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MAJOR AMPHIBIAN GROUPS

The following sections of this article consist of a detailed discussion of the three orders of living amphibians, the salamanders and newts (Caudata), the frogs and toads (Anura), and the caecilians (Apoda).

Caudata (salamanders and newts)

Salamanders and newts constitute the order Caudata (Urodela), one of the major extant groups of the class Amphibia. The relatively small and inconspicuous salamanders are important members of north temperate and some tropical ecosystems, in which they are locally abundant and play important roles. They are important as subjects of experimental studies in embryology, developmental biology, physiology, anatomy, biochemistry, genetics, and behaviour. Convenient size, low food requirements, low metabolic rate, and hardiness make them useful laboratory animals.

GENERAL FEATURES

Size range and diversity of structure. The most typical salamanders are short-bodied, four-legged, moist-skinned vertebrates about 100 to 150 millimetres (about 4 to 6 inches) long. The tail is usually about as long as the body. There is much variation in size, and terrestrial salamanders range from 40 to nearly 350 millimetres, with a few exceeding 1 metre (39 inches) in length. Members of most species live in moist places on land but must return to water to breed. Others are completely terrestrial. Wholly aquatic salamanders attain larger sizes than do terrestrial ones, the former reaching a maximum of 180 centimetres (about 6 feet). Salamanders may retain gills throughout life, lose the gills but retain a spiracle or gill slit, completely metamorphose and lose both gills and gill slits, or entirely bypass the aquatic larval stage and develop directly, hatching as miniature adults. Many aquatic species resemble their terrestrial relatives in body form, but the aquatic genera *Siren* and *Pseudobranchus* lack hindlimbs, and *Amphiuma* has an extremely elongated body, short tail, and diminutive legs; several cave-dwelling forms (*Proteus, Haideotriton, Typhlomolge*) are blind and almost without pigment.

Distribution and abundance. Salamanders are classic examples of animals with a distribution restricted to the north temperate regions of both the Eastern and Western hemispheres; 9 of the 10 families are found almost entirely in northern regions that lie outside the tropics. Typically, salamanders occur in moist, forested habitats, where they are often common in aquatic and terrestrial communities. Members of the family Salamandridae extend south to extreme northern Africa, the southern foothills of the Himalayas, northern Vietnam, and the islands of Hainan, Taiwan, and Okinawa. Some ambystomatids reach the southern margins of the Mexican Plateau, but only the lungless salamanders (plethodontids) have truly entered the tropics. One group of plethodontids, the bolitoglossines, occupies a wide variety of tropical habitats in the New World—from northern Mexico to southern Brazil and central Bolivia—and contains nearly half of all recognized species of salamanders, which is an indication that the plethodontids have been extremely successful in the tropical environment. Other areas in which salamanders are both speciose and abundant include temperate North America (Appalachian and Ozark uplands; Pacific coastal areas with a moist habitat), western Europe, Japan, and China.

NATURAL HISTORY

Life cycle and reproduction. Most salamanders are terrestrial or semiterrestrial as adults, but many return to aquatic habitats to breed. Courtship, which is relatively simple in hynobiids and cryptobranchids, is increasingly elaborate and prolonged in the more highly evolved families. In primitive species constituting the suborder Cryptobranchoidea, the egg is fertilized externally. The females deposit sacs or strings of eggs that may be grasped by the male, who then sheds milt (which contains the sperm) over them. Nothing is known of courtship in sirens, but they, too, may have external fertilization, for the males lack the cloacal glands that produce the spermatophore, or sperm case, in species with internal fertilization, and the females lack spermathecae—chambers inside the cloaca used for sperm storage. However, sirens also lay single eggs, a behaviour that would not be facilitated by external fertilization.

