

Introductory Herpetology

Nadine Swann

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Email: info@wtbooks.com

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Introduction



Herpetology is the branch of zoology concerned with the study of amphibians (including frogs, toads, salamanders, newts, and gymnophionae) and reptiles (including snakes, lizards, amphisbaenids, turtles, terrapins, tortoises, crocodilians, and the tuataras). Batrachology is a further subdiscipline of herpetology concerned with the study of amphibians alone.

Herpetology is concerned with poikilothermic, ectothermic tetrapods. "Herps" (or sometimes "herptiles" or "herpetofauna") exclude fish. However, it is not uncommon for herpetological and ichthyological scientific societies to "team up", publishing joint journals and holding conferences in order to foster the exchange of ideas between the fields. One of the most prestigious organizations, the American Society of Ichthyologists and Herpetologists, is an example of this. Many herpetological societies exist today, having been formed to promote interest in reptiles and amphibians both captive and wild.

Herpetology offers benefits to humanity in the study of the role of amphibians and reptiles in global ecology, especially because amphibians are often very sensitive to environmental changes, offering a visible warning to humans that significant changes are taking place. Some toxins and venoms produced by reptiles and amphibians are useful in human medicine. Currently, some snake venom has been used to create anti-coagulants that work to treat stroke victims and heart attack cases.

The word "herpetology" is from Greek: ἑρπῆτόν, *herpeton*, "creeping animal" and -λογία, *-logia*. People with an avid interest in herpetology and who keep different reptiles or amphibians often refer to themselves as "herpers".

Careers

There are many careers in the field of herpetology. These include, but are not limited to, field research, public and private breeding, zoological staff or curating, museum staff or curating and college teaching.

Those wishing to pursue a career in herpetology must have a strong science and math background. Few universities offer this program, and thus it is a highly competitive field.

In modern academic science, it is rare for individuals to consider themselves a herpetologist first and foremost. Most individuals focus on a particular field such as ecology, evolution, taxonomy, physiology, or molecular biology, and within that field ask questions pertaining to or best answered by examining reptiles and amphibians. For example, an evolutionary biologist who is also a herpetologist may choose to work on how warning coloration evolved in coral snakes.

Chapter- 1

Amphibian

Amphibians

Temporal range: Late Devonian–present



Strawberry Poison-dart Frog, *Oophaga pumilio*

Scientific classification

Kingdom:	Animalia
Phylum:	Chordata
Superclass:	Tetrapoda
Class:	Amphibia Linnaeus, 1758

Subclasses and Orders

Order Temnospondyli – *extinct*
Subclass Lepospondyli – *extinct*
Subclass Lissamphibia
Order Anura
Order Caudata
Order Gymnophiona

Amphibians (class Amphibia, from Amphi- meaning "on both sides" and -bios meaning "life"), such as frogs, salamanders, and caecilians, are ectothermic (or cold-blooded) animals that metamorphose from a juvenile water-breathing form, either to an adult air-breathing form, or to a paedomorph that retains some juvenile characteristics. Mudpuppies, for example, retain juvenile gills in adulthood. The three modern orders of amphibians are Anura (frogs and toads), Caudata (salamanders and newts), and Gymnophiona (caecilians, limbless amphibians that resemble snakes), and in total they numbers approximately 6,500 species. Many amphibians lay their eggs in water. Amphibians are superficially similar to reptiles, but reptiles are amniotes, along with mammals and birds. The study of amphibians is called batrachology.

Amphibians are ecological indicators, and in recent decades there has been a dramatic decline in amphibian populations around the globe. Many species are now threatened or extinct.

Amphibians evolved in the Devonian Period and were top predators in the Carboniferous and Permian Periods, but many lineages were wiped out during the Permian–Triassic extinction. One group, the metoposaurs, remained important predators during the Triassic, but as the world became drier during the Early Jurassic they died out, leaving a handful of relict temnospondyls like *Koolasuchus* and the modern orders of Lissamphibia.

Etymology

Amphibian is derived from the Ancient Greek term ἀμφίβιος *amphibios* which means both kinds of life, *amphi* meaning “both” and *bio* meaning life. The term was initially used for all kinds of combined natures. Eventually it was used to refer to animals that live both in the water and on land.

Evolutionary history

The first major groups of amphibians developed in the Devonian Period from fish similar to the modern coelacanth and lungfish which had evolved multi-jointed leg-like fins that enabled them to crawl along the sea bottom. These amphibians were as much as one to five meters in length. However, amphibians never developed the ability to live their entire lives on land, having to return to water to lay their shell-less eggs.

In the Carboniferous Period, the amphibians moved up in the food chain and began to occupy the ecological position currently occupied by crocodiles. These amphibians were notable for eating the mega insects on land and many types of fishes in the water. During the Triassic Period, the better land-adapted proto-crocodiles began to compete with amphibians, leading to their reduction in size and importance in the biosphere.

Taxonomic history

Traditionally, amphibians have included all tetrapod vertebrates that are not amniotes. They are divided into three subclasses, of which two are only known as extinct subclasses:

- Subclass Labyrinthodontia† (diverse Paleozoic and early Mesozoic group)
- Subclass Lepospondyli† (small Paleozoic group, sometimes included in the Labyrinthodontia)
- Subclass Lissamphibia (frogs, toads, salamanders, newts, etc.)

Of these only the last subclass includes recent species.

With the phylogenetic classification Labyrinthodontia has been discarded as it is a paraphyletic group without unique defining features apart from shared primitive characteristics. Classification varies according to the preferred phylogeny of the author, whether they use a stem-based or node-based classification. Generally amphibians are defined as the group that includes the common ancestors of all living amphibians (frogs, salamanders and caecilians) and all their descendants. This may also include extinct groups like the temnospondyls (traditionally placed in the subclass “Labyrinthodontia”), and the Lepospondyls. This means that cladistic nomenclature list a large number of basal Devonian and Carboniferous tetrapod groups, undoubtedly were “amphibians” in biology, that are formally placed in Amphibia in Linnaean taxonomy, but not in cladistic taxonomy.

All recent amphibians are included in the subclass Lissamphibia, superorder Salientia, which is usually considered a clade (which means that it is thought that they evolved from a common ancestor apart from other extinct groups), although it has also been suggested that salamanders arose separately from a temnospondyl-like ancestor.

Authorities also disagree on whether Salientia is a Superorder that includes the order Anura, or whether Anura is a sub-order of the order Salientia. Practical considerations seem to favor using the former arrangement now. The Lissamphibia, superorder Salientia, are traditionally divided into three orders, but an extinct salamander-like family, the Albanerpetontidae, is now considered part of the Lissamphibia, besides the superorder Salientia. Furthermore, Salientia includes all three recent orders plus a single Triassic proto-frog, *Triadobatrachus*.

Class **Amphibia**

- Subclass Lissamphibia
 - - Family Albanerpetontidae — Jurassic to Miocene (extinct)
 - Superorder Salientia
 - Genus *Triadobatrachus* — Triassic (extinct)
 - Order Anura (frogs and toads): Jurassic to recent — 5,602 recent species in 48 families
 - Order Caudata or Urodela (salamanders, newts): Jurassic to recent — 571 recent species in 9 families
 - Order Gymnophiona or Apoda (caecilians): Jurassic to recent — 174 recent species in 3 families

The actual number of species partly also depends on the taxonomic classification followed, the two most common classifications being the classification of the website AmphibiaWeb, University of California (Berkeley) and the classification by herpetologist Darrel Frost and The American Museum of Natural History, available as the online reference database Amphibian Species of the World. The numbers of species cited above follow Frost.

Respiration

The lungs in amphibians are primitive compared to that of the amniotes, possessing few internal septa, large alveoli and therefore a slow diffusion rate of oxygen into the blood. Ventilation is accomplished by buccal pumping. However, most amphibians are able to exchange gasses with the water or air via their skin. To enable sufficient cutaneous respiration, the surface of their highly vascularized skin must remain moist in order for the oxygen to diffuse at a sufficient rate. Because oxygen concentration in the water increases at both low temperatures and high flow rates, aquatic amphibians in these situations can rely primarily on cutaneous respiration, as in the Titicaca water frog or hellbender salamanders. In air, where oxygen is more concentrated, some small species can rely solely on cutaneous gas exchange, most famously the plethodontid salamanders which have neither lungs nor gills. Many aquatic salamanders and all tadpoles have gills in their larval stage, with some (such as the axolotl) retaining gills as aquatic adults.

Reproduction



Caecilian from the San Antonio zoo

For the purpose of reproduction most amphibians require fresh water. A few (e.g. *Fejervarya raja*) can inhabit brackish water and even survive (though not thrive) in seawater, but there are no true marine amphibians. Several hundred frog species in adaptive radiations (e.g., *Eleutherodactylus*, the Pacific Platymantines, the Australo-Papuan microhylids, and many other tropical frogs), however, do not need any water for breeding in the wild. They reproduce via direct development, an ecological and evolutionary adaptation that has allowed them to be completely independent from free-standing water. Almost all of these frogs live in wet tropical rainforests and their eggs hatch directly into miniature versions of the adult, passing through the tadpole stage within the egg. Reproductive success of many amphibians is dependent not only on the quantity of rainfall, but the seasonal timing.

Several species have also adapted to arid and semi-arid environments, but most of them still need water to lay their eggs. Symbiosis with single celled algae that lives in the jelly-like layer of the eggs has evolved several times. The larvae of frogs (tadpoles or polliwogs) breathe with exterior gills at the start, but soon a pouch is formed that covers the gills and the front legs. Lungs are also formed quite early to assist in breathing. Newt larvae have large external gills that gradually disappear and the larvae of newts are quite similar to the adult form from early age on.

Frogs and toads however have a tadpole stage, which is a totally different organism that is a grazing algae or ongrowth or filtering plankton until a certain size has been reached,

where metamorphosis sets in. This metamorphosis lasts typically only 24 hours and consists of:

- The disappearance of the gill pouch, making the front legs visible.
- The transformation of the jaws into the big jaws of predatory frogs (most tadpoles are scraping of algae or are filter feeders)
- The transformation of the digestive system: the long spiral gut of the larva is being replaced by the typical short gut of a predator.
- An adaptation of the nervous system for stereoscopic vision, locomotion and feeding
- A quick growth and movement of the eyes to higher up the skull and the formation of eyelids.
- Formation of skin glands, thickening of the skin and loss of the lateral line system
- An eardrum is developed to lock the middle ear.

