AMPHIBIA

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Keywords: Gymnophiona, Caudata, Anura, frog, salamander, caecilian, morphology, life-history, distribution, tadpole, vocalization, metamorphosis, pharmaceuticals, chytrid

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Summary

The Amphibia are vertebrates classified into three orders: Gymnophiona (caecilians), Caudata (salamanders), and Anura (frogs). The group is widely distributed and species-rich, and its success is in part due to a remarkable diversity of reproductive strategies. Most lay eggs that develop into feeding free-swimming larvae, but there are numerous other strategies. The caecilians are worm-like, adapted for burrowing. Salamanders are confined to the moist tropics, and possess a tail. The frogs are adapted for jumping, with no tail and specialized girdles to attach the limbs to the vertebral column. There are more than 3500 frog species in almost all habitats, from lakes and rainforests to deserts. The amphibians eat a wide range of food, and are eaten by larger vertebrates. Many groups have free-swimming larvae (tadpoles), and these usually occupy a different habitat and utilize a different food resource from the adults. The frogs make extensive use of sound communication for breeding. More than ten species have become extinct in pristine habitats in contemporary times. Many factors have been implicated, including the discovery of a chytrid fungus that infects the skin. Amphibians are sensitive to pollutants, especially the species or stages in water, and may serve as an early-warning system for habitat monitoring. Amphibians are useful as components of the ecosystem, and as potential sources of novel pharmaceuticals. Once discovered, these substances can be synthesized in the laboratory without harming the amphibians.

1. Introduction

Amphibians are widespread and important components of many ecosystems. They are vertebrates, intermediate in many respects between fish and reptiles. They have soft skins, and most species require water in which the free-swimming and feeding larvae can develop. They are able to obtain oxygen through their moist skin. Many life-history strategies are found in this group, and their success is due to their ability to eat a wide variety of prey, to occupy burrows, to live in water, on land, or high in vegetation. Apart from their ecological role, they are assuming more importance to humans as a potential source of active pharmaceuticals.

2. Classification of Amphibia

The class Amphibia groups soft-skinned vertebrates, most of which have lungs and lay eggs in water. The eggs develop into free-swimming larvae, which in turn metamorphose into adults. Living amphibians are placed in the subclass Lissamphibia (in some classifications regarded as the class Lissamphibia). This subclass consists of three orders: Gymnophiona, Caudata, and Anura.

The order Gymnophiona includes the caecilians and their relatives. They are all elongated, limbless animals that superficially resemble large earthworms. There are nearly 200 species in five families: Caeciliidae, Ichthyophiidae, Rhinatrematidae,

Scolecomorphidae, and Uraeotyphlidae.

The order Caudata includes the salamanders and their relatives, which all have a long tail and two pairs of limbs. There are ten families, with about 525 species: Ambystomatidae, Amphiumidae, Cryptobranchidae, Dicamptodontidae, Hynobiidae, Plethodontidae, Proteidae, Rhyacotritonidae, Salamandridae, and Sirenidae.

The order Anura consists of the tailless amphibians, and includes all the common frogs. This is the dominant order of amphibians, with more than 3500 species in 28 families. These are the Allophrynidae, Arthroleptidae, Ascaphidae, Astylosternidae, Bombinatoridae, Brachycephalidae, Bufonidae, Centrolenidae, Dendrobatidae, Discoglossidae, Heleophrynidae, Hemisotidae, Hylidae, Hyperoliidae, Leiopelmatidae, Leptodactylidae, Megophryidae, Microhylidae, Myobatrachidae, Pelobatidae, Pelodytidae, Pipidae, Pseudidae, Ranidae, Rhacophoridae, Rhinodermatidae, Rhinophrynidae, and Sooglossidae.

3. Gymnophiona

The caecilians could be mistaken for earthworms or legless lizards. Most burrow in leaf litter and damp loose soil in forests or along waterways. They are mainly blue, gray, or purple, sometimes with pale heads. The species range in length from 70 mm to 1.5 m. Many species have minute scales embedded in the skin.

3.1. Morphology

Caecilians display remarkable adaptations for a burrowing lifestyle. The skull is bony, strengthened on the sides by a complete roof, and flattened in front to allow them to move soil efficiently. There are two rows of fine sharp recurved teeth that enable the animal to capture and retain prey. There is a modified vertebra (the atlas) articulating with the head, followed by between about 100 and nearly 300 vertebrae in different species. Despite the large number of vertebrae, only a few caecilians have a tail. The body-wall musculature is well developed and separate from the muscles of the vertebral column. This allows them to move efficiently while burrowing, both by side-to-side snakelike actions, and by slightly folding to increase friction with the surroundings and then extending the body to push the head forward. Although the eyes are reduced or absent, a tentacle on the side of the head provides chemosensory information probably associated with feeding and finding a mate. The skin and body-wall muscles form a tough covering that protects the body while burrowing.