Fertilization

All other species of salamanders have internal fertilization and more complex courtship behaviour, which often differs in details between species. The male deposits from one to many spermatophores on the ground or other surface. These consist of a gelatinous base, which is produced by cloacal glands, and a so-called sperm cap at the tip. The female moves by herself or is led by the male onto the spermatophore, and she takes the sperm mass into her cloaca. Breeding often occurs in ponds, but some salamandrids and most plethodontids breed on land. Egg deposition may take place shortly after mating but in many plethodontids may be delayed for several months, the eggs being fertilized by stored sperm. Eggs are laid in masses in streams or ponds, often in the shallows near shore. Many salamandrids lay eggs singly, while plethodontids typically lay eggs in clusters in terrestrial sites—*e.g.*, under surface objects, in rotting logs, or underground. Some species deposit eggs in tree cavities, and tropical species may deposit them in bromeliad plants (various genera of the family Bromeliaceae), the leaves of which are arranged so that they often hold water and thus provide a moist habitat. Frequently, the female stays with the eggs until they hatch, a period of several weeks to many months. The number of eggs varies greatly and is correlated with adult size. Aquatic forms deposit as many as 400 eggs, terrestrial forms as few as 5 or 6.

Members of most families pass through an aquatic larval stage that lasts for a period ranging from a few days to several years. A short period of metamorphosis usually

From K. Adler (ed.), *Herpetology: Current Research on Amphibians and Reptiles* (1992), published by the Society for the Study of Amphibians and Reptiles, Oxford, Ohio

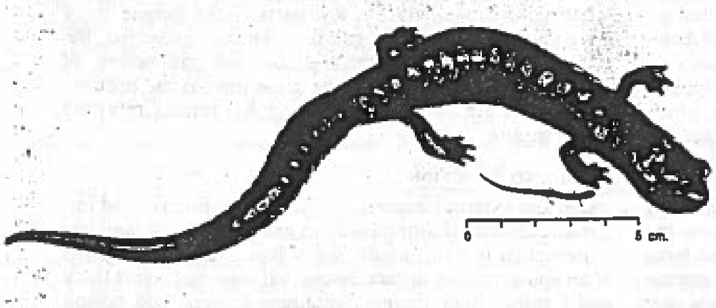

Figure 4: Two species of plethodontids illustrate the great size variation that exists in this family.

occurs before the terrestrial phase of the life cycle begins. The newly metamorphosed salamander is usually very small, and up to several years may elapse before it is sexually mature.

Paedomorphosis

Some salamander species never metamorphose and thus retain most of their larval characteristics. In other species, individuals or populations may occasionally fail to metamorphose. Still other species undergo partial metamorphosis, a state in which the adult retains larval or juvenile features (paedomorphosis). This condition characterizes all salamanders to a degree but is particularly evident in species such as *Necturus maculosus* (mud puppy) and *Ambystoma mexicanum* (axolotl), which retain gills and other larval structures throughout life. These animals breed in what is essentially a larval state. This extreme condition, which characterizes the Proteidae, Necturidae, and Sirenidae, is also found in the Dicamptodontidae, Plethodontidae, and Ambystomatidae. In most species the permanent larval state is determined by heredity, but in some it is induced by environmental factors, such as unfavourable terrestrial conditions resulting from drought or cold. The most complete metamorphosis is found in the families Hynobiidae, Salamandridae, Ambystomatidae, Dicamptodontidae, and Plethodontidae.

Most species of the family Plethodontidae differ from members of all other families in that their eggs develop entirely on land, with no aquatic larval stage. The hatchling has either rudimentary gills that soon disappear or none at all and, in virtually all respects, is a miniature of the adult.

Females of the genera *Salamandra* and *Mertensiella* (Salamandridae) may retain the fertilized eggs in the reproductive tract for a variable amount of time. The fire salamander (*Salamandra salamandra*) deposits relatively advanced larvae in the water. In the Alpine salamander (*Salamandra atra*) and *Mertensiella*, fully metamorphosed individuals are born. One individual develops from the first egg in each oviduct, the tube leading from the ovary to the outside. Initially, the young salamander lives on its own yolk supply; later it eats the yolk of the other eggs. It develops enlarged gills that form an intimate association with the walls of the oviduct to convey nutrients to itself. The gills are lost shortly before birth. Such salamanders are the only members of the order that bear live young.

