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Adaptive Radiation

Fields of Study

Biology; Genetics; Environmental Sciences; Ecology; Botany

Abstract

Many different forms of evolutionary adaptations may occur among animals that started with a common ancestor. In this way, evolutionary divergences can take place, and the occupation of a variety of ecological niches is made possible. The ability to adapt is not shared by all species. Therefore, in many instances, either evolutionary divergence has been modest or the species involved has become extinct.

Key Concepts

allele: an alternative form of a gene that is located at the same position on a chromosome

evolution: the process of change through time by which the characteristics of a species of plant or animal are altered by adaptation to the environment and produce a new species distinct from the parent species

fossil: any recognizable remains of an organism preserved in the earth's crust; it may be a footprint, bones, or even feces

gene: the biological unit of heredity, which is composed of DNA and is located on a chromosome

genotype: the total genetic composition of an organism

habitat: the place where an organism normally lives or where individuals of a population live

natural selection: the process of evolution whereby organisms that are the best adapted are the most successful in reproducing and therefore in passing along their genotypes to successive generations

niche: the role of an organism in an ecological community—its unique way of life and its relationship to other biotic and abiotic factors

phenotype: the visible expression of the genetic makeup of an individual

species: a taxonomic subdivision of a genus, containing populations of similar organisms that interbreed and that usually do not interbreed with other species

ADAPTATION

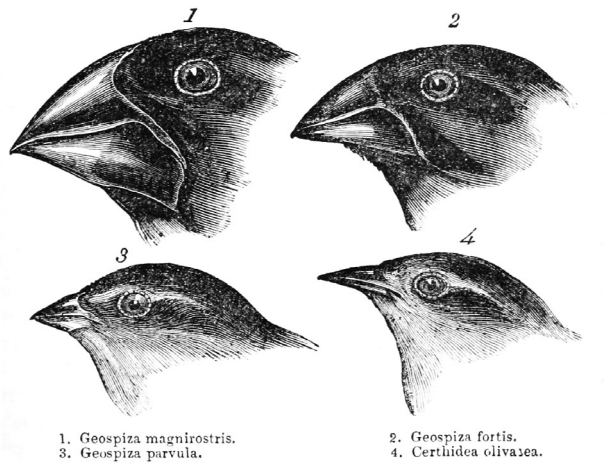
In 1898, Henry F. Osborn developed the concept of adaptive radiation. According to Osborn, many different forms of evolutionary adaptations may occur among animals that started with a common ancestor. In this way, evolutionary divergences can take place, and the occupation of a variety of ecological niches is made possible according to the adaptive nature of the invading species. As may be seen with certain forms of animal life, however, the ability to adapt is not shared by all species. Therefore, in many instances, either evolutionary divergence has been modest or the species involved has become extinct.

THE PRINCIPLES OF NATURAL SELECTION

In order to understand how adaptive radiation operates, it is necessary to become familiar with the principles of natural selection. The concept of natural selection, frequently expressed as "survival of the fittest," is at the core of Charles Darwin's theory of evolution. Darwin did not mean to suggest that there was a physical struggle among organisms in order to survive. Instead, he meant that organisms compete for food, space, shelter, water, and other things necessary for existence. Rather, he meant only that those organisms best adapted for a particular habitat will have the greatest ability to survive in a particular environment. According to the concept of natural selection, all organisms of a given species will show variation in color, size, physiology, and many other characteristics; in nature, all organisms produce more offspring than can survive, so the offspring must

therefore compete for the limited environmental resources. Organisms that are the best adapted (most fit) to compete are most likely to live to reproduce and pass their successful traits on to their offspring. The others, which are less fit, will be most likely to die without reproducing. When different parts of an animal population are faced with slightly different environments, they will diverge from one another and in time will become different enough to form new species, typically unable to interbreed. Natural selection also has the effect of producing different patterns of evolution. It may bring about widely different phenotypes (variable characteristics) in closely related animals, for example, or similar phenotypes in distantly related organisms. The organisms themselves may also become forces of selection through their interrelationships with other species.