3.2. Life Cycle

Most caecilians are live-bearers, while others lay eggs near water and develop into free-swimming larvae, or directly into juveniles. Within the live-bearers, some produce larvae, while others produce juveniles. All species that have been investigated have internal fertilization, accomplished with the use of an intromittent organ, the phallodeum. The breeding season may be extended in some groups, or be limited to the start of the rains in others. The primitive mode of laying eggs (oviparity) that develop into free-swimming larvae is replaced by ovivivparity, where the eggs develop directly

into young, to live-bearing (viviparity). The single family that is viviparous with free-swimming larvae appears to have evolved this strategy independently. All larvae hatch at an advanced stage. Table 1 summarizes the various reproductive modes by family. It must be emphasized that this information is based upon few samples.

Family	Reproductive Mode
Caeciliidae	Oviparous with aquatic larvae, or ovoviviparous, or viviparous
Ichthyophiidae	Oviparous with aquatic larvae
Rhinatrematidae	Oviparous with aquatic larvae
Scolecomorphidae	Viviparous, based on embryo morphology
Uraeotyphlidae	Oviparous with direct development

Table 1. Reproductive modes of caecilians

3.3. Distribution

The five families of caecilians are restricted to the tropics (Table 2).

The distributions suggest an ancient origin, with the present patterns largely the result of continental drift (see *Earth System: History and Natural Variability*).

The species are not equally distributed, with the highest number (85) in the Neotropical Realm, followed by the Oriental Realm with 45, and the Ethiopian Realm with about 30 (see *Zoogeographic Realms*).

Family	Distribution
Caeciliidae	North America, South America, India, East and West Africa, and the islands off Africa: the Seychelles, Fernando Po, Sao Tome, and Principe
Ichthyophiidae	The Philippines and India to southern China, Thailand, and the Malayan Archipelago
Rhinatrematidae	Northern South America
Scolecomorphidae	Africa
Uraeotyphlidae	India

Table 2. Distribution of caecilians

3.4. Feeding and Predators

Prey, generally earthworms, is found by tracking using the sensory tentacle. The prey is grabbed from the side, held by making use of the many recurved teeth, then swallowed whole or broken by twisting the body while the prey is held against the burrow walls. The worms are found on the surface or located underground. Caecilians have a powerful jaw-closing mechanism relying on the leverage produced when the quadrate bone is used as a fulcrum. Various species feed on crickets, termites, and beetle larvae in addition to earthworms. The larger species can eat vertebrates such as small lizards.

Birds and snakes are known to eat caecilians.

3.5. Little-known Caecilians

Caecilians are rarely seen in nature. They emerge from their burrows during heavy rain, but spend most of their time underground. Scientists find them by digging in suitable habitats, and much of what is known is deduced from preserved specimens or laboratory observations of a limited number of species. For many species, no life-history information is available. They occur in moist forests, a habitat threatened in many parts of the tropics.

4. Caudata

The tailed amphibians are small, generally less than 150 mm long, and active mostly at night. They are abundant in habitats such as the Appalachian Mountains of North America, where they may attain the highest biomass of any vertebrate group. There are species that are completely aquatic, some that are terrestrial, and many that utilize both habitats. A remarkable habitat occupied by some specialized species is water bodies in underground caves.

4.1. Morphology

Salamanders have small heads, short bodies, and long tails. Most have four limbs, enabling them to be active on land, while others are fully aquatic. The skull is not as robust as that of the caecilians. A hearing apparatus is present. The salamander skull has four articulation points with the vertebral column, which is two more than other vertebrates. The extra articulation points may increase the stability of the lightly muscled head. A cartilaginous hyoid apparatus at the back of the floor of the mouth allows them to protrude the tongue just beyond the jaw. The eyes are well developed, as is the ability to smell. The muscles that lift the eye also increase the volume of the mouth, and may be involved in feeding. Despite the incomplete roofing of the skull, the brain and the sensory nasal capsules are protected by cartilaginous elements. Teeth are present on the upper and lower jaws. These are replaced from the inside as they wear.

The vertebral column terminates in a tail consisting of up to 100 vertebrae. Salamanders can deliberately lose the tail when threatened. Tail autotomy occurs, with the skin break being one segment posterior to the muscle break, allowing the wound to be covered to promote healing.

The forelimbs attach to a pectoral girdle that is cartilaginous. The front limbs end in four fingers, and the hind limbs in five toes. The hind limbs attach to the vertebral column by the pelvic girdle that consists of a number of bony elements, including a short ilium on each side. Below the girdle is a specialized, Y-shaped cartilage that can be raised or lowered to control the bouyancy of the head. By shifting air forward, the head can float with the eyes just out of the water. The limbs of terrestrial salamanders produce a rather slow movement on land. They can move quickly by a snake-like undulation that does not rely on the limbs. Aquatic species swim with side-to-side movements.

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Biographical Sketch

Alan Channing is a professor of Zoology with strong research interests in all aspects of African amphibians.