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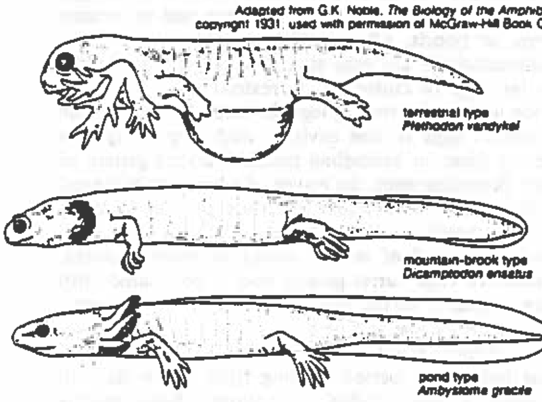

Figure 5: Principal types of urodele larvae.

Larval feeding habits

Larval salamanders are exclusively aquatic. They may occur in a variety of habitats, from temporary ponds to permanent swamps, rivers, slow-moving streams, mountain brooks, springs, and subterranean waters. In all habitats they are exclusively carnivorous, feeding primarily on aquatic invertebrates. In most salamander larvae, feeding is accomplished by a "gape-and-suck" method, in which the throat is expanded, or gaped, to produce a suction that draws water and prey into the opened mouth. Skin flaps around the mouth direct the water movement. The larvae are well equipped with teeth, which aid in holding and shredding prey. Pond larvae have a high fin on the upper side of the tail that extends far anteriorly and large gills. Limbs are rather slow to develop. By contrast, stream larvae have a low, short tail fin, small gills, and limbs that develop early.

Metamorphosis, although a period of major reorganization, is not so dramatic as that in frogs. In the final stages, metamorphosis is usually a rapid process; it is mediated by several hormones produced by the thyroid and pituitary glands. The following events typically occur during metamorphosis: loss of the gills, closure of the gill slits, appearance of a tongue pad and reorganization of the gill skeleton and musculature to produce the mechanical system necessary for projecting and retracting the tongue, enlargement of the mouth and eyes, development of eyelids, and major changes in the structure of the skull and skin.

Locomotion. Locomotion is by means of limbs and by sinuous body movements. Elongated species of the genera *Phaeognathus, Batrachoseps, Oedipina*, and *Lineatriton* have reduced limbs and rely mainly on body movements for rapid locomotion. Species of the genus *Aneides* have arboreal (tree-dwelling) tendencies, and their long legs and digits, expanded toe tips, and prehensile (grasping) tails make them effective climbers. Some salamanders of the genera *Ixalotriton, Nyctanolis, Dendrotriton, Pseudoeurycea*, and *Chiropterotriton*, found in the New World tropics, are similarly adapted. Others, members of the genus *Bolitoglossa*, have extensively webbed forefeet and hindfeet with indistinct digits, allowing them to move across moist leaves and other smooth surfaces.

Behaviour and ecology. Adult salamanders are nearly all nocturnal (*i.e.*, active mainly at night) animals. They may be highly seasonal, remaining hidden underground until the breeding season, or they may emerge from hiding places on any evening when moisture and temperature are at the proper levels. Fallen logs, rocks, crevices in soil, and surface litter commonly provide daytime refuge. Home ranges of salamanders are small, often less than 3 or 4 square metres (30 to 40 square feet), and in favourable areas some of the smaller species can be very abundant, occasionally numbering thousands per acre.

Habitat

Most terrestrial species live near the surface of the ground, often in thick leaf litter and rock piles. Some enter subterranean retreats, sometimes by way of burrows made by mammals and invertebrates. Caves are often occupied during cold or dry periods. Climbing species live on rock faces and in crevices, in trees, on broad-leaved herbs and shrubs, and in bromeliads. Many species are semiaquatic, frequenting streamside and spring habitats throughout their lives. The terrestrial species that have direct development have been able to free themselves entirely from reliance on standing or flowing water. Among the bolitoglossine plethodontids, species are found in habitats ranging from true deserts and frigid Alpine areas to tropical rain forests and from sea level to elevations of more than 4,000 metres (13,000 feet).