The process of adaptive radiation illustrates how natural selection operates. The most frequently cited example is the evolution of Darwin's finches on the Galápagos Islands, off the west coast of South America. The islands were formed from volcanic lava about one million years ago. At first they were devoid of life, but bit by bit, several species of plants and animals arrived at them from the South American mainland. Since the nearest island is about 950 kilometers from the coast of Ecuador, it is anybody's guess how the different species arrived. It has been suggested that the birds may have been carried to the islands by strong winds, since finches are not known for their lengthy flights. Other organisms may have been carried by floating debris. In any event, the islands became populated. The mainland ancestor of the finches is not known, but it was no doubt a nonspecialized finch (a finch is about the size of a sparrow). Since there were no other birds with which to compete on the islands, the original population of finches began to adapt to the various unoccupied niches. The early offshoots of the original population were modified again and again as adaptations continued. This process resulted in the evolution of fourteen species of finches. The main feature that makes each species different is the size of their beaks, which have adapted for the various types of available foods. Today the finches live on fifteen different islands. Some of the species are found in the same area (sympatric), while others occur in different areas (allopatric). The most noteworthy example of an adaptation to a particular niche



Darwin's finches or Galapagos finches. Darwin, 1845. Journal of researches into the natural history and geology of the countries visited during the voyage of H.M.S. Beagle round the world, under the Command of Capt. Fitz Roy, R.N. 2d edition.

is the woodpecker finch. A true woodpecker has an extremely long tongue that it uses to probe for insects. Since the woodpecker finch does not have a long tongue, it has learned to use a cactus spine for insect probing, and it can therefore occupy a niche normally filled by true woodpeckers.

A more recent example of adaptive radiation in its early stages has taken place in an original population of brown bears. The brown bear can be found throughout the Northern Hemisphere, ranging from the deciduous forests up into the tundra. During one of the glacier periods, a small population of the brown bear was separated from the main group; according to fossil evidence, this small population, under selection pressure from the Arctic environment, evolved into the polar bear. Although brown bears are classified as carnivores, their diets are mostly vegetarian, with occasional fish and small animals eaten as supplements. On the other hand, the polar bear is mostly carnivorous. Besides its white coat, the polar bear is different from the brown bear in many ways, including its streamlined head and shoulders and the stiff bristles that cover the soles of its feet, which provide traction and insulation, enabling it to walk on ice.

EVOLUTION

All the genes of any population of living organisms at any given time make up its gene pool, and the ratio of alternative characteristics (alleles) in the gene pool

can change because of selection pressures during the passage of time. As the ratio of alleles changes, evolution occurs. Evolution may be a random change, or it may occur because of the directive influences of natural selection. In the former case, occasional and unpredictable permanent random changes called mutations take place in the DNA molecules that compose the genes. These mutations also may be selected for by the environment or selected against by the environment. It is simply an accident if the newly mutated genes help the organism to become better adapted to its particular habitat niche. Genes may not change or become mutated through several generations (the Hardy-Weinberg law), but may change in terms of survival value if the environment changes or the species population is subjected to new mutations or natural selection.

The relative numbers of one form of allele decrease in a divergent population, while the relative numbers of a different gene increase. This progressive change is all-important in the evolutionary process that takes place between the origin of a new gene by random mutation and the replacement of the original form of the gene by descendants having the newer, better-adapted form of the gene. The result in the long term is that enough of the DNA changes, either slowly or rapidly, through divergent populations or organisms, that the new generations have become so different from the original population that they are considered new species. Many times in earth's history, a single parental population has given rise not to one or two new species but to an entire family of species. The rapid multiplication of related species, each with its unique specializations that fit it for a particular ecological niche, is called adaptive radiation, or divergent evolution.

STUDYING ADAPTIVE RADIATION

Not all scientific information is gained by experimentation: A considerable portion of science is descriptive and is based upon observation. In determining that adaptive radiation has occurred and is indeed taking place among living species, much supporting evidence has come from the study of fossils and from observations of the structural, physiological, and behavioral adaptations of current animals. Clearly, wide-scale experimentation would be out of the question. No matter how well an experiment may be designed to test the concept of adaptive radiation, the scientist could not be around thousands or millions of years from now to gather the data. Therefore, scientific observation of animal remains is the best method.