The disappearance of the tail is somewhat later (occurs at higher thyroxin levels) and after the tail has been resorbed the animals are ready to leave the water. The material of the tail is being used for a quick growth of the legs. The disappearance of the larval structures is a regulated process called apoptosis.

The transformation of newts when leaving the water is reversible except for the loss of the external gills. When the animals enter the water again for reproduction changes are driven by prolactin, when they return to the land phase by thyroxin

Conservation



The Golden Toad of Monteverde, Costa Rica was among the first casualties of amphibian declines. Formerly abundant, it was last seen in 1989.

Dramatic declines in amphibian populations, including population crashes and mass localized extinction, have been noted in the past two decades from locations all over the world, and amphibian declines are thus perceived as one of the most critical threats to global biodiversity. A number of causes are believed to be involved, including habitat destruction and modification, over-exploitation, pollution, introduced species, climate change, endocrine-disrupting pollutants, destruction of the ozone layer (ultraviolet radiation has shown to be especially damaging to the skin, eyes, and eggs of amphibians), and diseases like chytridiomycosis. However, many of the causes of amphibian declines are still poorly understood, and are a topic of ongoing discussion. A global strategy to stem the crisis has been released in the form of the Amphibian Conservation Action Plan. Developed by over 80 leading experts in the field, this call to action details what would be required to curtail amphibian declines and extinctions over the next 5 years - and how much this would cost. The Amphibian Specialist Group of the World Conservation Union (IUCN) is spearheading efforts to implement a comprehensive global strategy for amphibian conservation. Amphibian Ark is an organization that was formed to implement the ex-situ conservation recommendations of this plan, and they have been working with zoos and aquaria around the world encouraging them to create assurance colonies of threatened amphibians. One such project is the Panama Amphibian Rescue and Conservation Project that built on existing conservation efforts in Panama to create a country-wide response to the threat of chytridiomycosis rapidly spreading into eastern Panama

On January 21, 2008, Evolutionarily Distinct and Globally Endangered (EDGE), as given by chief Helen Meredith, identified nature's most endangered species: "The EDGE amphibians are amongst the most remarkable and unusual species on the planet and yet an alarming 85% of the top 100 are receiving little or no conservation attention." The top 10 endangered species (in the List of endangered animal species) include: the Chinese giant salamander, a distant relative of the newt, the tiny Gardiner's Seychelles, the limbless *Sagalla caecilian*, South African ghost frogs, lungless Mexican salamanders, the Malagasy rainbow frog, Chile's Darwin frog (*Rhinoderma rufum*) and the Betic Midwife Toad.

Chapter- 2

Reptile



Clockwise from above left: Spectacled Caiman (*Caiman crocodilus*), Green Sea Turtle (*Chelonia mydas*), Tuatara (*Sphenodon punctatus*) and Eastern Diamondback Rattlesnake (*Crotalus adamanteus*).

Scientific classification

Kingdom:	Animalia
Phylum:	Chordata
Superclass:	Tetrapoda
(unranked):	Reptiliomorpha
(unranked):	Amniota
Class:	Reptilia Laurenti, 1768

Subgroups

- Anapsida (=Parareptilia?)

- Testudines (traditional)
- Eureptilia
 - Crocodilia
 - Sphenodontia
 - Squamata
 - Testudines (molecular)

Reptiles are animals in the (Linnaean) class Reptilia. They are characterized by breathing air, laying shelled eggs, and having skin covered in scales and/or scutes. Reptiles are classically viewed as having a "cold-blooded" metabolism. They are tetrapods (either having four limbs or being descended from four-limbed ancestors). Modern reptiles inhabit every continent with the exception of Antarctica, and four living orders are currently recognized:

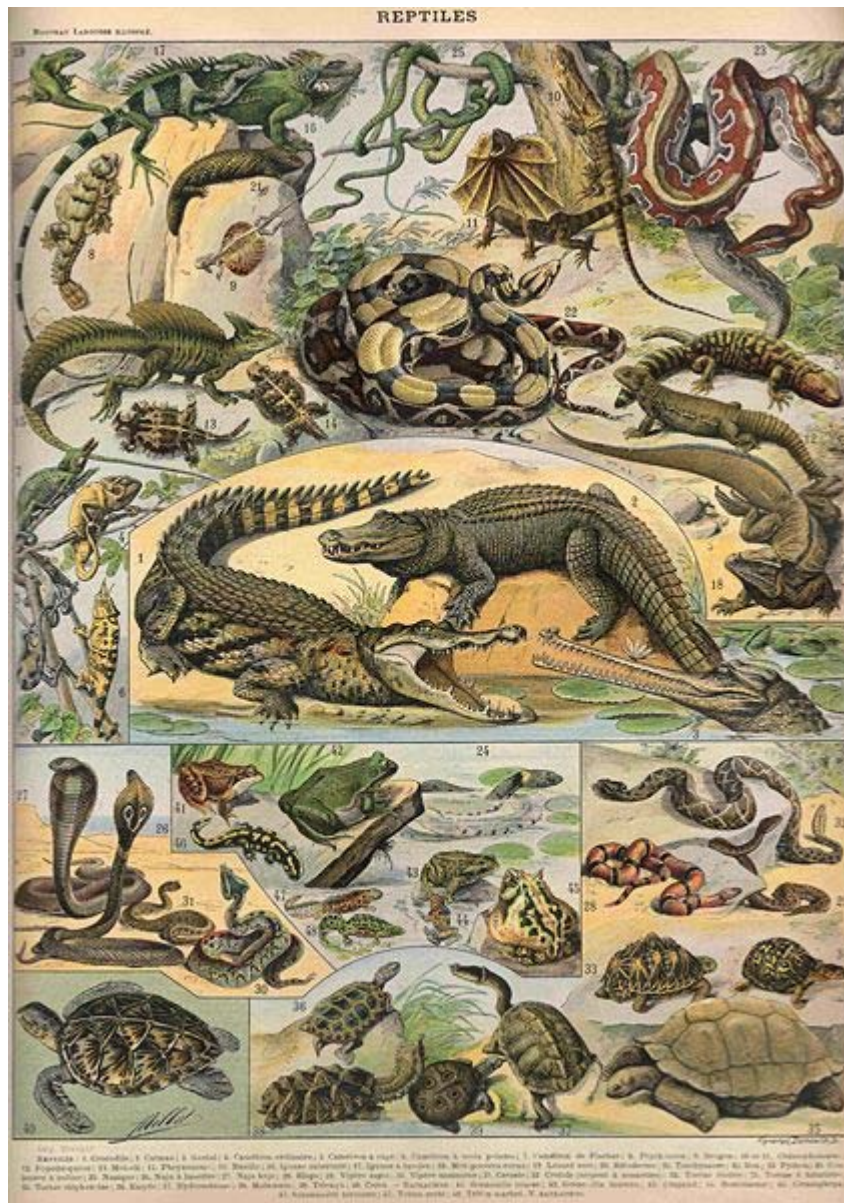
- Crocodilia (crocodiles, gavials, caimans, and alligators): 23 species
- Sphenodontia (tuataras from New Zealand): 2 species
- Squamata (lizards, snakes, and worm lizards): approximately 7,900 species
- Testudines (turtles and tortoises): approximately 300 species

Unlike amphibians, reptiles do not have an aquatic larval stage. As a rule, reptiles are oviparous (egg-laying), although certain species of squamates are capable of giving live birth. This is achieved by either ovoviviparity (egg retention) or viviparity (birth of offspring without the development of calcified eggs). Many of the viviparous species feed their fetuses through various forms of placenta analogous to those of mammals, with some providing initial care for their hatchlings. Extant reptiles range in size from a tiny gecko, *Sphaerodactylus ariasae*, that grows to only 1.6 cm (0.6 in) to the saltwater crocodile, *Crocodylus porosus*, which may reach 6 m in length and weigh over 1,000 kg.

The science dealing with reptiles is called herpetology.

Classification

History of classification



Reptiles, from *Nouveau Larousse Illustré*, 1897-1904. Notice the inclusion of amphibians (below the crocodiles).

Linnaeus and the 18th century

The reptiles were from the outset of classification grouped with the amphibians. Linnaeus, working from species-poor Sweden, where the common adder and grass snake are often found hunting in water, included all reptiles and amphibians in class "III – Amphibia" in his *Systema Naturæ*. The terms "reptile" and "amphibian" were largely interchangeable, "reptile" (from Latin *reperere*, "to creep") being preferred by the French.

Josephus Nicolaus Laurenti was the first to formally use the term "Reptilia" for an expanded selection of reptiles and amphibians basically similar to that of Linnaeus. It is today still common to treat the two groups under the same heading as herpetiles.