Food and feeding. Insects are by far the most important food of salamanders. All terrestrial salamanders initially contact the prey with the tongue, which retracts quickly to deliver the quarry into the mouth. Some members of the Salamandridae and Plethodontidae, however, have evolved highly specialized tongue-protrusion mechanisms. These are especially well developed in the tropical plethodontids, many of which are arboreal. The tongue can be extended from the mouth for a considerable distance and retracted almost instantaneously, with the prey attached to the sticky tongue pad. The gill skeleton found in larvae has evolved into a biomechanically efficient tongue-projection mechanism in adults, and most of the tongue skeleton is shot from the mouth with the tongue pad on the end; in contrast, in frogs only the soft parts of the tongue leave the mouth. When the tongue is maximally projected, the retractor muscles are stretched; because contraction of these muscles takes place at the same time as the protractor muscles are contracted, the tongue is rapidly returned to the mouth.

FORM AND FUNCTION

Skin and external features. The most distinctive and important feature of amphibians in general and salamanders in particular is their smooth, moist skin. This organ consists of an epidermis, or surface tissue, that is several layers thick and a rather thick dermis containing mucous and poison glands as well as pigment cells. The integument, or skin,

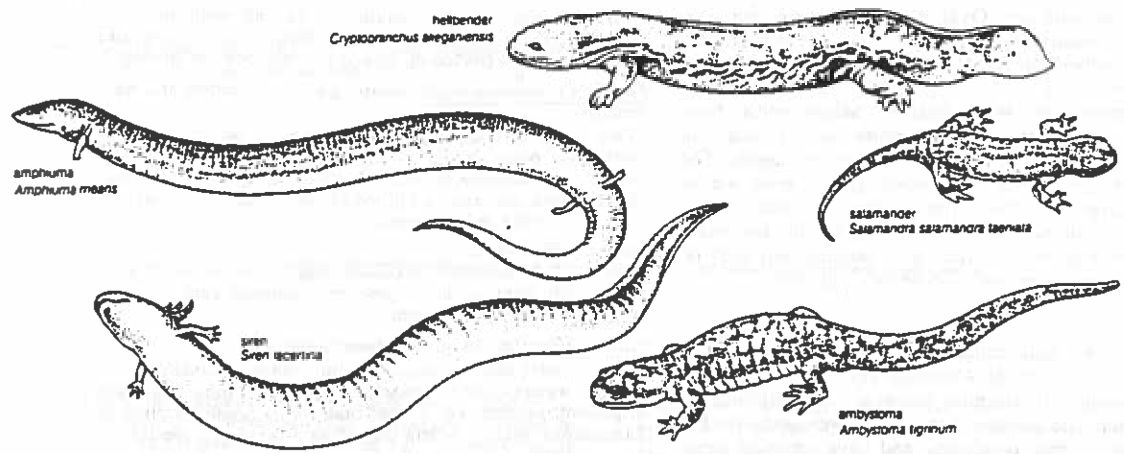

Figure 6: Representative urodeles.
From *The Life of Vertebrates* by J.Z. Young, 1st ed. 1950, 3rd ed. © J.Z. Young 1981; published by Oxford University Press

is highly vascular and serves a major respiratory function. The poison glands of some species produce some of the most virulent toxins known. The fleshy tongue pad contains many mucus-secreting glands.

Most species are drab gray or brown; but many species, especially the more poisonous ones, are spectacularly coloured, with bright spots, blotches, or streaks. The few integumentary specializations include keratinized skins of the terrestrial stages of many salamandrids, keratinized claws in stream-dwelling hynobiids, and glands that to some degree stimulate sexual activity by making the female more receptive. Cryptobranchids have large, lateral folds of skin that serve respiratory functions.

Bones and cartilage. The rather weak skull of adults is composed of various paired and unpaired bones. These bones may fuse or be lost in different groups, and their presence and arrangement are important in classification. Much of the fusion and loss of skull bones is associated with a trend toward tongue feeding. Small, double-cusped teeth line the margins of the jaw and spread over parts of the palate. They are important in holding but not chewing the prey.

