Urodela

Salamanders, constituting the order Urodela (Caudata), together with frogs (order Anura) and caecilians (order Gymnophiona) comprise the three living groups of the class Amphibia. The relatively small and inconspicuous salamanders are important members of north temperate and some tropical animal communities. 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 hardness make them good 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 four to six 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 500 millimetres (about 1.6 to 14 inches) in length. Some live in moist places on land but must go 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 six feet). Salamanders may retain gills throughout life, lose the gills but retain a spiracle (breathing pore) or gill slit, or completely metamorphose (i.e., alter radically in structure and appearance) and lose both gills and gill slits. Many aquatic species resemble their terrestrial relatives in body form, but aquatic genera such as Siren and Pseudobranchus lack hindlimbs, and Amphiuma has an extremely elongated body, short tail, and diminutive legs; several cave-dwelling forms (Proteus, Hadroleptodon, Typhlonolus) are blind and almost without pigment.

Distribution and abundance. Salamanders are classic examples of animals with a Holartic distribution (i.e., in the north-temperate regions of both the Eastern and Western hemispheres); eight of the nine families (see below Annotated classification) are found almost entirely in northern regions that lie outside the tropics. Typically, they 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, North Vietnam, and the island of Okinawa. Some ambyastosids reach the southern margins of the Mexican Plateau, but only the lungless salamanders (plethodontids) have truly entered the tropics. One group of plethodontids, which occupies a wide variety of tropical habitats in the New World—from northern Mexico to southern Brazil and central Bolivia—contains nearly half of all recognized species of salamanders, an indication that the plethodontids have been highly successful in the tropical environment. Other areas in which salamanders have been successful include temperate North America (Appalachian and Ozark uplands; Pacific coast 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 simple or nonexistent in hynobids and cryptobranchids, is increasingly elaborate and prolonged in the more highly evolved families. In primitive species comprising the suborder Cryptobranchida, fertilization of the egg is external. 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. All other species of salamanders have more complex courtship behaviour—often differing in details between species—and internal fertilization. The male deposits from one to many spermatophores on the ground or other surface. These are produced by a cloacal gland, 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 pachydontids 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. In most pachydontid and other species of other families, eggs are laid singly, in short strings, or in small groups 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 or in water plants which are arranged so that they often hold water. Frequently, the female stays with the eggs until they hatch, a period of several weeks. 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 five or six.

Typical salamanders undergo an aquatic larval stage that lasts for a period ranging from a few days to several years. A short period of metamorphosis usually occurs before the terrestrial phase of the life cycle begins. The newly metamorphosed salamander is usually very small, and from one to several years elapse before it achieves sexual maturity.

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. This phenomenon, known as paedomorphism—i.e., retention of larval or juvenile features by adults—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 several species of the 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, and Plethodontidae.

Most species of the family Plethodontidae develop entirely on land, with no aquatic larval stage. The hatching 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 genus Salamandra (Salamandridae) may retain the fertilized eggs in the reproductive tract for a varying amount of time. The first salamander (Salamana-
dra saumandra) deposits a relatively advanced larva in the water. In the Alpine salamander (Salamandra atra) and some other Salamandra species, fully metamorphosed individuals are born. One individual develops from the first egg in each ovipositor, 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, and finally 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 live-bearing members of the order.

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Figure 2: Principal types of urodela larvae.

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 (toward the head) and large gills (see Figure 2, above). 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 (i.e., chemical substances that serve to regulate the function of various organs) produced by the thyroid and pituitary glands. The following 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 a 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. Some very elongated species of the genus Phaeognathus, Batrachoepis, Oedipina, and Lineatriton have reduced limbs and rely mainly on body movements for rapid locomotion. Species of the genus Ancides have arboreal (i.e., tree-climbing) tendencies, and their long legs and digits, expanded toe tips, and prehensile (grasping) tails make them effective climbers. Some salamanders of the genera Pseudoeurycea and Chirotecton, 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 three or four 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.

Insects are by far the most important food of salamanders. Primitive salamanders seize their prey by a combination of jaw and tongue movements. 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.

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. Cavities 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 semi-aquatic, 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 wa-
ter. Among one group of 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 meters (13,000 feet).

