URODELA

by

David B. Wake

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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 hardiness 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 350 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*, *Haideotriton*, *Typhlomolge*) are blind and almost without pigment.

Distribution and abundance. Salamanders are classic examples of animals with a Holarctic 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 ambystomatids 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 hynobiids and cryptobranchids, is increasingly elaborate and prolonged in the more highly evolved families. In primitive species comprising the suborder Cryptobranchoidea, 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 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. In most plethodontids and in some 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, the leaves of 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.

Fertilization

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 paedomorphosis —*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.

Paedomorphosis

Most species of the family Plethodontidae 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 genus *Salamandra* (Salamandridae) may retain the fertilized eggs in the reproductive tract for a varying amount of time. The fire salamander (*Salaman-*

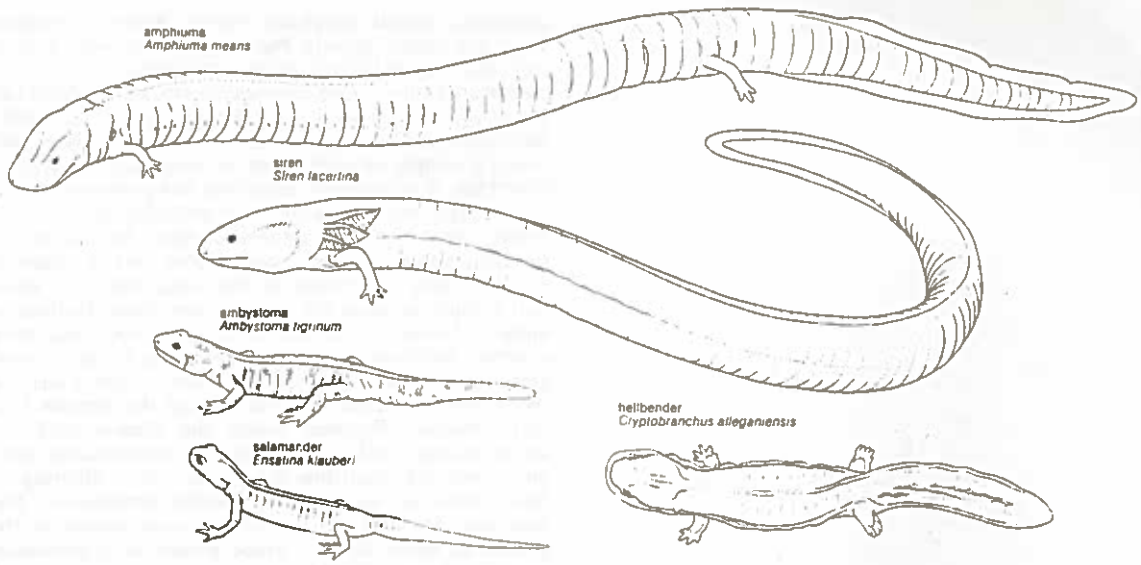

Figure 1: Representative urodeles.

dra salamandra) 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 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, 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.

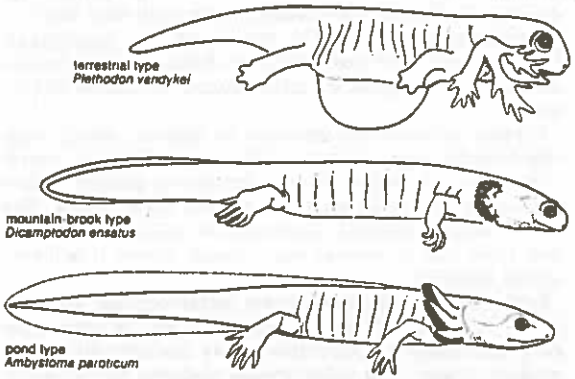

Figure 2: Principal types of urodele larvae.

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 (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 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 (*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 *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 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.

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 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 metres (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 tissue, that is 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 coloured, with bright spots, blotches, or streaks on 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 salamandrids; keratinized claws in stream-dwelling hynobiids; and so-called hedonic 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.

Bones and cartilage. 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 larvae and permanently gilled species the tongue is not developed.

The vertebrae comprising 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 one or two usually bearing ribs. Most salamanders have from 14 to 20 trunk vertebrae. One sacral vertebra, two to four caudosacral vertebrae, and from about 20 to over 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; all elements are fused and remain largely in a cartilaginous condition. An ypsiloid cartilage, used in exhalation, is present in several groups, especially ambystomatids 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 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 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. 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 branchiomeric muscles and some abdominal muscles (rectus abdominis) are highly specialized in 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 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.