"Antediluvian monsters"



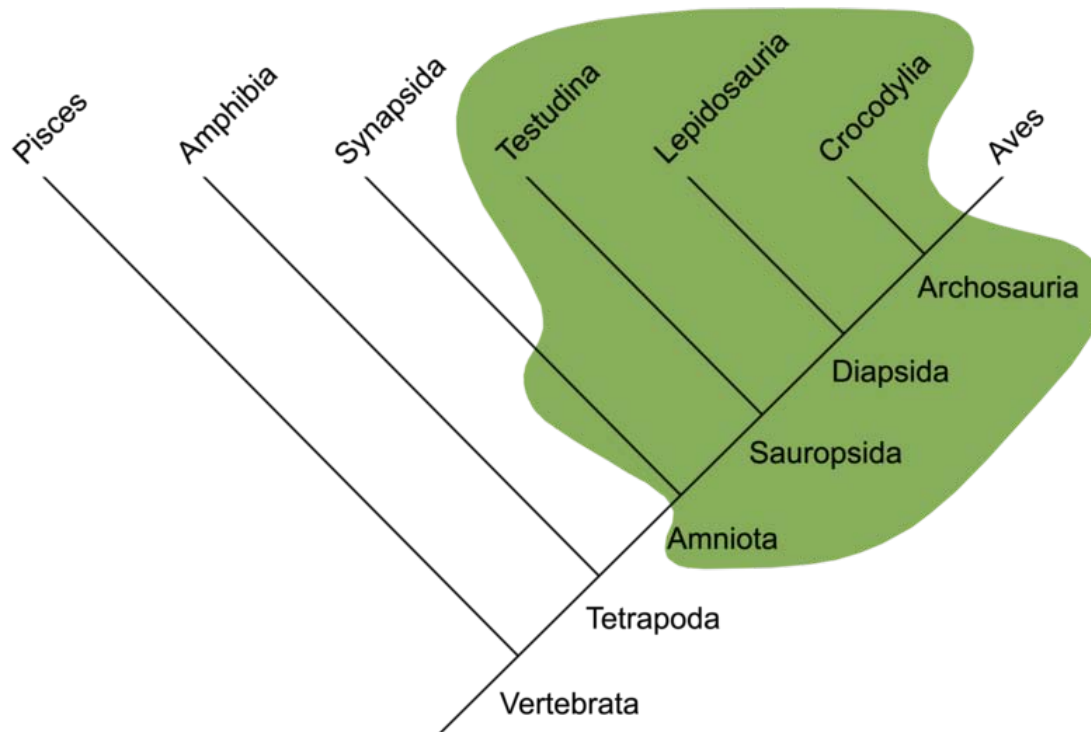
An "antediluvian monster", a *Mosasaurus* discovered in a Maastricht limestone quarry, 1770 (contemporary engraving)

Not until the beginning of the 19th century did it become clear that reptiles and amphibians are in fact quite different animals, and Pierre André Latreille erected the class *Batrachia* (1825) for the latter, dividing the tetrapods into the four familiar classes of reptiles, amphibians, birds and mammals.

The British anatomist Thomas Henry Huxley made Latreille's definition popular, and together with Richard Owen expanded Reptilia to include the various fossil "antediluvian monsters", including dinosaurs and the mammal-like (synapsid) *Dicynodon* he helped describe. This was not the only possible classification scheme: In the Hunterian lectures delivered at the Royal College of Surgeons in 1863, Huxley grouped the vertebrates into mammals, sauroids, and ichthyoids (the latter containing the fishes and amphibians). He subsequently proposed the names of Sauropsida and Ichthyopsida for the two.

The terms "Sauropsida" ("lizard faces") and "Theropsida" ("beast faces") were used again in 1916 by E.S. Goodrich to distinguish between lizards, birds, and their relatives on the one hand (Sauropsida) and mammals and their extinct relatives (Theropsida) on the other. Goodrich supported this division by the nature of the hearts and blood vessels in each group, and other features such as the structure of the forebrain. According to Goodrich, both lineages evolved from an earlier stem group, Protosauria ("first lizards") which included some Paleozoic amphibians as well as early reptiles.

In 1956 D.M.S. Watson observed that the first two groups diverged very early in reptilian history, and so he divided Goodrich's Protosauria between them. He also reinterpreted Sauropsida and Theropsida to exclude birds and mammals, respectively. Thus his Sauropsida included Procolophonia, Eosuchia, Millerosauria, Chelonia (turtles), Squamata (lizards and snakes), Rhynchocephalia, Crocodylia, "thecodonts" (paraphyletic basal Archosauria), non-avian dinosaurs, pterosaurs, ichthyosaurs, and sauropterygians.



Reptiles (green field) are a paraphyletic group comprising all non-avian and non-mammalian amniotes.

In 1866, Haeckel demonstrated that vertebrates could be divided based on their reproductive strategies, and that reptiles, birds and mammals were united by the amniotic egg. By the end of the 19th century, the class Reptilia had come to include all the amniotes except birds and mammals. Thus reptiles were defined as the set of animals that includes the extant crocodiles, alligators, tuatara, lizards, snakes, amphisbaenians, and turtles, as well as fossil groups like dinosaurs, synapsids and the primitive pareiasaurs. This is still the common definition of the term.

Skull openings in 20th century classification

The synapsid/sauropsid division supplemented, but was never as popular during the 20th century as a Linneanean approach splitting the reptiles into four subclasses based on the number and position of *temporal fenestrae*, openings in the sides of the skull behind the eyes. This classification was initiated by Henry Fairfield Osborn and elaborated and made popular by Romer's classic *Vertebrate Paleontology*. Those four subclasses were:

- Anapsida – no fenestrae - cotylosaurs and Chelonia (turtles and relatives)
- Synapsida – one low fenestra - pelycosaurs and therapsids (the 'mammal-like reptiles')
- Euryapsida – one high fenestra (above the postorbital and squamosal) - protosauropsids (small, early lizard-like reptiles) and diverse marine reptiles like plesiosaurs and ichthyosaurs, the latter called Parapsida in Osborn's work.
- Diapsida – two fenestrae - most reptiles, including lizards, snakes, crocodylians, dinosaurs and pterosaurs

The composition of Euryapsida was uncertain. Ichthyosaurs were at times considered to have arisen independently of the other euryapsids, and given the older name Parapsida. Parapsida was later discarded as a group for the most part (ichthyosaurs being classified as *incertae sedis* or with Euryapsida). This schema remained more or less universal for non-specialist work throughout the 20th century, and has only been challenged with the rising popularity of phylogenetic nomenclature.

Phylogenetics and modern definition

By the 21st century, most vertebrate paleontologists had adopted phylogenetic taxonomy, in which all groups are defined in such a way as to be monophyletic; that is, groups include all descendants of a particular ancestor. The reptiles as historically defined would be paraphyletic, since they exclude both birds and mammals, although these also evolved from the original reptiles. Colin Tudge wrote:

Mammals are a clade, and therefore the cladists are happy to acknowledge the traditional taxon Mammalia; and birds, too, are a clade, universally ascribed to the formal taxon Aves. Mammalia and Aves are, in fact, subclades within the grand clade of the Amniota. But the traditional class Reptilia is not a clade. It is just a section of the clade Amniota: the section that is left after the Mammalia and Aves have been hived off. It cannot be defined by synapomorphies, as is the proper way. It is instead defined by a combination of the features it has and the features it lacks: reptiles are the amniotes that lack fur or feathers. At best, the cladists suggest, we could say that the traditional Reptilia are 'non-avian, non-mammalian amniotes'.

Despite the early proposals for replacing the paraphyletic Reptilia for a monophyletic Sauropsida, that term was never adopted widely or, when it was, applied consistently. When Sauropsida was used, it often had the same content or even the same definition as Reptilia. In 1988 Jacques Gauthier proposed a cladistic definition of Reptilia as a monophyletic node-based crown group containing turtles, lizards and snakes, crocodylians, and birds, their common ancestor and all its descendants. The proposal suffered under the actual relationship of turtles to other reptiles not being fully understood. A variety of other definitions were proposed by other scientists in the years following Gauthier's paper. The first which attempted to adhere to the standards of the PhyloCode was published by Modesto and Anderson in 2004. They reviewed the many previous definitions, and proposed a modified definition which they intended to retain most traditional content of the group while keeping it stable and monophyletic. They

defined Reptilia as all amniotes closer to *Lacerta agilis* and *Crocodylus niloticus* than to *Homo sapiens*. This stem-based definition is equivalent to that of Sauropsida, which Modesto and Anderson synonymized with Reptilia, since the latter is more well known and more frequently used, despite their definition including birds.

Taxonomy

Classification to order level, after Benton, 2004.

- **Series Amniota**
 - **Class Synapsida**
 - Order Pelycosauria*
 - Order Therapsida
 - **Class Mammalia**
 - **Class Sauropsida**
 - **Subclass Anapsida**
 - Order Testudines (turtles)
 - A series of unassigned anapsid families, corresponding to Captorhinida, Mesosauria and Procolophonomorpha
 - **Subclass Diapsida**
 - Order Araeoscelidia
 - Order Younginiformes
 - **Infraclass Ichthyosauria**
 - **Infraclass Lepidosauromorpha**
 - Superorder Sauropterygia
 - Order Placodontia
 - Order Nothosauroida
 - Order Plesiosauria
 - Superorder Lepidosauria
 - Order Sphenodontia (tuatara)
 - Order Squamata (lizards & snakes)
 - **Infraclass Archosauromorpha**
 - Order Prolacertiformes
 - Division Archosauria
 - Subdivision Crurotarsi
 - Superorder Crocodylomorpha
 - Order Crocodilia
 - Order Phytosauria
 - Order Rauisuchia
 - Order Rhynchosauria
 - Subdivision Avemetatarsalia
 - Infradivision Ornithodira
 - Order Pterosauria
 - Superorder Dinosauria
 - Order Saurischia