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 layer, and several layers thick and a rather thick dermis containing mucus and poison glands as well as pigment cells. The integument, or skin, 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 colored. Juvenile salamander bodies are smaller and brightly colored. Adults tend to be drab and cryptic in coloration. Young salamanders of some species have a contrasting dark background. The few integumentary specializations include keratinized (i.e., infused with a tough, horny material; keratin) skins of the terrestrial stages of many salamanders; keratinized claws in stream-dwelling hydropsids; and so-called epidermic glands (believed to stimulate sexual activity of the opposite sex) that are variously distributed in many species. Cryptobranchids have large, lateral folds of skin that serve respiratory functions.

Fingers and toes. The rather weak skull of adults is comprised of various paired 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 frequently 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 urodele 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 that display tongue protrusion often have flexible, cartilaginous tongue skeletons. In most and permanently gilled species the tongue is not developed.

The vertebral column is generally used with centra (i.e., ventral, or lower, sections connecting with the adjacent vertebrae) that are rather poorly developed. The notochord, a flexible rod of specialized cells passing through the vertebral column, is usually present in adults. An intervertebral cartilage forms between vertebrae. If it remains cartilaginous, the vertebrae are said to be amphichordal, whereas if the cartilage is depressed on both the anterior and posterior sides, but, if it mineralizes or ossifies, the vertebrae are termed ophistochordal (bulged on the anterior side and depressed on the posterior side). There is one cervical vertebra with a characteristic projection called the neural arch process, and two large facets for articulation with the skull. There may be from 11 (Ambystoma talpoideum) to 60 (Amphithymus) dorsal, or trunk, vertebrae, but usually less than half in the more highly evolved species. Six sacral vertebrae are found in most species, and at least one pair of caudal vertebrae is present in all species. These are similar to those of generalized vertebrates. The pectoral, or chest, girdle, supporting the forelimbs, is relatively reduced; all elements are fused and remain largely in a cartilaginous condition. An episcapoid cartilage, used in exhalation, is present in several groups, especially ambyostomats and salamanders. Digita! toes have been lost in many different groups. There are never more than four fingers, but nearly all species have five toes.

Nervous system and sense organs. The nervous system is the simplest found in any four-legged animal. 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 eyes, usually large and well developed, are reduced and nearly lost in some cave-dwelling species. 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 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.

The elements are variously fused or lost in different groups. 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 supplying the limbs.

Muscles and organ systems. The generalized trunk musculature shows little differentiation. The abdominal muscles are increasingly differentiated in the higher groups. The hyobranchial and branchiomerid muscles and some abdominal muscles (rectus abdominis) are highly specialized in species that use the tongue to capture the prey.

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

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 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 highly evolved groups with a spermatheca in females and several sets of cloacal glands in both sexes.

Evolution and relationships. Amfibians have contributed little, as yet, to the understanding of salamander evolution. The earliest definitive salamander is one of unknown affinities from the Jurassic Period (about 156–150 million years old). The oldest known ambystomatid families (Prosirenidae, Scapherpetonidae, Batrachosaurusidae) are known only from fossils.

The relationships of urodeles to other living and fossil amphibians are unclear, but recent workers consider the three living groups to form the subclass Liss amphibia.

Distinguishing taxonomic features. The features used to establish the limits of the order and 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 vertebral and intervertebral articulations; number of vertebrae; number and organization of the hand and foot elements; anatomy of the pelvic girdle; anatomy of external structures, such as gill (sex-attractant) glands, body and tail fins, webbing of hands and feet, and cloacal glands. Distinctive also is the general way of life, whether permanently aquatic, semi-aquatic, or terrestrial.

Annotated classification. The classification below is based on that of A.H. Brame, Jr. (1967). There is as yet no widely accepted scheme for classification below the order level. The plethodontids of the New World tropics remain poorly known, taxonomically.

ORDER URODELA (OR CAUDATA)
Tailed amphibians with 2 or 4 legs; moist, usually smooth, glandular skin; the most generalized of the living amphibi-
Some authorities place the sireniids in a separate order, Trachystomata, while others separate the Necturidae from the Proteidae, but neither scheme has been widely accepted. Chromosomal evidence of proteidnucid relatedness has recently been presented. Close association of Ambystomatidae and plethodontid families is now accepted, but placement of Amphiumidae remains controversial. Compare AMBLYSTOMA: Annotated classification.


Urticales