Gonads

Evolution and classification. *Paleontology.* Fossils 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 136,000,000 to 190,000,000 years ago). Several ambystomatoid families (Prosirenidae, Scapherpetonidae, Batrachosauroididae) 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 Lissamphibia.

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; numbers of vertebrae; number and organization of the hand and foot elements; anatomy of the pelvic girdle; anatomy of external structures, such as hedonic (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-

ans not only in structure but also in way of life; about 320 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, semi-aquatic, and terrestrial.

Family Hynobiidae (Asiatic salamanders)

Generalized, medium-sized (to about 250 mm, or about 10 in.), semi-aquatic and terrestrial; lacrimal and septomaxillary bones present in skull; vomerine teeth not parallel to marginal teeth; Paleocene(?) (54,000,000–65,000,000 years ago) to present; northern Asia from Ural Mountains to Japan and Taiwan; about 30 species.

Family Cryptobranchidae (giant salamanders and hellbender)

Very large, to about 180 cm (about 6 ft.), aquatic; no lacrimal or septomaxillary bones in skull; vomerine teeth parallel to marginal teeth; Oligocene (26,000,000–38,000,000 years ago) to present; Japan, China, and eastern United States; 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 (about 40 in.), predators; inhabitants of lowland waters; Late Cretaceous (65,000,000–90,000,000 years ago) to present; southeastern United States from South Carolina to Tamaulipas, Mexico; 3 species.

Suborder Salamandroidea

Fertilization internal; angular bone fused with prearticular bone in lower jaw; no septomaxillary bones in skull; tooth replacement of vomerine teeth from medial side in metamorphosed forms; 2 pairs of limbs; external gills in a few species; aquatic, semi-aquatic, and terrestrial.

Family Proteidae (olms)

Blind; lacking pigment, cave-dwelling; elongated body, length to 30 cm (about 1 ft), and slender limbs (3 fingers, 2 toes); external gills present; Pliocene (2,500,000–7,000,000 years ago) to present; 1 species, native to Yugoslavia.

Family Necturidae (mud puppies)

Small to moderately large, to 45 cm (about 1½ ft), permanently aquatic, lake and stream dwellers; eyes and skin pigmentation present; 4 fingers and 4 toes; external gills present; no fossil record; eastern North America; 5 species, of genus *Necturus*.

Family Amphiumidae (congo eels)

Large, to over 100 cm (about 40 in.); very elongated, aquatic to semi-aquatic; 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; 3 species, of genus *Amphiuma*.

Family Salamandridae (salamanders and newts)

Generalized form and habit; moderate size, to 32 cm (about 13 in.); limbs with 4 fingers, 4 to 5 toes; usually no external gills or spiracle; Upper Cretaceous (?) to present; Europe, North Africa; Middle East; Afghanistan to Japan, China, and North Vietnam; eastern and western North America; about 42 species.

Suborder Ambystomatoidea

Fertilization internal; angular bone fused with prearticular bone in lower jaw; septomaxillary bones present primitively in skull; tooth replacement of vomerine teeth from posterior or lateral direction; 2 pairs of limbs; external gills in some species; aquatic, semi-aquatic, or terrestrial.

Family Ambystomatidae (mole salamanders and others)

Small to moderate size, to 35 cm (about 14 in.); usually with well developed lungs; no nasolabial grooves; ypsiloid cartilage present; Paleocene to present; North America; about 33 species, including *Ambystoma*.

Family Plethodontidae (lungless salamanders)

Very small to moderate size, 4 to about 30 cm (about 1.6 to 12 in.); includes the most specialized and most terrestrial salamanders, and the only truly tropical species; lungless; nasolabial grooves present; no ypsiloid cartilage; Pliocene to present; North America, Central America, and most of South America; 2 species in Europe (Sardinia, southern France, and north central Italy); more than 200 species.

Critical appraisal. Some controversy exists concerning the classification of salamanders below the ordinal level. Some authorities place the sirenids in a separate order, Trachystomata, while others separate the Necturidae from the Proteidae, but neither scheme has been widely accepted. Chromosomal evidence of proteidnecturid similarity has recently been presented. Close association of Ambystomatidae and Plethodontidae is now accepted, but placement of Amphiumidae remains controversial. Compare AMPHIBIA: *Annotated classification.*

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(D.B.W.)

Urticales