- Class Aves
- Order Ornithischia

Evolutionary history

Rise of the reptiles



A early reptile *Hylonomus*



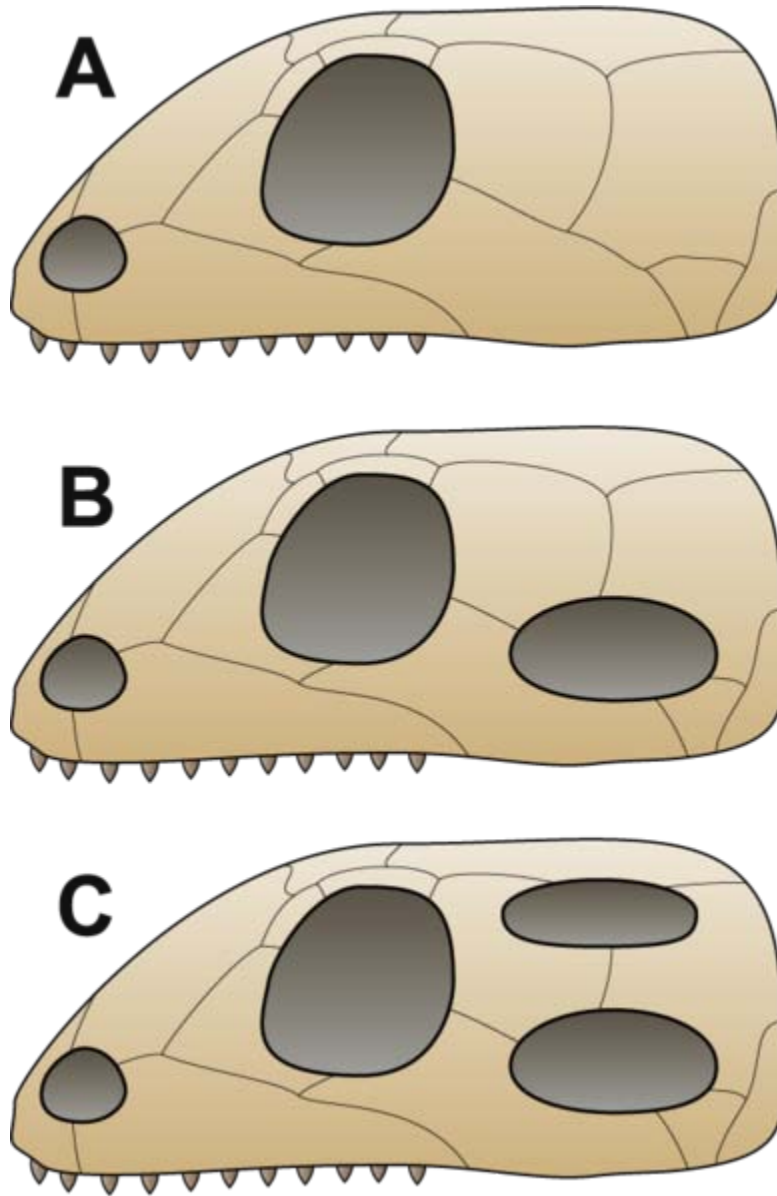
Mesozoic scene showing typical reptilian megafauna: the dinosaurs *Europasaurus holgeri* and *Iguanodon*, and the early bird *Archaeopteryx* perched on the foreground tree stump.



Megalania was a giant, carnivorous goanna that might have grown to as long as 7 metres, and weighed up to 1,940 kilograms (Molnar, 2004).

The origin of the reptiles lies about 320–310 million years ago, in the steaming swamps of the late Carboniferous period, when the first reptiles evolved from advanced reptiliomorph labyrinthodonts. The oldest known animal that may have been an amniote, i.e. a primitive reptile rather than an advanced amphibian is *Casineria*. A series of footprints from the fossil strata of Nova Scotia, dated to 315 million years show typical reptilian toes and imprints of scales. The tracks are attributed to *Hylonomus*, the oldest unquestionable reptile known. It was a small, lizard-like animal, about 20 to 30 cm (8–12 in) long, with numerous sharp teeth indicating an insectivorous diet. Other examples include *Westlothiana* (for the moment considered a reptiliomorph amphibian rather than a true amniote) and *Paleothyris*, both of similar build and presumably similar habit. One of the best known early reptiles is *Mesosaurus*, a genus from the early Permian that had returned to water, feeding on fish. The earliest reptiles were largely overshadowed by bigger labyrinthodont amphibians such as *Cochleosaurus*, and remained a small, inconspicuous part of the fauna until after the small ice age at the end of the Carboniferous.

Anapsids, synapsids, diapsids and sauropsids



A = Anapsid, B = Synapsid, C = Diapsid

The first reptiles were anapsids, having a solid skull with holes for only nose, eyes, spinal cord, etc. Very soon after the first reptiles appeared, they split into two branches. One branch, Synapsida (including both "mammal-like reptiles" and modern, extant mammals such as humans), had one opening in the skull roof behind each eye; the other branch, Diapsida, possessed a hole in their skulls behind each eye, along with a second hole located higher on the skull. The function of the holes in both groups was to lighten the skull and give room for the jaw muscles to move, allowing for a more powerful bite. Diapsids and later anapsids are classed as the "true reptiles", Sauropsida.

Turtles have been traditionally believed to be surviving anapsids, on the basis of their skull structure. The rationale for this classification was disputed, with some arguing that turtles are diapsids that reverted to this primitive state in order to improve their armor. Later morphological phylogenetic studies with this in mind placed turtles firmly within Diapsida. All molecular studies have strongly upheld the placement of turtles within diapsids, most commonly as a sister group to extant archosaurs.

Permian reptiles

With the close of the Carboniferous, reptiles became the dominant tetrapod fauna. While the terrestrial reptiliomorph labyrinthodonts still existed, the synapsids evolved the first truly terrestrial megafauna (giant animals) in the form of pelycosaurids such as *Edaphosaurus* and the carnivorous *Dimetrodon*. In the mid-Permian period the climate turned dryer, resulting in a change of fauna: The primitive pelycosaurids were replaced by the more advanced therapsids.

The anapsid reptiles, whose massive skull roofs had no postorbital holes, continued and flourished throughout the Permian. The pareiasaurs reached giant proportions in the late Permian, eventually disappearing at the close of the period (the turtles being possible survivors).

Early in the period, the diapsid reptiles split into two main lineages, the archosaurs (forefathers of crocodiles and dinosaurs) and the lepidosaurs (predecessors of modern snakes, lizards, and tuataras). Both groups remained lizard-like and relatively small and inconspicuous during the Permian.

The Mesozoic era, the "Age of Reptiles"

The close of the Permian saw the greatest mass extinction known. Most of the earlier anapsid/synapsid megafauna disappeared, being replaced by the archosauromorph diapsids. The archosaurs were characterized by elongated hind legs and an erect pose, the early forms looking somewhat like long-legged crocodiles. The archosaurs became the dominant group during the Triassic period, developing into the well-known dinosaurs and pterosaurs, as well as crocodiles and phytosaurs. Some of the dinosaurs developed into the largest land animals ever to have lived, making the Mesozoic era popularly known as the "Age of Reptiles". The dinosaurs also developed smaller forms, including the feather-bearing smaller theropods. In the mid-Jurassic period, these gave rise to the first birds.

The lepidosauromorph diapsids may have been ancestral to the sea reptiles. These reptiles developed into the sauropterygians in the early Triassic and the ichthyosaurs during the Middle Triassic. The mosasaurs also evolved in the Mesozoic era, emerging during the Cretaceous period.

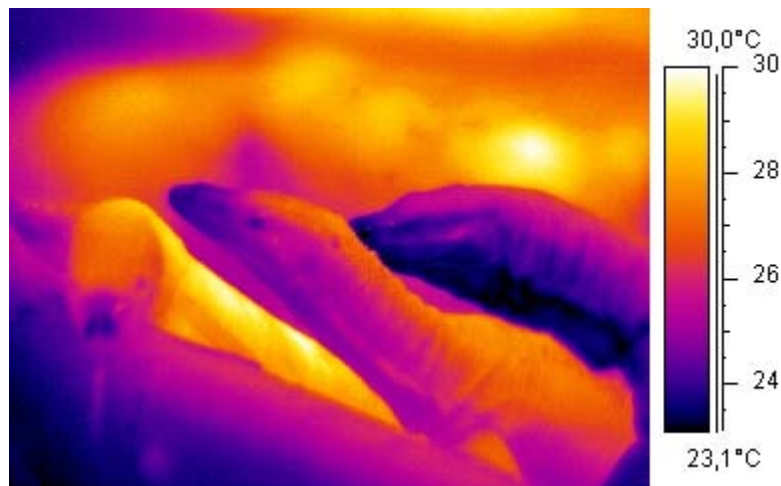
The therapsids came under increasing pressure from the dinosaurs in the early Mesozoic and developed into increasingly smaller and more nocturnal forms, the first mammals being the only survivors of the line by the late Jurassic.

Demise of the dinosaurs

The close of the Cretaceous period saw the demise of the Mesozoic era reptilian megafauna. Of the large marine reptiles, only sea turtles are left, and, of the dinosaurs, only the small feathered theropods survived in the form of birds. The end of the “Age of Reptiles” led into the “Age of Mammals”. Despite the change in phrasing, reptile diversification continued throughout the Cenozoic, with squamates undergoing a greater radiation than they did in the Mesozoic. Today squamates make up the majority of extant reptiles today (over 90%). There are approximately 8,700 extant species of reptiles, compared with 5,400 species of mammals.

Systems

Circulation



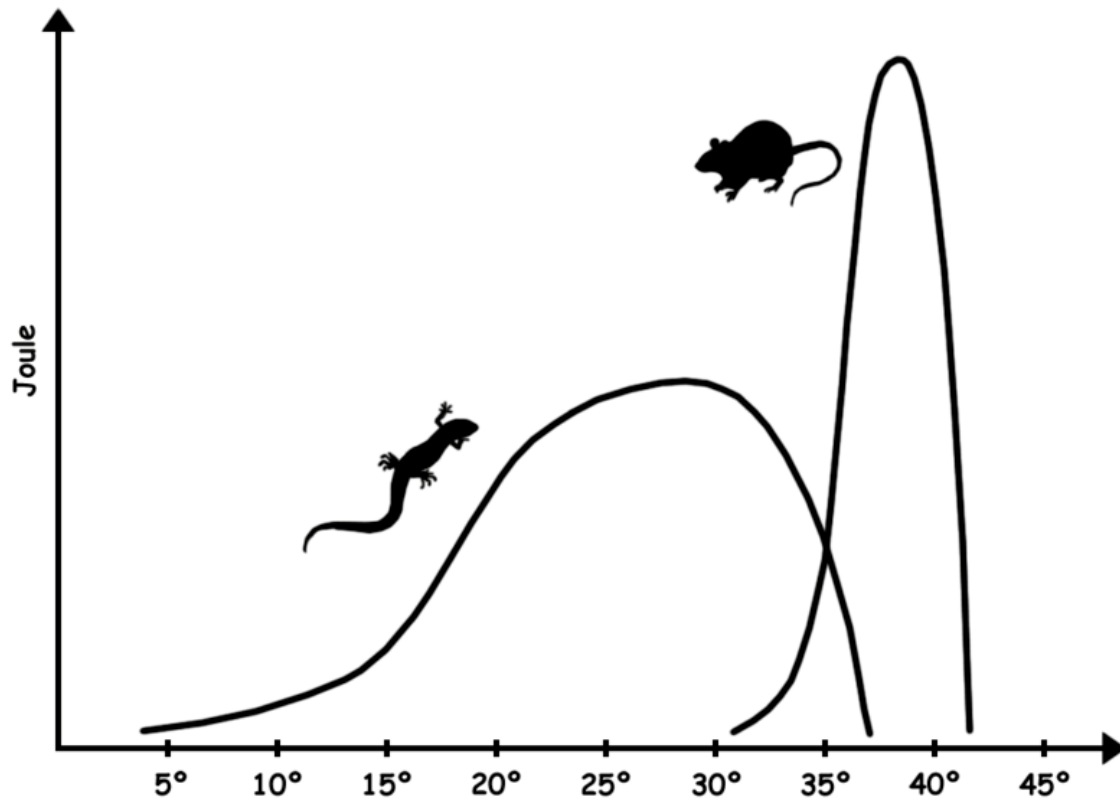
Thermographic image of a monitor lizard

Most reptiles have a three-chambered heart consisting of two atria, one variably partitioned ventricle, and two aortas that lead to the systemic circulation. The degree of mixing of oxygenated and deoxygenated blood in the three-chambered heart varies depending on the species and physiological state. Under different conditions, deoxygenated blood can be shunted back to the body or oxygenated blood can be shunted back to the lungs. This variation in blood flow has been hypothesized to allow more effective thermoregulation and longer diving times for aquatic species, but has not been shown to be a fitness advantage.

