (**2**) *Diadectes*, 3m (10ft), and (**3**) *Eryops*, 1.5m (5ft).

film. Other frogs and a few salamanders form a cocoon of shed skin to reduce water loss, and some tree frogs reduce evaporative water loss by wiping fat-like skin secretions over the body surface.

On the other hand, loss of body water through the skin is used in some species as a method of temperature regulation through evaporative cooling. In most species the skin and surfaces in the mouth cavity also serve a respiratory function, since dissolved gases pass across them; the numerous members of one family of salamanders (Plethodontidae) have lost lungs altogether and depend entirely upon this method of gas exchange.

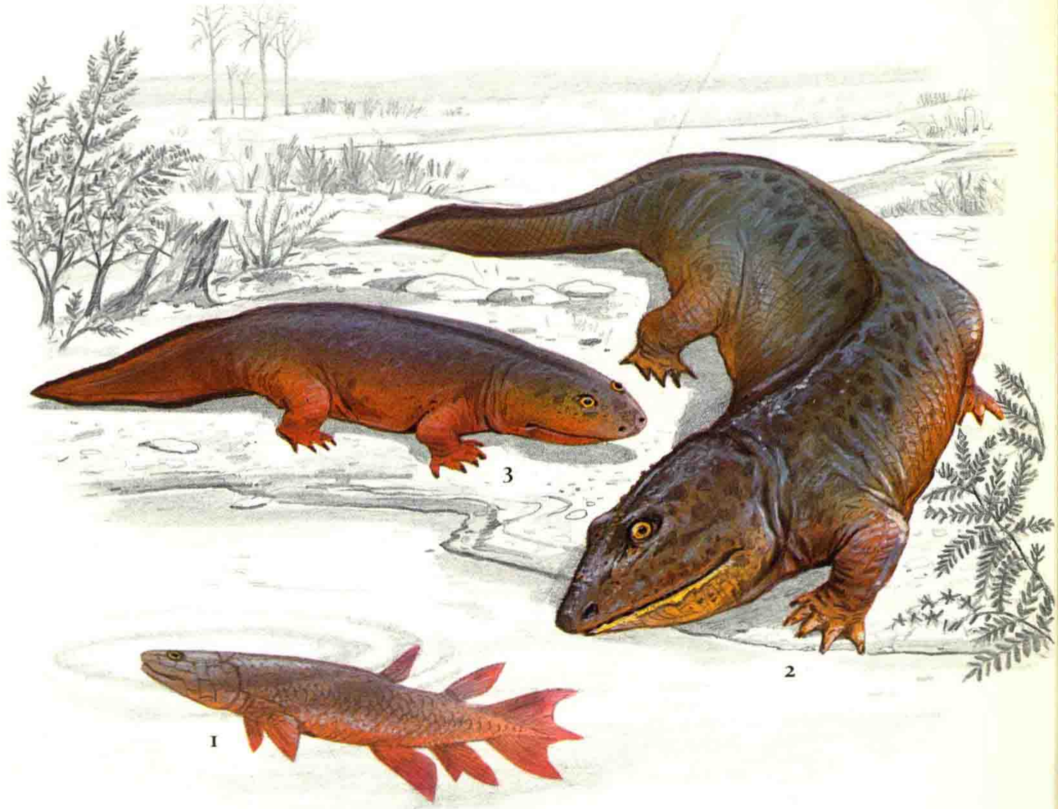
Practically nothing is known about the skin of the earliest amphibians. By inference, it is often assumed that they too had soft naked skin, but recent fossil evidence suggests instead that scutes covered their undersides. Some types had osteoderms on the upper surfaces.

After the appearance of the first amphibians in the late Devonian, a period of rapid evolution occurred resulting in an enormous diversity of amphibian types. However, by the end of the Triassic, about 155 million years later, nearly all of them had become extinct. Some were truly enormous in size. The largest, *Mastodonsaurus*, had a skull 125cm (49in) long and a length estimated at 4m (13ft); the largest living amphibians, by comparison, are the Asiatic representatives of the giant salamanders, which reach 170cm (67.5in).