Cartilage plays an important role in the salamander head, especially in supportive structures in the throat region. These are ossified (bony) to different degrees, with more cartilage in the more highly evolved groups. Species such as the bolitoglossine plethodontids that display tongue protrusion often have flexible, cartilaginous tongue skeletons. In larvae and permanently gilled species the tongue is not developed.

The vertebrae constituting the spinal column are generalized with centrums (*i.e.*, ventral, or lower, sections connecting with the adjacent vertebrae) that are rather poorly developed. The notochord (*i.e.*, a resilient, flexible cord of specialized cells passing through the vertebral column) is usually persistent in adults. An intervertebral cartilage forms the articulation between vertebrae. If it remains cartilaginous, the vertebrae are said to be amphicoelous (biconcave, or depressed on both the anterior and posterior sides), but, if it mineralizes or ossifies, the vertebrae are termed opisthocoelous (bulged on the anterior side and depressed on the posterior side). There is one cervical vertebra with a characteristic projection called the odontoid process and two large facets for articulation with the skull. There may be from 11 (*Ambystoma talpoideum*) to 60 (*Amphiuma*) dorsal, or trunk, vertebrae, all but the last 1 or 2 usually bearing ribs. Most salamanders have from 14 to 20 trunk vertebrae. One sacral vertebra, 2 to 4 caudosacral vertebrae, and from about 20 to more than 100 (*Oedipina*) caudal, or tail, vertebrae complete the column. Many plethodontids are capable of autotomizing, or dropping off, the tail, a valuable defense mechanism in the event that the tail is grasped or bitten by a predator. These salamanders have various specialized features associated with the last caudosacral and the first caudal vertebrae, between which the break usually occurs.

The limbs and girdles are similar to those of generalized vertebrates. The pectoral, or chest, girdle, supporting the forelimbs, is relatively reduced, and the fused elements remain largely in a cartilaginous condition. An ypsiloid cartilage, attached to the front of the pelvic girdle, is used in exhalation in several groups, especially ambystomatids, dicamptodontids, hynobiids, and salamandrids. Digits and digital bones have been lost in many different groups. There are never more than four fingers, but nearly all species have five toes. Fingers and toes

Nervous system and sense organs. The nervous system is almost diagrammatically simple in anatomy, although this apparent simplicity is not primitive but mainly a secondary evolutionary derivation. The generalized brain is rather small. The relatively large cerebrum (collectively, the two large anterior lobes of the brain) is associated with the large and important olfactory and vomeronasal organs, both of which are used for smelling. The surprisingly complex social organization of these organisms is largely based on olfaction. The eyes, usually large and well developed, are reduced and nearly lost in some cave-dwelling species. Vision is especially important in terrestrial foraging, because the projection of the tongue is guided visually. Certain parts of the inner ear are large and well developed. Hearing mechanisms of the salamander are not fully understood. There is no middle ear cavity and no external ear. One middle ear bone rests in the structure known as the vestibular fenestra. The other bone of the middle ear rests in the posterior part of the fenestra and is joined by muscles to the pectoral girdle. In most species these bones are variously fused or lost, so that only one survives. The spinal cord and the peripheral nervous system—*i.e.*, the paired cranial and spinal nerves—are generalized in their structure, and there are distinct brachial and sacral plexuses, both of which are important nerve networks that supply the limbs.

Muscles and organ systems. The generalized musculature of the trunk exhibits little differentiation. The abdominal muscles show increasing degrees of differentiation in the fully metamorphosed, more derived taxa. The hyobranchial and branchiomeric muscles and some abdominal muscles (rectus abdominis) are highly specialized in those species that use the tongue to capture prey.

The simple digestive system includes a short, nearly straight gut. The lungs are relatively simple, saclike organs in primitive groups. In stream-dwelling members of several families, the lungs are greatly reduced; they are entirely absent in all plethodontids.

The circulatory system is characterized by a highly developed vascularization of the body surface. The heart is simple, with one ventricle (*i.e.*, a chamber that pumps blood out of the heart) and two atria (chambers that receive blood from the rest of the body); separation between the two atria is not distinct in lungless forms.