There are some exceptions to the general physiology. For instance, crocodylians have an anatomically four-chambered heart, but also have two systemic aortas and are therefore capable of bypassing only their pulmonary circulation. Also, some snake and lizard species (e.g., pythons and monitor lizards) have three-chambered hearts that become functionally four-chambered hearts during contraction. This is made possible by a muscular ridge that subdivides the ventricle during ventricular diastole and completely divides it during ventricular systole. Because of this ridge, some of these squamates are

capable of producing ventricular pressure differentials that are equivalent to those seen in mammalian and avian hearts.

Metabolism



Sustained energy output (Joule) of a typical reptile versus a similar size mammal as a function of core body temperature. The mammal has a much higher peak output, but can only function over a very narrow range of body temperatures.

All reptiles exhibit some form of cold-bloodedness (i.e. some mix of poikilothermy, ectothermy, and bradymetabolism). This means that most reptiles have limited physiological means of keeping the body temperature constant, and often rely on external sources of heat. Due to a less stable core temperature than birds and mammals, reptilian biochemistry requires enzymes capable of maintaining efficiency over a greater range of temperatures than warm-blooded animals. The optimum body temperature range varies with species, but is typically below that of warm-blooded animals, in the 24°–35°C range for many lizards, while extreme heat adapted species like the American desert iguana *Dipsosaurus dorsalis* can have optimal physiological temperatures in the mammalian range, between 35 and 40°C. While the optimum temperature is often encountered when the animal is active, the low basal metabolism makes body temperature drop rapidly when the animal is inactive.

Like in all animals, reptilian muscle action produces heat. In large reptiles, like leatherback turtles, the low surface to volume ratio allows this metabolically produced

heat to keep the animals warmer than their environment, despite not having a warm-blooded metabolism. This form of homeothermy is called gigantothermy, and has been suggested as having been common in large dinosaurs and other extinct large-bodied reptiles.

The benefits of a low resting metabolism is that it requires far less fuel to sustain bodily functions. By using temperature variations in their surroundings or by remaining cold when they do not need to move, reptiles can save considerable amounts of energy compared to endotherm animals of the same size. A crocodile need from a fifth to a tenth of the food necessary for a lion of the same weight, and can live half a year without eating. Lower food requirements and adaptive metabolisms allow reptiles to dominate the animal life in regions where net calorie production is too low to sustain large-bodied mammals and birds.

It is generally assumed that reptiles are unable to produce the sustained high energy output necessary for long distance chases or flying. Higher energetic capacity might have been responsible for the evolution of warm-bloodedness in birds and mammals. However, investigation of correlations between active capacity and thermophysiology show a weak relationship. Most extant reptiles are carnivores with a sit-and-wait feeding strategy, and whether reptiles are cold blooded due to their ecology, or if their metabolism is a result of their ecology is not clear. Energetic studies on some reptiles have shown active capacities equal to, or greater than similar sized warm-blooded animals.

Respiration

Reptilian lungs

All reptiles breathe using lungs. Aquatic turtles have developed more permeable skin, and some species have modified their cloaca to increase the area for gas exchange. Even with these adaptations, breathing is never fully accomplished without lungs. Lung ventilation is accomplished differently in each main reptile group. In squamates, the lungs are ventilated almost exclusively by the axial musculature. This is also the same musculature that is used during locomotion. Because of this constraint, most squamates are forced to hold their breath during intense runs. Some, however, have found a way around it. Varanids, and a few other lizard species, employ buccal pumping as a complement to their normal "axial breathing." This allows the animals to completely fill their lungs during intense locomotion, and thus remain aerobically active for a long time. Tegu lizards are known to possess a proto-diaphragm, which separates the pulmonary cavity from the visceral cavity. While not actually capable of movement, it does allow for greater lung inflation, by taking the weight of the viscera off the lungs. Crocodylians actually have a muscular diaphragm that is analogous to the mammalian diaphragm. The difference is that the muscles for the crocodylian diaphragm pull the pubis (part of the pelvis, which is movable in crocodylians) back, which brings the liver down, thus freeing space for the lungs to expand. This type of diaphragmatic setup has been referred to as the "hepatic piston."

Turtles and tortoises



Red-eared slider taking a gulp of air

How turtles and tortoises breathe has been the subject of much study. To date, only a few species have been studied thoroughly enough to get an idea of how turtles do it. The results indicate that turtles and tortoises have found a variety of solutions to this problem.

The difficulty is that most turtle shells are rigid and do not allow for the type of expansion and contraction that other amniotes use to ventilate their lungs. Some turtles such as the Indian flapshell (*Lissemys punctata*) have a sheet of muscle that envelops the lungs. When it contracts, the turtle can exhale. When at rest, the turtle can retract the limbs into the body cavity and force air out of the lungs. When the turtle protracts its limbs, the pressure inside the lungs is reduced, and the turtle can suck air in. Turtle lungs are attached to the inside of the top of the shell (carapace), with the bottom of the lungs attached (via connective tissue) to the rest of the viscera. By using a series of special muscles (roughly equivalent to a diaphragm), turtles are capable of pushing their viscera up and down, resulting in effective respiration, since many of these muscles have attachment points in conjunction with their forelimbs (indeed, many of the muscles expand into the limb pockets during contraction).

Breathing during locomotion has been studied in three species, and they show different patterns. Adult female green sea turtles do not breathe as they crutch along their nesting

beaches. They hold their breath during terrestrial locomotion and breathe in bouts as they rest. North American box turtles breathe continuously during locomotion, and the ventilation cycle is not coordinated with the limb movements. This is because they use their abdominal muscles to breathe during locomotion. The last species to have been studied is the red-eared slider, which also breathes during locomotion, but takes smaller breaths during locomotion than during small pauses between locomotor bouts, indicating that there may be mechanical interference between the limb movements and the breathing apparatus. Box turtles have also been observed to breathe while completely sealed up inside their shells.

Palate

Most reptiles lack a secondary palate, meaning that they must hold their breath while swallowing. Crocodilians have evolved a bony secondary palate that allows them to continue breathing while remaining submerged (and protect their brains against damage by struggling prey). Skinks (family Scincidae) also have evolved a bony secondary palate, to varying degrees. Snakes took a different approach and extended their trachea instead. Their tracheal extension sticks out like a fleshy straw, and allows these animals to swallow large prey without suffering from asphyxiation.

Skin



The foot of a skink, showing squamate reptiles iconic scales

Reptilian skin is covered in a horny epidermis, making it watertight and enabling reptiles to live on dry land, in contrast to amphibians. Compared to mammalian skin, that of reptiles is rather thin and lacks the thick dermal layer that produces leather in mammals. Exposed parts of reptiles are protected by scales or scutes, sometimes with a bony base, forming armor. In lepidosaurians such as lizards and snakes, the whole skin is covered in

overlapping epidermal scales. Such scales were once thought to be typical of the class Reptilia as a whole, but are now known to occur only in lepidosaurians. The scales found in turtles and crocodiles are of dermal, rather than epidermal, origin and are properly termed scutes. In turtles, the body is hidden inside a hard shell composed of fused scutes.

Lacking a thick dermis, reptilian leather is not as strong as mammalian leather. It is used in leather-wares for decorative purposes for shoes, belts and handbags, particularly crocodile skin. Due to reptiles lacking feathers or fur, reptiles are used as pets by people with allergies.

Excretion

Excretion is performed mainly by two small kidneys. In diapsids, uric acid is the main nitrogenous waste product; turtles, like mammals, excrete mainly urea. Unlike the kidneys of mammals and birds, reptile kidneys are unable to produce liquid urine more concentrated than their body fluid. This is because they lack a specialized structure called a loop of Henle, which is present in the nephrons of birds and mammals,. Because of this, many reptiles use the colon to aid in the reabsorption of water. Some are also able to take up water stored in the bladder. Excess salts are also excreted by nasal and lingual salt glands in some reptiles.

Digestion



Watersnake *Malpolon monspessulanus* eating a lizard. Most reptiles are carnivorous, and many primarily eat other reptiles.

Most reptiles are carnivorous and have rather simple and comparatively short digestive tracts, meat being fairly simple to break down and digest. Digestion is slower than in mammals, reflecting their lower resting metabolism and their inability to divide and masticate their food. Their poikilotherm metabolism has very low energy requirements, allowing large reptiles like crocodiles and the large constrictors to live from a single large meal for months, digesting it slowly.

While modern reptiles are predominately carnivorous, during the early history of reptiles several groups produced some herbivorous megafauna: in the Paleozoic the pareiasaurs and the synapsid dicynodonts, and in the Mesozoic several lines of dinosaurs. Today the turtles are the only predominantly herbivorous reptile group, but several lines of agamas and iguanas have evolved to live wholly or partly on plants.