Many species were aquatic and possessed gills, whereas others were adapted to land. Although many were heavy-bodied and lizard-like in build, there were some truly bizarre types including legless, eel-shaped forms and others with extremely wide heads drawn back into peculiar horns.

These ancient amphibians were found on all land masses and were the dominant land animals of their day. Mammals and birds did not evolve until after most of these ancient amphibian types had become extinct, but the first reptiles evolved from amphibians very early in the Carboniferous period (about 345 million years ago). The earliest known reptiles resemble members of the amphibian order Anthracosauria.

As evidence of this close similarity, one anthracosaur (*Seymouria*) was long considered to be a primitive reptile. Recently, however, fossilized aquatic larvae were found, suggesting that seymouriamorphs did not lay shelled eggs. Nevertheless, the earliest reptiles were generally small and their great adaptive radiation did not begin until late in the Permian (about 225 million years ago) at which time few of the ancient groups of amphibians still survived.

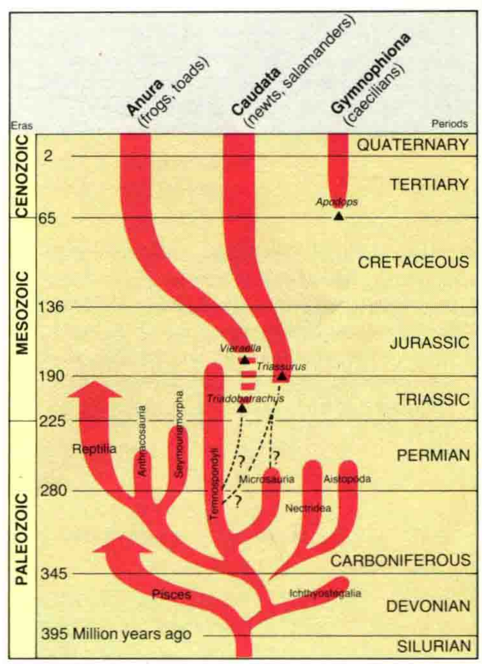


Modern Amphibians

In contrast to our knowledge about the origin of reptiles, the ancestry of modern amphibians is a puzzle, largely because there are no fossils linking the ancient Paleozoic forms to any of the three living orders. The earliest known fossil (*Triadobatrachus*, of the early Triassic) is already frog-like in some of its features and the earliest true salamanders (from the late Triassic), true frogs (from the early Jurassic) and caecilians (from the early Tertiary, about 65 million years ago) are already as specialized, each in its own way, as modern forms.

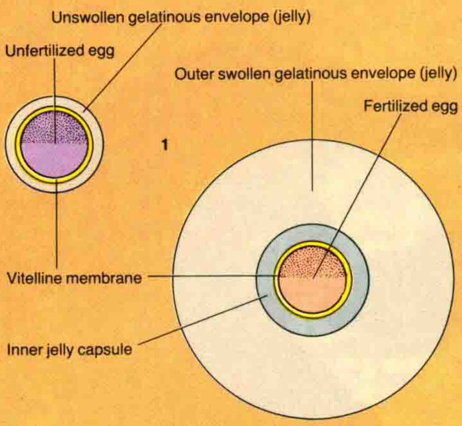
Thus, the incomplete fossil record provides little help. Indeed, it prompts the question why these animals were not readily fossilized, since even very small and fragile labyrinthodont larvae have been recovered. The reason may be ecological: the ancestors of living amphibians probably occupied very shallow waters or rushing mountain streams where the large species of ancient amphibians could not pursue them and, coincidentally, places where fossilization is relatively rare.