The urogenital system consists of an elongated kidney Gonads with a distinct sexual segment and a posterior concentration of large renal units, which filter urine from the blood. Testes, the male sex glands, are small and compact, increasing in size with age. Ovaries of females are thin sacs. The cloaca is relatively complex in more derived groups, with a spermatheca in females and several sets of cloacal glands in both sexes.

Cell structure and biochemistry. Salamanders have enormous genomes that contain more nucleic acid and larger chromosomes in each cell than any tetrapods. The genomes vary greatly in size among species, even within a family. Large genomes impose large cell size, which means that small salamanders have relatively few cells. The apparent anatomic simplicity of salamanders may be a direct and phylogenetically secondary outcome.

EVOLUTION

Main patterns. Salamanders are very ancient survivors of a Mesozoic (245 to 66.4 million years ago) radiation. The cryptobranchids, sirenids, proteids, and amphiumids are all unusual, considering that they are tetrapods, in that they are fully to mainly aquatic and have retained larval traits (paedomorphosis) to a great degree. The other families have adults that are generalized terrestrial tetrapods, but several of these families have few species and limited distributional ranges. The hynobiids, plethodontids, and salamandrids are the most diverse in structure and ecology. These groups have evolved along parallel lines, and features such as highly projectile tongues, loss of lungs, and loss of fifth toes have evolved repeatedly, even within the same family. The combination of parallel evolution and paedomorphic evolution has made phylogenetic analysis difficult. Several genera—such as *Ambystoma, Bolitoglossa, Hynobius,* and *Plethodon*—are very speciose, and within the Plethodontidae there has been much cryptic speciation that has been revealed by application of biochemical techniques.

Paleontology. Fossils have contributed little as yet to the understanding of salamander evolution. The earliest definitive salamander from the Middle to Late Jurassic Period (187 to 144 million years ago) may be the sister taxon (Karauridae) of all other salamanders. Several other families (Prosirenidae, Scapherpetonidae, Batrachosauroididae) are known only from fossils. The relationships of salamanders to other living and fossil amphibians are unclear, but recent workers consider the three living groups to form the subclass Lissamphibia.

CLASSIFICATION

Distinguishing taxonomic features. The features used to establish the limits of the order and of the groups within it include general body size and organization—*e.g.,* presence or absence of external gills; numbers and relative proportions of limbs and digits; number and arrangement of skull bones; organization of the hyobranchial apparatus (cartilage in the throat region); structure and distribution of the teeth; structure of the vertebrae and intervertebral articulations; number of vertebrae; number and organization of the hand and foot elements; anatomy of the pelvic girdle; and anatomy of external structures, such as skin glands, body and tail fins, webbing of hands and feet, and cloacal glands. Distinctive, too, is the general way of life, whether permanently aquatic, semiaquatic, or terrestrial.

Annotated classification. The classification below is based on that of D.R. Frost (1985) and more recent work. There is as yet no widely accepted scheme for classification below the order level. The plethodontids of the New World tropics and the hynobiids across western China and Central Asia remain poorly known taxonomically.

ORDER CAUDATA (URODELA)
Tailed amphibians with 2 or 4 legs; moist, usually smooth, glandular skin; the most generalized of the living amphibians not only in structure but also in way of life; 61 genera and about 400 species.

Suborder Cryptobranchoidea
The most primitive salamanders; external fertilization; angular bone separate from the prearticular bone in the lower jaw; 2 pairs of limbs; no external gills; aquatic, semiaquatic, and terrestrial.

Family Hynobiidae (Asiatic salamanders)
Generalized, medium-sized (to about 250 mm), semiaquatic and terrestrial; lacrimal and septomaxillary bones present in the skull; vomerine teeth not parallel to marginal teeth; no fossil record; northern Asia from the Ural Mountains to Japan and Taiwan; 9 genera (including *Hynobius*) and about 36 species.

Family Cryptobranchidae (Asiatic giant salamanders and hellbenders)
Very large, to about 180 cm; aquatic; no lacrimal or septomaxillary bones in skull; vomerine teeth parallel to marginal teeth; Late Paleocene (63.6–57.8 million years ago) to present; Japan, China, and eastern United States; 2 genera (*Andrias* and *Cryptobranchus*) and 3 species.