Herbivorous reptiles face the same problems of mastication as herbivorous mammals but, lacking the complex teeth of mammals, many species swallow rocks and pebbles (so called gastroliths) to aid in digestion: The rocks are washed around in the stomach, helping to grind up plant matter. Fossil gastroliths have been found associated with sauropods. Sea turtles, crocodiles, and marine iguanas also use gastroliths as ballast, helping them to dive.

Nerves

The reptilian nervous system contains the same basic part of the amphibian brain, but the reptile cerebrum and cerebellum are slightly larger. Most typical sense organs are well developed with certain exceptions, most notably the snake's lack of external ears (middle and inner ears are present). There are twelve pairs of cranial nerves. Due to their short cochlea, reptiles use electrical tuning to expand their range of audible frequencies.

Reptiles are generally considered less intelligent than mammals and birds. The size of their brain relative to their body is much less than that of mammals, the encephalization quotient being about one tenth of that of mammals. Though larger reptiles show more complex brain development. Larger lizards like the monitors are known to exhibit complex behavior, including cooperation. Crocodiles have relatively larger brains and show a fairly complex social structure. The Komodo dragon is even known to engage in play.

Vision

Most reptiles are diurnal animals. The vision is typically adapted to daylight conditions, with color vision and more advanced visual depth perception than in amphibians and most mammals. In some species, such as blind snakes, vision is reduced. Some snakes have extra sets of visual organs (in the loosest sense of the word) in the form of pits sensitive to infrared radiation (heat). Such heat-sensitive pits are particularly well developed in the pit vipers, but are also found in boas and pythons. These pits allow the snakes to sense the body heat of birds and mammals, enabling pit vipers to hunt rodents in the dark.

Reproduction



Most reptiles reproduce sexually such as this *Trachylepis maculilabris* skink



Reptiles have amniotic eggs with hard or leathery shells, requiring internal fertilization.

Most reptiles reproduce sexually, though some are capable of asexual reproduction. All reproductive activity occurs through the cloaca, the single exit/entrance at the base of the tail where waste is also eliminated. Most reptiles have copulatory organs, which are usually retracted or inverted and stored inside the body. In turtles and crocodylians, the male has a single median penis, while squamates, including snakes and lizards, possess a pair of hemipenes. Tuataras, however, lack copulatory organs, and so the male and female simply press their cloacas together as the male excretes sperm.

Most reptiles lay amniotic eggs covered with leathery or calcareous shells. An amnion, chorion, and allantois are present during embryonic life. There are no larval stages of development. Viviparity and ovoviviparity have evolved only in squamates, and many species, including all boas and most vipers, utilize this mode of reproduction. The degree of viviparity varies: some species simply retain the eggs until just before hatching, others provide maternal nourishment to supplement the yolk, and yet others lack any yolk and provide all nutrients via a structure similar to the mammalian placenta.

Asexual reproduction has been identified in squamates in six families of lizards and one snake. In some species of squamates, a population of females is able to produce a unisexual diploid clone of the mother. This form of asexual reproduction, called parthenogenesis, occurs in several species of gecko, and is particularly widespread in the teiids (especially *Aspidocelis*) and lacertids (*Lacerta*). In captivity, Komodo dragons (Varanidae) have reproduced by parthenogenesis.

Parthenogenetic species are suspected to occur among chameleons, agamids, xantusiids, and typhlopids.

Some reptiles exhibit temperature-dependent sex determination (TDSD), in which the incubation temperature determines whether a particular egg hatches as male or female. TDSD is most common in turtles and crocodiles, but also occurs in lizards and tuataras. To date, there has been no confirmation of whether TDSD occurs in snakes.

Defense mechanisms

Many small reptiles such as snakes and lizards which live on the ground or in the water are vulnerable to being preyed on by all kinds of carnivorous animals. Thus avoidance is the most common form of defense in reptiles. At the first sign of danger, most snakes and lizards crawl away into the undergrowth, and turtles and crocodiles will plunge into water and sink out of sight.



A camouflaged *Phelsuma deubia* on a palm frond

Reptiles may also avoid confrontation through camouflage. Using a variety of grays, greens, and browns, these animals can blend remarkably well into the background of their natural environment.

If the danger arises so suddenly that flight may be harmful, then crocodiles, turtles, some lizards, and some snakes hiss loudly when confronted by an enemy. Rattlesnakes rapidly vibrate the tip of the tail, which is composed of a series of nested, hollow beads.

If all this does not deter an enemy, different species will adopt different defensive tactics.

Snakes use a complicated set of behaviors when attacked. Some will first elevate their head and spread out the skin of their neck in an effort to look bigger and more threatening. Failure of this may lead to other measures practiced particularly by cobras, vipers, and closely related species, who use venom to attack. The venom is modified saliva, delivered through fangs from a venom gland. Some non-venomous snakes, such as the corn snake, play dead when in danger.

When a crocodile is concerned about its safety, it will gape to expose the teeth and yellow tongue. If this doesn't work, the crocodile gets a little more agitated and typically begins to make hissing sounds. After this, the crocodile will start to change its posture dramatically to make itself look more intimidating. The body is inflated to increase apparent size. If absolutely necessary it may decide to attack an enemy.



A White-headed dwarf gecko with shed tail

Some species try to bite immediately. Some will use their heads as sledgehammers and literally smash an opponent, some will rush or swim toward the threat from a distance, even chasing them onto land or galloping after them.

Geckos, skinks, and other lizards that are captured by the tail will shed part of the tail structure through a process called autotomy and thus be able to flee. The detached tail will continue to wiggle, creating a deceptive sense of continued struggle and distracting the predator's attention from the fleeing prey animal. The animal can partially regenerate its tail over a period of weeks. The new section will contain cartilage rather than bone, and the skin may be distinctly discolored compared to the rest of the body. The tails are often a separate and dramatically more vivid color than the rest of the body, as to attract potential predators to strike for the tail first.

Chapter- 3

Evolution of Reptiles

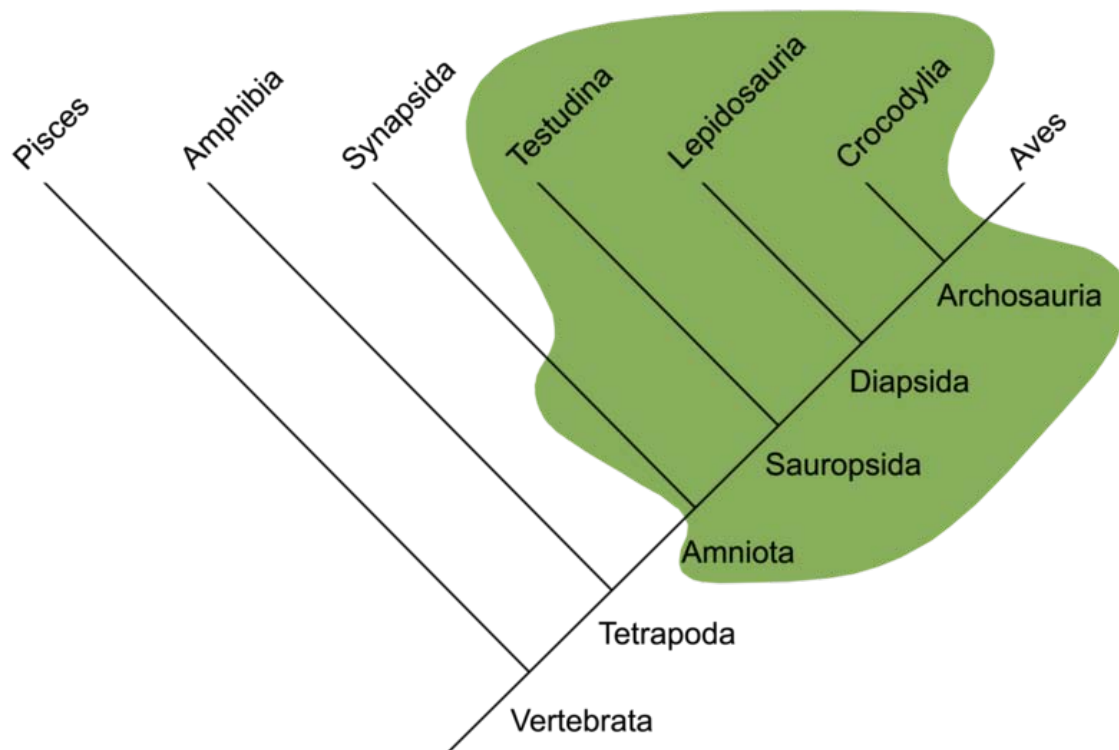


A fossil of a Casineria. The earliest evidence of amniotes, although an amphibian, it laid eggs on land as reptiles do.

Reptiles arose about 310-320 million years ago during the Carboniferous period. Reptiles are defined as animals that have scales, lay land based hard shelled eggs, and possessing cold-blooded metabolisms. Today reptiles generally rank low in most ecological food chains, containing very few apex predators, but many examples of apex reptiles have existed in the past. Although reptiles have lower specie variation than in the past, they have an extremely diverse evolutionary history that has led to biological successes such as dinosaurs, mammals, and birds.

First reptiles

Rise from water



Reptiles (green field) are a paraphyletic group comprising all non-avian and non-mammalian amniotes.

Reptiles first arose from amphibians in the swamps of the late Carboniferous. Increasing evolutionary pressure and the vast untouched niches of the land powered the evolutionary changes in amphibians to gradually become more and more land based. Environmental selection propelled the development of certain traits, such as a stronger skeletal structure, muscles, and more protective coating (scales) became more favorable, the basic foundation of reptiles were founded. The evolution of lungs and legs are the main transitional steps towards reptiles, but the development of hard-shelled external eggs replacing the amphibious water bound eggs is the defining feature of the class reptilia (with the exception of certain squamates) and is what allowed amphibians to fully leave water. Another major difference from amphibians is the increased brain size, more

specifically, the enlarged cerebrum and cerebellum. Although their brain size is small when compared to mammals and birds, these enhancements prove vital in hunting strategies of reptiles. The increased size of these two regions of the brain allowed for improved motor skills and an increase in sensory development.