Based upon scientific observations, it has been well established that the phenomenon known as adaptive radiation is a general feature of the evolution of most organisms. Studies of the morphological features of fossilized remains help determine relationships among prehistoric animals and enable the scientist to trace adaptive radiations from a more primitive ancestral stock. In order to establish time intervals, techniques such as radioactive carbon dating, potassium-argon dating, and fluorine dating have been used.

Zoologists have also made use of the uneven distribution of blood groups (A, B, AB, and O) among different groups of animals. As more blood subgroups were discovered, they became useful in helping chart migrations and indicating relationships between species.

THE EVIDENCE AND ITS IMPLICATIONS

Adaptive radiation as an important aspect of evolution means that modern organisms have attained their diversity in form and behavior through hereditary modifications after having been separated from ancestral populations. Adaptive radiation, therefore, is attributable to the genetic changes in isolated groups of organisms or, more specifically, to a change in the relative frequency of their genes from one generation to the next that eventually results in the formation of new species.

Evidence in several areas supports the concept of adaptive radiation as an important aspect of evolution: the fossil record (the most direct evidence), biogeographic distribution of organisms, comparative anatomy and embryology, homologous and analogous structures, vestigial organs, and comparative biochemistry. Regarding comparative biochemistry, scientists agree that blood group similarities confirm evolutionary relationships among the nonhuman primates. It has been shown that the blood of higher primates, such as orangutans and chimpanzees, is closer to human blood than to that of the more primitive monkeys.

—Jon P. Shoemaker

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AGING

FIELDS OF STUDY

Medicine; Biology; Geriatrics; Thanatology

ABSTRACT

When change is reversible or self-maintaining, the effects of aging are often not observable. However, in animals some change is not reversible. The changes in the cells of the body accumulate over time and result in a steady downward trend. The end point of this trend is the death of the organism. Aging occurs within body systems as a result of unseen changes at the molecular and cellular levels. Although the mechanisms through which aging occurs may be understood, the causes are less clear.

KEY CONCEPTS

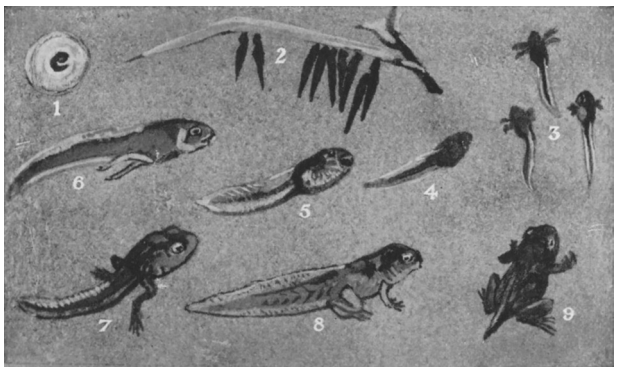
aging: a process common to all living organisms, eventually resulting in death or conclusion of the life cycle
cognition: ability to perceive or understand
death: the cessation of all body and brain functions
function: ability, capacity, performance
life span: length of life from birth to death
longevity: length of life

CHANGE AND AGING

Progressive and irreversible change has been called the single common property of all aging systems. When change is reversible or self-maintaining, such as one would see in a forest, for example, the effects of aging are often not observable. Growth of the forest is evident, but with the right conditions, trees within the forest may grow for hundreds of years in the absence of disease. Certain conditions of the forest system help to regenerate, renew, and reverse changes that happen within that system.

However, in animals some change is not reversible. The changes in the cells of the body accumulate over time and result in a steady downward trend. The end point of this trend is the death of the organism. Aging is a normal part of the life cycle. This is known to be true because aging changes within populations are rather predictable. The changes associated with aging that are seen in all animal species may occur for similar reasons. These may include chemical aging, extracellular aging, intracellular aging, and aging of cells.