Without critical fossil material, evolutionary relationships must be inferred from



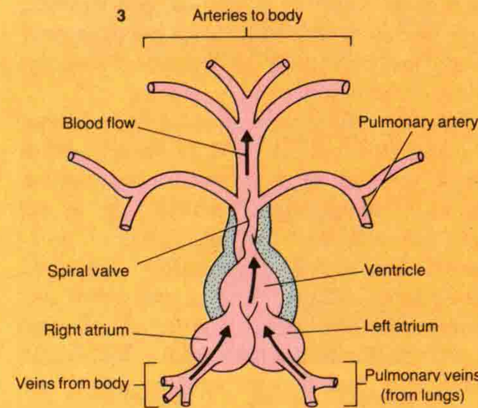
▲ **The evolution of amphibians.** ABOVE From fish to amphibian. (1) Crossopterygian fish, *Eusthenopteron*. (2) *Ichthyostega* one of the earliest amphibians (360 million year ago). (3) *Elpistostege*, remains of which were until recently believed to be those of an amphibian, with the form shown, but are now considered to be those of a fish. BELOW Chart showing the main evolutionary branches of amphibians and their ancestors.

AMPHIBIAN BODY PLAN

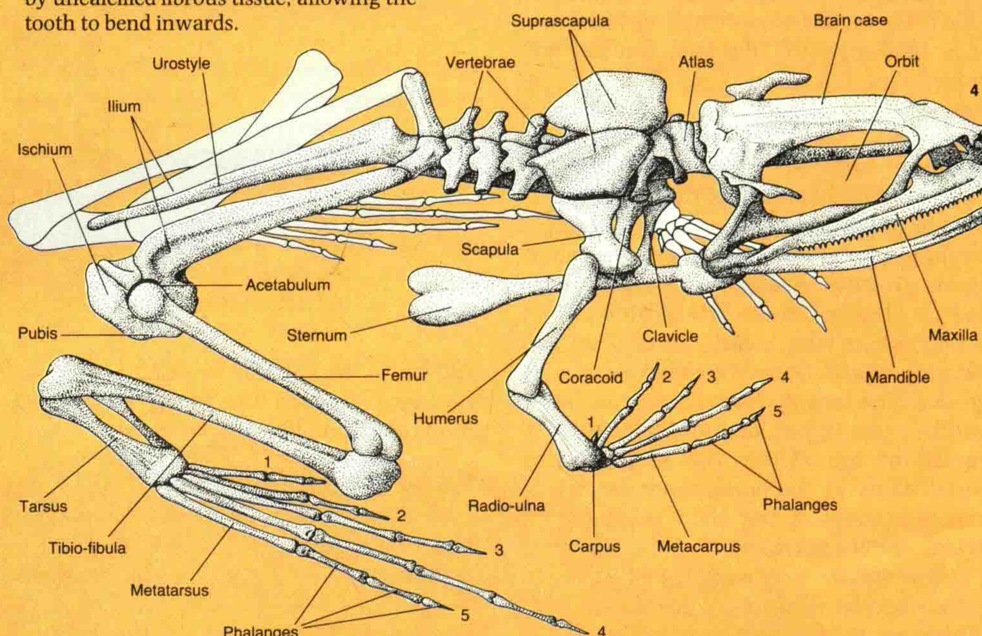


▸ **The heart** (3) has three chambers, two atria and a ventricle, which may be partly divided. Amphibians have paired lungs, but in four families of salamanders these are sometimes reduced or completely absent; in caecilians, the left lung is greatly reduced.

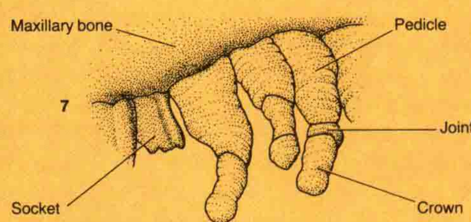
▾▸ **The skull** is flattened, and in the modern forms, eg frogs (4) and salamanders (5), articulates with the vertebral column by means of two knob-like occipital condyles (6), a condition found also in mammals; the extinct forms have a single condyle. Like fish, living amphibians have only ten pairs of cranial nerves. Primitive fossil forms had twelve, as do higher vertebrates. Living amphibians also have pedicellate teeth (7), with the crown attached to a narrow pedicel by uncalcified fibrous tissue, allowing the tooth to bend inwards.