Suborder Sirenoidea
Mode of fertilization unknown; angular bone fused with prearticular bone in lower jaw; only anterior pair of limbs present; external gills; aquatic.

Family Sirenidae (sirens and dwarf sirens)
Small to very large, to about 100 cm, predators; inhabitants of lowland waters; Late Cretaceous (97.5–66.4 million years ago) to present; southeastern United States from South Carolina to Tamaulipas, Mex.; 2 genera (including *Siren*) and 3 species.

Suborder Salamandroidea
Fertilization internal; angular bone fused with prearticular bone in lower jaw; 2 pairs of limbs; external gills in a few species that remain permanently aquatic; aquatic, semiaquatic, and terrestrial.

Family Ambystomatidae (mole salamanders)
Small to moderate size, to 35 cm; usually with well-developed lungs; no nasolabial grooves; ypsiloid cartilage present; Oligocene (36.6–23.7 million years ago) to present; North America; 2 genera (including *Ambystoma*) and about 32 species.

Family Amphiumidae (congo eels)
Large, to more than 100 cm; very elongated; aquatic to semiaquatic; predaceous, with powerful jaws and teeth; limbs diminutive, 1 to 3 fingers and toes; external gills absent, but spiracle open; Late Cretaceous to present; eastern North America; 1 genus, *Amphiuma*, and 3 species.

Family Dicamptodontidae (giant salamanders)
Large salamanders, to 35 cm; stout-bodied and large-headed with large, long limbs; larvae live for several years, and 1 species is permanently larval; Paleocene (66.4–57.8 million years ago) to present; northwestern United States and extreme southwestern Canada; 1 genus, *Dicamptodon*, and 4 species.

Family Plethodontidae (lungless salamanders)
Very small to moderate size, 3.5 to about 30 cm; includes the most specialized and most terrestrial salamanders and the only truly tropical species; lungless; nasolabial grooves present; no ypsiloid cartilage; Early Miocene (23.7–16.6 million years ago) to present; North America, Central America, and most of South America; 6 species in Europe (Sardinia, southern France, and north-central Italy); 25 genera, placed in 2 subfamilies: Desmognathinae, with 3 genera (including *Desmognathus*) and about 14 species in eastern North America, and Plethodontinae, with 22 genera (including *Plethodon* in North America and the bolitoglossines *Bolitoglossa* in Central and South America, *Batrachoseps* in western North America, and *Hydromantes* in western North America and the central Mediterranean region) and about 232 species.

Family Proteidae (olms and mud puppies)
The olm is blind, has little pigment, has an elongated body, and is cave-dwelling; mud puppies live in lakes and streams, have eyes, and are normally pigmented; elongate bodies, length to 45 cm; limbs with 3 (olm) or 4 fingers, 2 (olm) or 4 toes; external gills present; Late Paleocene to present; 2 genera (*Proteus*, native to the northern Balkan Peninsula, and *Necturus*, of eastern North America) and 6 species.

Family Rhyacotritonidae (torrent salamanders)
Small dwellers of streams, springs, and seeps; length to 9 cm; 4 fingers and 5 toes; no gills in adults; no fossil record; northwestern United States; 1 genus, *Rhyacotriton*, and 4 species.

Family Salamandridae (salamanders and newts)
Generalized form and habit; moderate size, to 30 cm; limbs with 4 fingers, 4 to 5 toes; usually no external gills or spiracle; Paleocene to present; Europe; North Africa; Middle East; Afghanistan to Japan, China, and northern Vietnam; eastern and western North America; 14 genera (including *Triturus* and *Salamandra* in Europe, *Notophthalamus* and *Taricha* in North America, and *Cynops* in Japan) and about 56 species.

Critical appraisal. There is disagreement concerning the classification of salamanders below the ordinal level. Some authorities recognize no suborders, and some separate the genus *Necturus* into the family Necturidae, distinct from the Proteidae. Molecular data (nucleic acid sequence comparisons) have cast into doubt the former separation of the Salamandroidea into two suborders. (D.B.W.)

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