Aging occurs within body systems as a result of unseen changes at the molecular and cellular levels. Although the mechanisms through which aging



Before hatching Newly hatched larvæ hanging on to water-weed With external gills External gills are covered over and are absorbed Limbless larva about a month old with internal gills Tadpole with hind-legs, about two months old With the fore-limbs emergin.

occurs may be understood, the causes are less clear. The fact remains that due to changes in chemical balances such as those of hormones, and to the dying of cells within the body, each of the bodily systems shows deterioration over time.

Changes that occur in domestic animals over the life span can be similar to those that occur in humans. Dogs experience the graying of their hair, a decrease in vision, and a slowing of movement with age. They also experience cataract formation, arthritis, skin problems, cancer, and diabetes. Certain breeds of animals may demonstrate a tendency toward specific illnesses or diseases. For example, German shepherds often develop hip problems, and collies commonly develop progressive arthritis that may seriously inhibit mobility by around ten years of age.

COMMON EFFECTS OF AGING

There are many variations in the effects of aging among the species of animals. The life span of animals may range from a few days (among insects) to thirty years or more, with great variation depending upon many factors. Animals that live in captivity, as pets or in zoos where they are sheltered from the effects of predation, disease, and adverse climate, also tend to live significantly longer than animals in the wild.

Very little research has been done on the aging of most animal species. The reasons for this include the difficulty of observing animals over a long period of time in their natural habitat. Aging in monkeys has been studied more than that in other animals because of the notion that aging patterns may closely reflect those of humans.

Aging monkeys show changes in their circulatory systems similar to those found in humans: There is notable atherosclerosis and arteriosclerosis, or hardening of the arteries. The heart pumps less effectively, and vessels show buildup of plaque. These changes often result in cardiac problems, including heart attacks. The respiratory system also shows a decrease in elasticity. Senile emphysema has been noted. The kidneys show signs of atrophy and sclerosis in aged monkeys. The kidneys of humans may lose up to half of the functioning nephrons with advanced age and thus become less effective in filtering waste products from the body.

Physical function or capacity tends to decline with age. This is largely due to the atrophy of muscles, which is more common as the body gets older. The joints tend to become stiffer and less mobile. Range of motion may be restricted. Changes in bone density may lead to loss of teeth, osteoporosis, and subsequent fractures. Tooth loss and osteoporosis have been documented in monkeys over the age of twenty years. Pictures of such older monkeys reveal a stooped posture, with shoulders hunched forward, similar to the kyphosis observed in many older human women.

Physical function among animals has been less studied than that in humans, but certain physiological characteristics are similar. For example, survival times after severe physical injury with blood loss and trauma decreases in both humans and animals as age increases. Male monkeys do not lose reproductive capabilities until toward the end of the life span, while females have a more restricted period of time to bear offspring. Fertility among all females tends to decline with age after its peak.

The immune system functions less effectively as age increases. This leaves the body more susceptible to a range of illnesses and diseases. Neoplasms, or tumors, are most common among mammals as they age. An impaired immune system allows various types of tumors or cancers to spread more rapidly in the older body. Response to stress and ability to adapt to stressors also decline with age. For example, older mice become less able to adapt to cold temperatures.

Social roles and behaviors among animals may also change with age. Longitudinal studies on animals in the wild are scarce, so only generalities may

be speculated upon. Even studies done within controlled laboratory settings yield only broad suggestions, since numbers of animals available for study are limited. Males generally tend to dominate the females in both physical strength and social ranks. Some nonhuman primates show different characteristics with advanced age. That is, some monkeys and baboons allow older males to remain part of the social group, while other species support the male leader in the group only as long as the female harem supports him, whether younger or older. Individual monkeys in stable groups have been observed to resort less frequently to aggressive behavior to maintain their status within the group.

CAUSES OF DEATH

Among nonhuman primates, the leading cause of spontaneous death is digestive problems. Older animals that die do not always show advanced signs of tissue aging. Since much less research has been done on aging among animals than among humans, data about causes of death are rare. However, it appears that there is an increased probability of dying from trivial illnesses, perhaps due to decreased resistance factors, as animals age.