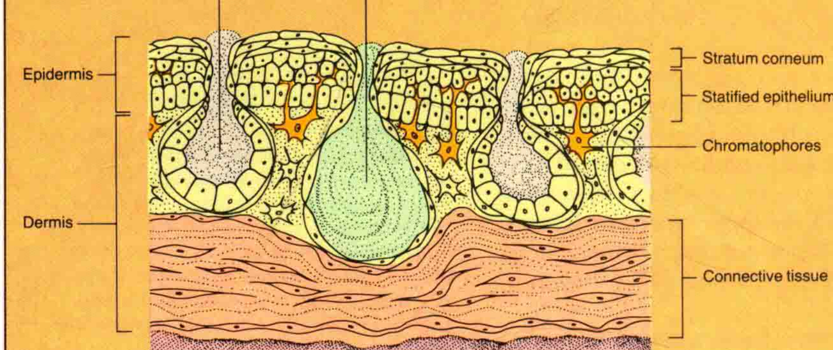


▴ **Embryos** (fertilized eggs) of amphibians (1), like those of fish, have gelatinous envelopes but lack the protective membranes found in all higher vertebrates. Amphibian eggs also lack shells and therefore must be laid in fresh water or in moist places to avoid drying out, although a few species give birth to fully-formed young. Larvae, even those of the earliest extinct forms, possess external gills, and in frog tadpoles these become enclosed inside a chamber by a flap of skin (the operculum). The larva undergoes an abrupt metamorphosis (see pp10–11) to the adult stage, from which it often differs markedly in structure.



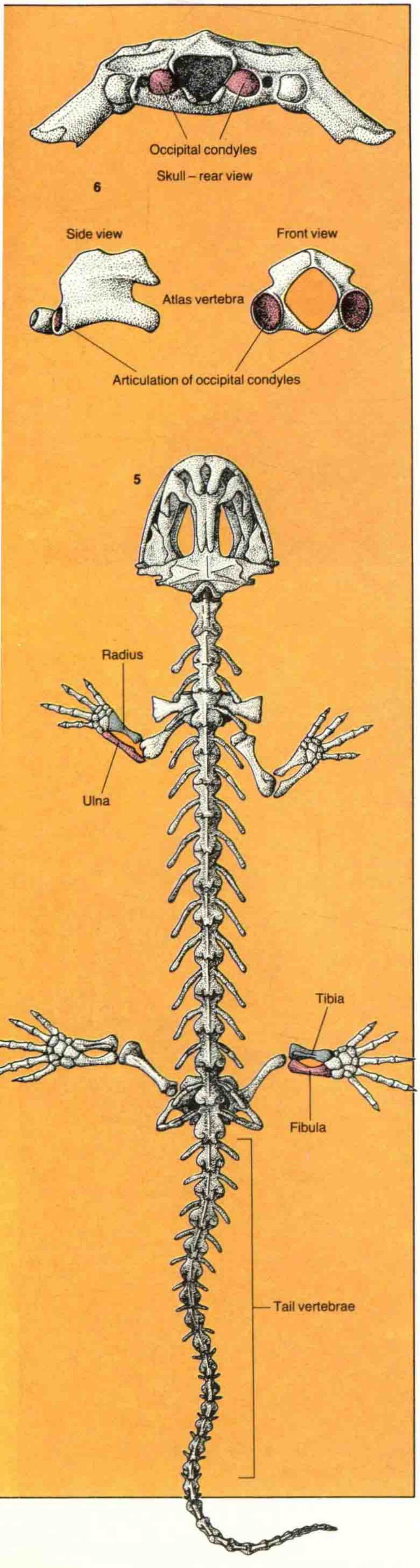
▾ **Skin.** Living forms have a moist, glandular skin (2), without scales or true claws. Some caecilians, however, have scales embedded in the dermis of the skin and a few frogs have plates of bone (osteoderms) in the skin, as do many reptiles. Some species of frogs and salamanders have claw-like epidermal tips on the toes.