Early reptiles



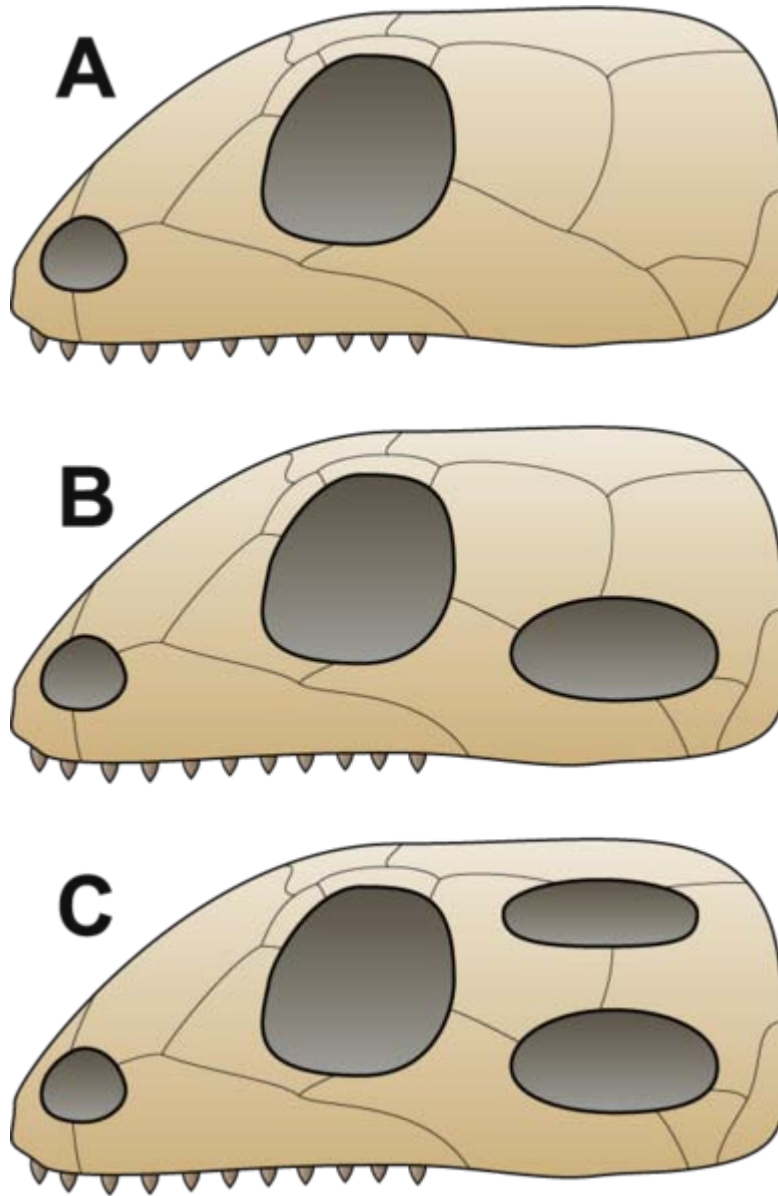
An early reptile *Hylonomus*



Mesozoic scene showing typical reptilian megafauna: the dinosaurs *Europasaurus holgeri* and *Iguanodon*, and the early bird *Archaeopteryx* perched on the foreground tree stump.

The origin of the reptiles lies about 320–310 million years ago, in the steaming swamps of the late Carboniferous period, when the first reptiles evolved from advanced reptiliomorph labyrinthodonts. The oldest known animal that may have been an amniote, i.e. a primitive reptile rather than an advanced amphibian is *Casineria*. A series of footprints from the fossil strata of Nova Scotia, dated to 315 million years show typical reptilian toes and imprints of scales. The tracks are attributed to *Hylonomus*, the oldest unquestionable reptile known. It was a small, lizard-like animal, about 20 to 30 cm (8–12 in) long, with numerous sharp teeth indicating an insectivorous diet. Other examples include *Westlothiana* (for the moment considered a reptiliomorph amphibian rather than a true amniote) and *Paleothyris*, both of similar build and presumably similar habit. One of the best known early reptiles is *Mesosaurus*, a genus from the early Permian that had returned to water, feeding on fish. The earliest reptiles were largely overshadowed by bigger labyrinthodont amphibians such as *Cochleosaurus*, and remained a small, inconspicuous part of the fauna until after the small ice age at the end of the Carboniferous.

Anapsids, synapsids, diapsids and sauropsids



A = Anapsid, B = Synapsid, C = Diapsid

The first reptiles were anapsids, having a solid skull with holes for only nose, eyes, spinal cord, etc. Very soon after the first reptiles appeared, they split into two branches. One branch, Synapsida (including both "mammal-like reptiles" and modern, extant mammals), had one opening in the skull roof behind each eye; the other branch, Diapsida, possessed a hole in their skulls behind each eye, along with a second hole located higher on the skull. The function of the holes in both groups was to lighten the skull and give room for the jaw muscles to move, allowing for a more powerful bite. Diapsids and later anapsids are classed as the "true reptiles", Sauropsida.

Turtles have been traditionally believed to be surviving anapsids, on the basis of their skull structure. The rationale for this classification was disputed, with some arguing that turtles are diapsids that reverted to this primitive state in order to improve their armor. Later morphological phylogenetic studies with this in mind placed turtles firmly within Diapsida. All molecular studies have strongly upheld the placement of turtles within diapsids, most commonly as a sister group to extant archosaurs.

Mammalian evolution

The main points to the transition from reptile to mammal was the evolution from scales to hair or fur, the evolution of warm-bloodedness, the loss of external eggs (except for in monotremes who have retained this trait), and the evolution mammary glands (the most defining trait in mammals that allow them to produce milk for offspring). The evolution of mammals was a gradual process that took approximately 70 million years, beginning in the mid-Permian. By the mid-Triassic, there were many species that looked like modern mammals, and the first true mammals appeared in the early Jurassic. The earliest known marsupial, *Sinodelphys*, appeared 125 million years ago in the early Cretaceous, around the same time as *Eomaia*, the first known eutherian (member of placentals' "parent" group); and the earliest known monotreme, *Teinolophos*, appeared two million years later.

Rise of dinosaurs

Permian reptiles

With the close of the Carboniferous, reptiles became the dominant tetrapod fauna. While the terrestrial reptiliomorph labyrinthodonts still existed, the synapsids evolved the first truly terrestrial megafauna (giant animals) in the form of pelycosaurs such as *Edaphosaurus* and the carnivorous *Dimetrodon*. In the mid-Permian period the climate turned dryer, resulting in a change of fauna: The primitive pelycosaurs were replaced by the more advanced therapsids.

The anapsid reptiles, whose massive skull roofs had no postorbital holes, continued and flourished throughout the Permian. The pareiasaurs reached giant proportions in the late Permian, eventually disappearing at the close of the period (the turtles being possible survivors).

Early in the period, the diapsid reptiles split into two main lineages, the archosaurs (forefathers of crocodiles and dinosaurs) and the lepidosaurs (predecessors of modern snakes, lizards, and tuataras). Both groups remained lizard-like and relatively small and inconspicuous during the Permian.

The Mesozoic era, the "Age of Reptiles"

The close of the Permian saw the greatest mass extinction known. Most of the earlier anapsid/synapsid megafauna disappeared, being replaced by the archosauromorph

diapsids. The archosaurs were characterized by elongated hind legs and an erect pose, the early forms looking somewhat like long-legged crocodiles. The archosaurs became the dominant group during the Triassic period, developing into the well-known dinosaurs and pterosaurs, as well as crocodiles and phytosaurs. Some of the dinosaurs developed into the largest land animals ever to have lived, making the Mesozoic era popularly known as the "Age of Reptiles". The dinosaurs also developed smaller forms, including the feather-bearing smaller theropods. In the mid-Jurassic period, these gave rise to the first birds.

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The therapsids came under increasing pressure from the dinosaurs in the early Mesozoic and developed into increasingly smaller and more nocturnal forms, the first mammals being the only survivors of the line by the late Jurassic.

Bird evolution



An Archaeopteryx specimen in Berlin

The main points to the transition from reptile to bird is the evolution from scales to feathers, the evolution of the beak (although independently evolved in other organisms), the hallofication of bones, development of flight, and warm-bloodedness.

The evolution of birds is thought to have begun in the Jurassic Period, with the earliest birds derived from theropod dinosaurs. Birds are categorized as a biological class, Aves. The earliest known species Aves is *Archaeopteryx lithographica*, from the Late Jurassic period, though 'Archaeopteryx is not commonly considered to have been a true bird, but a transitional species between Aves and Reptiles. Modern phylogenetics place birds in the dinosaur clade Theropoda. According to the current consensus, Aves and a sister group of the order Crocodylia, together are the sole living members of an unranked "reptile" clade, the Archosauria.

Demise of the dinosaurs

The close of the Cretaceous period saw the demise of the Mesozoic era reptilian megafauna. Along with massive amount of volcanic activity at the time, the meteor impact that created the K-T boundary is accepted as the main cause for this mass extinction event. Of the large marine reptiles, only sea turtles are left, and, of the dinosaurs, only the small feathered theropods survived in the form of birds. The end of the "Age of Reptiles" led into the "Age of Mammals". Despite the change in phrasing, reptile diversification continued throughout the Cenozoic, with squamates undergoing a greater radiation than they did in the Mesozoic. Today squamates make up the majority of extant reptiles today (over 90%), filling many of the ecological niches left by the mammals who would take advantage of the niches left by the dinosaurs. There are approximately 8,700 extant species of reptiles, compared with 5,400 species of mammals.

Role reversal

After the Cretaceous-Tertiary extinction wiped out all of the non-avian dinosaurs (birds are generally regarded as the surviving dinosaurs) and several other mammalian groups, placental and marsupial mammals diversified into many new forms and ecological niches throughout the Tertiary era. Some reaching enormous sizes and almost as wide of a variation as the dinosaurs once did. Due to global climate changes such as a lowering in total oxygen levels and lower average temperatures, mammalian megafauna never quite reached the sky-scraper heights as did some sauropods. These evolutionary and climatic changes is what is responsible for all modern orders of mammals that are now on Earth, including humans.