Predator-prey relationships among animals are particularly significant as causes of death. Thus, the effect of the environment on animal aging and death requires more investigation. Do animals age more quickly if they are objects of prey? Do animals relate to stress in ways similar to those of people, thus showing signs of wear and tear that are seen with premature aging under stress? Are there risk factors among animals that affect their life span? These are some of the questions that remain to be answered on the topic of aging among animals.

—Kristen L. Mauk

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AMPHIBIANS

FIELDS OF STUDY

Biology; Taxonomy; Ecology; Environmental Studies

ABSTRACT

The term amphibian *is derived from the Greek word* amphibios*, which means "to live two lives." The majority of amphibians spend the first part of their lives as aquatic, gill-breathing larvae and then transform into terrestrial adults. The larval stage can be as short as a few weeks or as long as several years. Completion of the larval stage is triggered by hormonal events that initiate some dramatic developmental processes, collectively termed metamorphosis.*

KEY CONCEPTS

adaptive radiation: rapid speciation that occurs as the result of a particular group being able to exploit a new resource

convergence: a phenomenon in which two forms that are not closely related evolve structures that appear similar

disjunct distribution: a geographic distribution pattern in which two closely related groups are separated by large areas that are devoid of either group

metamorphosis: the complex developmental process of morphological change in which larval amphibians are transformed into adults

neoteny: the retention of larval features by adults, a process that has played a major role in the evolution of amphibians

phylogeny: the determination of the evolutionary history of a particular group of organisms

AMPHIBIAN LIFE

The term *amphibian* is derived from the Greek word *amphibios,* which means "to live two lives." The majority

of amphibians spend the first part of their lives as aquatic, gill-breathing larvae and then transform into terrestrial adults. The larval stage can be as short as a few weeks or as long as several years. Completion of the larval stage is triggered by hormonal events that initiate some dramatic developmental processes, collectively termed metamorphosis.

As adults, most amphibians seek out aquatic environments in which to deposit their eggs. These can range from fast-flowing mountain streams to ephemeral roadside ditches. Most male frogs have species-specific mating calls that serve both to attract females and to prevent interbreeding. Frogs reproduce by external fertilization: the male typically grasps the female and encourages her to deposit her eggs, which he promptly fertilizes. Normally, both parents abandon the eggs, but some variations of this pattern exist. In contrast, most salamanders practice internal fertilization, accomplished after the male has performed a type of species-specific courtship dance that culminates with the deposition of a packet of sperm cells, called a spermatophore. The female squats on the spermatophore, transferring the spermatozoa to a specialized holding structure called a spermatheca. The spermatozoa can be used to fertilize her eggs up to several months after mating.

EVOLUTION OF AMPHIBIANS

Amphibians were the first vertebrates to possess adaptations that allowed them to spend considerable periods of time out of the water. The earliest fossil amphibians, members of the order Ichthyostegalia, appear in the geologic record during the Devonian period, about 320 million years ago. Among experts, there is a general consensus that the ancestor of the amphibians is to be found in the primitive, lobe-finned fish (class Osteichthyes, subclass Sarcopterygii). This conclusion is based on a detailed analysis of the comparative anatomy of hard body parts that fossilized, such as the vertebrae, shoulder girdles, teeth, and skulls. Characteristics that the first amphibians shared with their fish ancestors include internal nasal openings (nares); a strange, hinged skull; and a distinctive tooth structure, in which the enamel is folded into intricate patterns.

The environmental conditions that led to the abandonment of aquatic habitats in favor of a more terrestrial existence remain a major topic of discussion. One scenario envisions the early amphibian ancestors in an environment that was gradually becoming more and more arid. To survive, it would have been advantageous to be able to crawl on land for short distances to escape drying pools in favor of more permanent bodies of water. Those that could migrate would have survived in higher numbers than those that lacked this adaptation. A second scenario suggests that heavy predation pressures from the jawed, carnivorous fish that are known to have been abundant in the shallow freshwater lakes of the time may have selected for individuals that could leave the water, even if only briefly. A third scenario depicts competition for food as strong in the aquatic environments and much weaker on land, where several groups of invertebrates were known to be abundant.