Many of the features first developed by the amphibians relate to their crucial transition from water to land. Amphibians were the first vertebrates to possess true tongues (to moisten and move food), the first eyelids (which, together with adjacent glands, wet the cornea), an outer layer of dead cells in the epidermis that can be sloughed off, the first true ears—and a voice-producing structure, the larynx—and the first Jacobson's organ, a chemosensory structure adjacent to the nasal cavities that reaches its developmental zenith in snakes and lizards (see pp87, 114).

There were also striking changes in the nervous system related to life in a more complex terrestrial environment. The spinal cord is enlarged in the regions adjacent to the limbs, correlated with the more intricate movement of limbs compared to the fins of their fish ancestors. Invasion of the outer layer of the cerebral hemispheres by nerve cells, foreshadowing the tremendous enlargement of the mammalian cerebrum, also first occurred in amphibians.



comparisons of the living species. For a long time, given the enormous differences between frogs and salamanders, it was believed that each had descended from different orders of Paleozoic amphibians. More recently, it was suggested that despite their different appearances, frogs, salamanders and caecilians have many basic features in common, particularly in the skin, ears, skull and teeth.

The possibility that all of these features evolved independently was so unlikely, it was argued, that it was more reasonable to assume a common origin. Therefore, many scientists place the three living groups in one subclass (Lissamphibia). But since that time new evidence has come to light, particularly concerning the vertebral column, skull and jaw musculature, which raises anew the possibility that the living forms arose from different orders of ancient stocks. Until critical fossil material from the late Paleozoic is found, the question is likely to remain unresolved.

Locomotion

Whatever their true origins, modern amphibians do share numerous features, in particular their highly permeable skin and pedicellate teeth; but there has been a striking adaptive radiation among them in terms of locomotion and reproduction.

Salamanders and caecilians swim like fish, with side-to-side sinusoidal movements. Frogs, on the other hand, swim (and jump) in a totally different way. The vertebral column has become progressively shortened, the hindmost vertebrae have fused into a single element (the urostyle), and the bones of the hind legs have become elongated. Thus, frogs have rather inflexible bodies and swim by means of simultaneous thrusts of the legs (see p56).

Terrestrial salamanders move by means of lateral undulations, advancing diagonally opposite feet each time the body bends; some species use the tail as a fifth leg. Caecilians are legless and, except for a few completely aquatic species, live in burrows. Since the burrow walls greatly restrict lateral undulations, caecilians move by an alternating fold-and-extension progression in which only the vertebral column bends, producing momentary points of contact with the substrate which allows extension of other parts of the body, superficially resembling the locomotion of an earthworm.

Reproduction

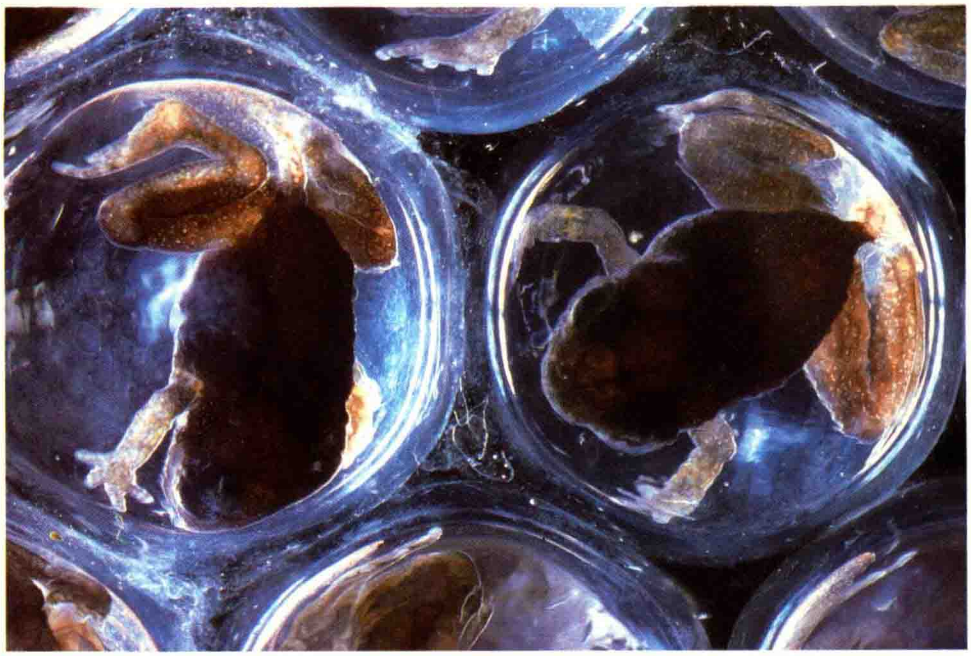
Amphibians exhibit the greatest diversity of reproductive modes of any vertebrate group. Fertilization can be external or internal. In the most primitive families (the giant and Asiatic salamanders) it is external, the sperm being shed into the water near the eggs. However, most salamanders transfer sperm in small packets called spermatophores that are picked up by the female with her cloacal lips during courtship. The sperm can then be used at once or, in most species, stored in specialized glands (spermatheca) in the cloaca for use during the following season. In two North American mole salamanders (genus *Ambystoma*) the sperm merely activate the developmental process and do not contribute genetically (a form of parthenogenesis).

With few exceptions, frogs fertilize externally. Usually sperm is deposited as the eggs are laid, with the male clasping the female with his forelegs (amplexus). Some poison-arrow frogs have no amplexus at all, the males fertilizing the eggs after deposition. In some narrow-mouthed frogs the bodies are temporarily glued together, and in a few other species the male's cloaca is held next to the female's while sperm is transferred, so that fertilization is internal, but there is no intromittent organ. However, in the North American Tailed frog the tail is, in fact, an extension of the male's cloaca which is inserted into the female's cloaca to transfer sperm. All caecilians fertilize internally, the male everting his cloaca and using it as an intromittent organ.

Most amphibian species lay eggs (they are oviparous) in fresh water or on land. Others are viviparous: the mother retains the eggs in her body and the embryos are nourished either by food stored in their own yolk sac (this is sometimes called "ovoviviparous" reproduction) or by materials obtained directly from the mother. Clutch size in frogs varies from species to species and ranges from a single egg to about 25,000; in salamanders, the number is generally no more than a few dozen.

Fertilized eggs may be laid singly, in clusters, or in long strands, but are always enclosed in gelatinous envelopes. If laid in water (or near enough that hatched larvae can crawl or be swept into it by floods), the larvae have gills and lead an aquatic existence, eventually metamorphosing into miniature adults (see pp10–11).

Amphibians use a variety of sites for laying eggs, including still or running water, mud basins constructed by the male, cavities beneath logs or stones, debris or burrows, leaves overhanging water, or the water-filled axils of plants. However, each



species generally has one preferred site. Those that lay eggs on land typically have no free-living larval stage and undergo direct development; this is true in many tropical frogs and in virtually all terrestrial species of salamanders. In many frogs and salamanders the eggs are defended by one of the parents and in several species of frogs the eggs or tadpoles are carried (see pp14–15).

Most amphibians giving birth to fully-developed young are ovoviviparous. In the Puerto Rican live-bearing frog, for example, only the embryo's own yolk is utilized; the embryo's tail is thin and rich in blood supply and may function in gas exchange. Several species of African live-bearing toads (genus *Nectophrynoides*) are ovoviviparous but in one, the West African live-bearing toad, the fetuses ingest a mucoprotein (uterine milk) secreted by the oviduct when the yolk supply is exhausted.

Two European species of salamanders are known to be viviparous. In the European Fire salamander the young are deposited as larvae into the water. In the Alpine salamander, a member of the same genus, only 1–4 young survive from as many as 60 fertilized ova. The survivors cannibalize their own siblings and they metamorphose before birth. The olm may also be viviparous under certain conditions. Although many caecilians lay eggs which are guarded by the mother, about half of the species are viviparous. After utilizing their own yolk, the large fetuses feed on uterine milk and also scrape material from the oviduct walls with their specialized teeth. Gas exchange occurs between the greatly-enlarged gills