TAXONOMY OF FOSSIL AMPHIBIANS

The taxonomy of fossil amphibians is confusing because of a series of problems. First, on the whole, the range of morphological variations within the group has been conservative. Striking differences of taxonomic value (which would have to fossilize) are not numerous. Second, many of the skeletal elements that are important in determining the relationships of living amphibians are composed of cartilage rather than bone, and this material does not fossilize well. Because of this limitation, bony elements such as the vertebrae and skull have played a major role in determining amphibian phylogeny. The molecular techniques that have greatly assisted modern taxonomists, such as electrophoresis, immunology, karyotyping, and deoxyribonucleic acid (DNA) sequencing, cannot be used on fossilized materials.

The class Amphibia is further divided into orders. The number of orders recognized by various authorities ranges from eight to thirteen. All but three of these are extinct. One extinct order is Ichthyostegalia, which includes the earliest recorded fossil amphibians. Most were small, with elongate bodies and weakly developed limbs. Many were almost assuredly aquatic, but at least some were capable of spending extended periods of time out of the water. By the time of the Devonian period, when they first appear in the fossil record, they were already diverse, with several different genera and species present.

Another extinct group is the order Temnospondyli, which was abundant during the late Permian period

and persisted until the end of the Triassic period. Most in this order were of moderate size (0.5 to 1.0 meter in body length), with low, stout profiles and flattened skulls. Some were highly aquatic and had short, weak appendages. One group, the clade Trematosauria, was marine, and they are apparently the only amphibians to have been successful at invading the oceans.

The order Anthracosauria appears in the fossil record during the Carboniferous period and was extinct by the end of the Permian. Common names of members of this group include the seymouriamorphs and the embolomeres. This order contains a mixture of terrestrial and aquatic amphibians. From an evolutionary standpoint, Anthracosauria is important because it gave rise to the ancestors of the reptiles.

Members of the order Aistopoda were eel-like, aquatic amphibians with elongate, limbless bodies. They are characterized by a large number of vertebrae—more than one hundred—that are clearly divisible into cervical, trunk, and caudal regions.

The order Nectridea consists of fully aquatic, salamander-like amphibians that persisted during the Carboniferous period. Appendages were weak or absent, and most fossils indicate body forms that were flattened dorsiventrally. They probably persisted by slowly crawling about the bottoms of ponds and lakes, where they preyed on unwitting animals that crossed their paths.

Amphibians of the order Microsauria were a diverse group of elongate, weak-limbed amphibians. Fossils of this group are fairly abundant in habitats that were swamplike during the Carboniferous period. The remarkable physical similarities between some microsaurs and some of the earliest reptiles are considered by most authorities to be the result of convergence of body form rather than an indication of a true evolutionary relationship.

The order Proanura consists of a single froglike fossil that dates from the Triassic period on the island of Madagascar. The skull is distinctly froglike, but a tail is present, and the hind limbs have not been modified for jumping.

The taxonomy of the living members of the class Amphibia is still under considerable debate. A central question revolves around whether all currently living amphibians are of monophyletic origin, meaning they derive from a single common ancestor, or whether they are of polyphyletic origin, meaning they arose independently from two or more separate stocks of fish. Based on the presence of unique features, such as pedicellate teeth, a distinctive part of the inner ear, and specialized eye receptors, most experts have concluded that all living amphibians are monophyletic and can be grouped in the superorder Lissamphibia. As recognized, living amphibians are placed in the orders Caudata, Anura, and Gymnophiona.

SALAMANDERS

Salamanders are grouped in the order Caudata. They are distributed over temperate parts of Europe, Asia, and North and South America. There are approximately 550 recognized species, grouped into eight different families. Eastern North America has the greatest overall diversity, with seven of the eight described families represented there. One family, Plethodontidae, invaded South America and underwent a period of such tremendous speciation that approximately 60 percent of the living species of salamanders are members of this family.

Almost everyone is quick to recognize a frog based on its appearance, but the same cannot be said for salamanders. The families Proteidae, Cryptobranchidae, Sirenidae, and Amphiumidae are entirely aquatic. The family Cryptobranchidae is disjunctly distributed and occurs today only in eastern Asia and eastern North America. It contains the genus *Andrias*, which includes the largest living salamanders; one species, *Andrias davidianus*, has been known to reach lengths as great as 1.8 meters. Members of the family Proteidae are today isolated in Europe and eastern North America. They are commonly called "water dogs" and are frequently dissected in comparative anatomy classes. Members of the families Sirenidae and Amphiumidae are restricted to the southeastern United States, where they are called sirens and amphiumas, respectively. Sirens have external gills and two front legs, while amphiumas have minute front and back legs and lack external gills.

The family Ambystomatidae is entirely North American in its distribution. Most species are highly secretive and are only encountered under objects or intercepted as they migrate to breeding ponds during spring rains.

The family Hynobildae is exclusively Asian in its present distribution. Reproduction in this family is considered to be primitive, in that the female lays

eggs that are enclosed in a loose sac and are subsequently fertilized externally by the male.

The family Salamandridae is widely distributed in Europe, North Africa, Asia, and North America, with the greatest diversity in the Eastern Hemisphere. Many species have developed highly toxic skin secretions to protect themselves from predators; human fatalities have been recorded from eating only one salamander. Many species advertise their toxicity by being very brightly and distinctly colored, a phenomenon known as aposematic coloration, while members of other, less toxic families also display these color patterns for protection from predators, a process called mimicry.

Members of the family Plethodontidae all share the unique feature of being lungless; respiration is accomplished by diffusion across their moist skins. Many species have abandoned laying eggs in water in favor of damp, terrestrial nests. Females guard the eggs until they hatch as miniatures of the adult, having completed their abbreviated metamorphosis while still in the egg.

CAECILIANS

The order Gymnophiona consists of a highly specialized group of wormlike, limbless amphibians called caecilians. They inhabit tropical regions of North and South America, Asia, and Africa. Most are terrestrial burrowers and are rarely observed. Some primitive forms have dermal scales embedded in their skin. All caecilians possess a unique sensory organ called a tentacle. Fertilization is internal, and male caecilians possess a copulatory organ that is derived from the cloaca. In the majority of caecilian species, the females retain their eggs in the oviduct and give birth to fully developed young. Fossil caecilians are extremely rare.

FROGS

The order Anura is composed of tailless amphibians called frogs. Their hind legs are typically modified for jumping, their presacral vertebrae are usually eight in number, and their postsacral vertebrae are fused to form a coccyx. Frogs occur on all continents except Antarctica but reach their greatest diversity in the tropics of South America, Africa, and Asia. They have successfully invaded deserts, rivers, cold mountain streams, and arboreal vegetation. Several families have undergone tremendous adaptive radiation in the tropics, so that today almost 80 percent of living amphibians are anurans.

Families that are widely distributed include Bufonidae (toads), Hylidae (tree frogs), Microhylidae (mostly small frogs), and Ranidae (true frogs). These families are almost worldwide in their geographic distributions, although Australia lacks Bufonidae, Ranidae, and Microhylidae and Africa lacks Hylidae. Toads often have dry, warty skins containing numerous glands that produce noxious, protective secretions. Tree frogs have expanded disks on the tips of their toes that have allowed them to occupy arboreal habitats unavailable to many other families.

The families Leptodactylidae, Brachycephalidae, Rhinodermatidae, Pseudidae, Centrolenidae, and Dendrobatidae reach their greatest abundance in Central and South America. The leptodactylids are a diverse assemblage of nearly seven hundred species. Many of these lay eggs in specially constructed foam nests; other species have taken this a step further and deposit their eggs in damp, terrestrial locations, thereby avoiding aquatic predators almost completely. The dendrobatids are often small, brightly colored frogs that have been given the common name of poison arrow frogs because of their extremely toxic skin secretions, which have been used by some indigenous tribes to poison the tips of hunting arrows. Members of the family Pseudidae are unique in producing very large tadpoles that metamorphose into rather small frogs. The rhinodermatids consist of only two species, but one is unique in that the larvae do not feed and are carried in the mouth of the adult until they complete metamorphosis.

The Discoglossidae are found mostly in Europe, and Pelodytidae are native to southwestern Europe and western Asia. The midwife toad (*Alytes obstetricians*), a discoglossid, has an unusual reproductive mode: after fertilizing the eggs, the male cements them on his back and carries them to and from the water until they are ready to hatch.

The Rhacophoridae are a moderate-sized family of about 180 species, distributed over southern Africa and southeast Asia. Most members have expanded terminal digits, and some even have extensive webbing between their toes, which allows them to glide between arboreal perches. Diverse reproductive

tactics occur in this family. Several species use water-filled tree holes in which to deposit their eggs.

The family Myobatrachidae is a diverse group of about ninety-nine species that occur in Australia and New Zealand. One species, *Rheobatrachus silus*, has a unique reproductive mode that includes brooding eggs in the stomach of the female.

The family Leiopelmatidae is a small group of frogs that are disjunctly distributed in western North America and New Zealand. The tailed frog (*Ascaphus truei*) is the only frog to possess an intromittent organ that is used to transfer sperm to the female for internal fertilization. This organ apparently evolved in response to the swift, cold streams in which the frog lives.

BASES OF CHARACTERIZATION

As a group, amphibians are easier to characterize by the morphological features that they lack than by the unique characteristics that they possess. Missing are the scales that cover fish and reptiles (although these are not closely related structures), as well as the hair and feathers associated with mammals and birds. Amphibians' skin is relatively thin and contains numerous glands. Large amounts of water can be lost or gained via the epidermis. In many forms, the skin serves as a major organ for respiration. Amphibians are ectothermic, which means that they do not have internal physiological mechanisms for maintaining a constant body temperature. The circulatory system is closed, and the heart is composed of three chambers—two atria and one ventricle.

The taxonomic relationships of salamanders are based primarily on the arrangement of bones of the skull, which of these bones possess teeth, and the shape of the centrum of the vertebrae. Living forms are further compared by the manner of reproduction. In general, salamanders have been relatively conservative, and characteristics such as the number of chromosomes have not proved especially useful in determining phylogenetic relationships. However, modern molecular techniques, such as electrophoresis, immunology, and the use of restriction enzymes, are adding to the understanding of selected groups. With these techniques, it has been possible to show that several forms that were indistinguishable based on morphological data are in fact genetically isolated from one another and are actually distinct sibling species.

The taxonomic relationships of frogs are also based largely on differences in bony anatomy. Skull morphology, the shape of the vertebral centrum and its manner of development, and the arrangement of the bones that make up the pectoral girdle are important diagnostic characters. In living forms, molecular techniques are also shedding new light on relationships. The number of chromosomes is more variable and has more value as a diagnostic tool in frogs than in salamanders. The morphology of the larvae is another important taxonomic tool.

THE IMPORTANCE OF AMPHIBIANS

There are about seven thousand recognized species of living amphibians. This number represents only a small fraction of the number of species that have been present on the earth over the past 350 million years. In many habitats, amphibians still represent a major portion of the biomass, and because ecologists often relate a group's "worth" to its biomass, amphibians can be considered major members of many terrestrial communities, often serving as keystone species for their ecological niches. Amphibians often exhibit traits such as low mobility, fidelity to breeding sites, and species-specific behaviors that are sought by ecologists and animal behaviorists for their studies. As a whole, salamanders and frogs represent some of the most thoroughly studied vertebrates.

Areas to which amphibians have contributed a significant portion of current knowledge include the evolution of mating systems, sexual selection, reproductive isolation mechanisms, niche partitioning, and community structure. Embryologists have long used amphibians to gain a basic understanding of complex development processes.

One area of extreme interest is the apparent decline of many populations of frogs and salamanders over large geographic areas, notably in western North America. Loss of breeding sites through habitat modification, acid rain, and competition from exotic species have all contributed to their demise. Another likely cause is chytridiomycosis, an infectious and deadly skin disease caused by the chytrid fungus *Batrachochytrium dendrobatidis*. The disease was first discovered in frogs in Queensland, Australia, in 1993 and was first described by Lee Berger et al. in 1998. The specific fungus was identified by Joyce E. Longcore, Allan P. Pessier, and Donald K. Nichols in 1999.

—Robert E. Herrington