The four orders of reptilia

Testudines

Testudines, or turtles, may have evolved from anaspids, but their exact origin is unknown and heavily debated. Fossils date back to around 220 million years ago and share remarkably similar characteristics. These first turtles retain the same body plan as do all

modern testudines and are mostly herbivorous. With some feeding exclusively on small marine organisms. The trade-mark shell is believed to have evolved from extensions from there backbone and widened ribs which fused together. This is supported by the fossil of *Odontochelys semitestacea*, which has an incomplete shell originating from the ribs and back bone. This species also had teeth with its beak, giving more support to it being a transitional fossil, although this claim is still controversial. This shell evolved to protect itself from predators, but also slows down the land based species by a great amount. This has caused many species to go extinct in recent times. Because of alien species out-competing the slow order for food and lack of ability to escape from humans, there are large amounts of endangered species in this order.

Sphenodontia

Sphenodontians arose in the mid Triassic and only consist of one genus tuatara, which only includes two endangered species on New Zealand and some other minor surrounding islands. Their evolutionary history is filled with many species. Recent paleogenetic discoveries show that tuataras are prone to quick speciation.

Squamata

The most recent order of reptiles, squamates are recognized by having a movable quadrate bone (giving them upper-jaw movement) and possessing horny scales. They originate from the early Jurassic and are made up of the three suborders Lacertilia, Serpentes, and Amphisbaenia. Although they are the most recent order, squamates contain more species than any of the other reptilian orders. Squamates are a monophyletic group that is a sister group to the Sphenodontia or tuataras. The squamates and tuatara together are a sister group to crocodiles and birds, the extant archosaurs. Although squamate fossils first appear in the early Jurassic, mitochondrial phylogenetics suggests that they evolved in the late Permian. Most evolutionary relationships within the squamates are not yet completely worked out, with the relationship of snakes to other groups being most problematic. From morphological data, Iguanid lizards have been thought to have diverged from other squamates very early, but recent molecular phylogenies, both from mitochondrial and nuclear DNA, do not support this early divergence. Because snakes have a faster molecular clock than other squamates, and there are few early snake and snake ancestor fossils, it is difficult to resolve the relationship between snakes and other squamate groups.

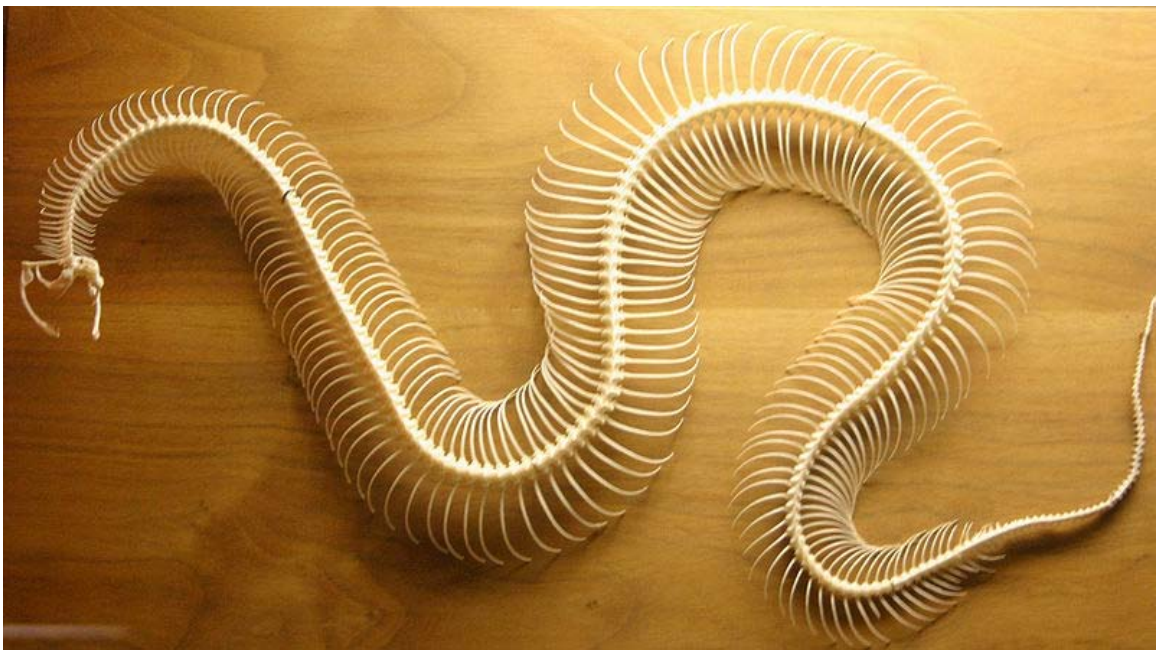
Crocodylia

The first organisms that showed similar characteristics of Crocodylians would be the Crurotarsi who appeared during the early Triassic 250 million years ago. This quickly gave rise to the Eusuchia clade 220 million years ago which would eventually lead to the order of Crocodylians, first of which arose about 85 million years ago during the late cretaceous, originating from the Eusuchia clade. The earliest fossil evidence of eusuchians is of the species *Isisfordia*. Early species mainly feed on fish and vegetation. They were land-based, most having long legs (when compared to modern crocodiles) and

many were bipedal. As diversification increased, many apex predators arose, all of which is now extinct. Modern Crocodylia arose through specific evolutionary traits. The complete loss of bipedalism in trade for generally low quadrupedal stance for an easy and less noticeable entrance to bodies of water. The shape of the skull/jaw changed to allow further grasp along with up-ward pointing nostrils and eyes. Mimicry is evident, as the back of all crocodylia resemble some type floating log along with their general color scheme of brown and green to mimic moss or wood. Their tail also took on a paddle shape to increase swimming speed. The only remaining groups to this order is the alligator, crocodile, caiman, and gharial.

Chapter- 4

Snake Skeleton



A **snake skeleton** consists primarily of the skull, vertebrae, and ribs, with only vestigial remnants of the limbs.

Skull

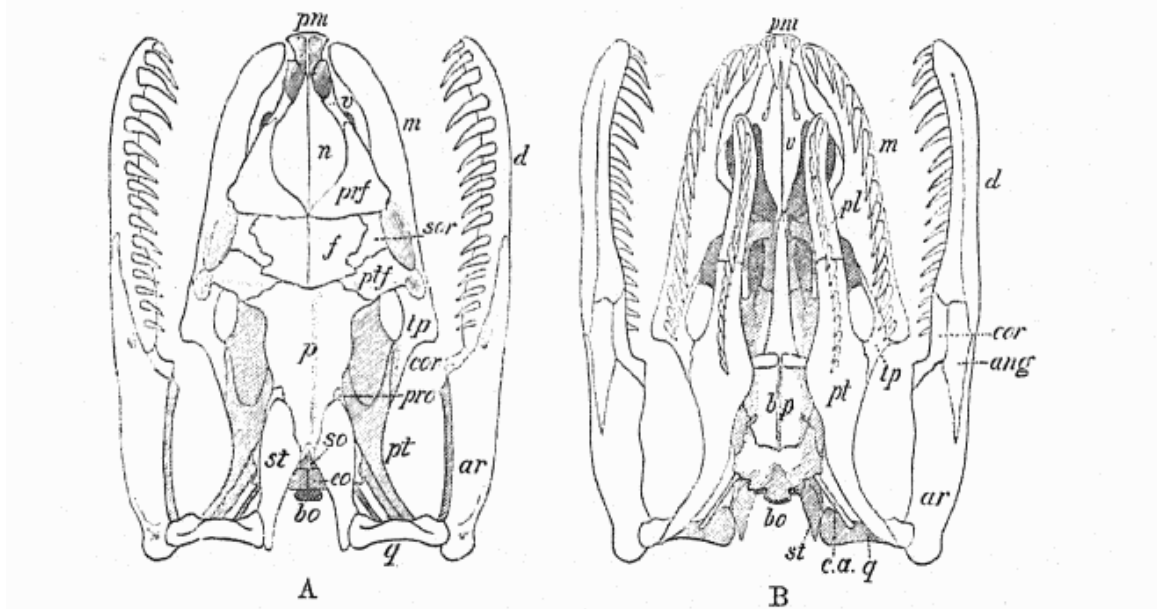


Fig. 73.—Skull of *Python reticulatus*.

A. Upper view. B. Lower view.

| | | |
|------------------------------|---------------------------|----------------------------|
| <i>ang.</i> Angular. | <i>f.</i> Frontal. | <i>pt.</i> Pterygoid. |
| <i>ar.</i> Articular. | <i>m.</i> Maxillary. | <i>ptf.</i> Postfrontal. |
| <i>bo.</i> Basioccipital. | <i>n.</i> Nasal. | <i>q.</i> Quadrate. |
| <i>bp.</i> Basisphenoid. | <i>p.</i> Parietal. | <i>so.</i> Supraoccipital. |
| <i>c.a.</i> Columella auris. | <i>pl.</i> Palatine. | <i>sor.</i> Supraorbital. |
| <i>cor.</i> Coronoid. | <i>pm.</i> Praemaxillary. | <i>st.</i> Supratemporal. |
| <i>d.</i> Dentary. | <i>prf.</i> Praefrontal. | <i>tp.</i> Transpalatine. |
| <i>co.</i> Exoccipital. | <i>pro.</i> Prootic. | <i>v.</i> Vomer. |

The skull of *Python reticulatus*

The skull of a snake is a very complex structure, with numerous joints to allow the snake to swallow prey far larger than its head.

The typical snake skull has a solidly ossified braincase, with the separate frontal bones and the united parietal bones extending downward to the basisphenoid, which is large and extends forward into a rostrum extending to the ethmoidal region. The nose is less ossified, and the paired nasal bones are often attached only at their base. The occipital condyle is either trilobate and formed by the basioccipital and the exoccipitals, or a simple knob formed by the basioccipital; the supraoccipital is excluded from the foramen magnum. The basioccipital may bear a strong, curved ventral process or hypapophysis in the vipers.

The prefrontal bone is situated, on each side, between the frontal bone and the maxilla, and may or may not be in contact with the nasal bone.

The postfrontal bone, usually present, borders the orbit behind, rarely also above, and in the pythons a supraorbital bone is intercalated between it and the prefrontal bone.

The premaxillary bone is single and small, and as a rule connected with the maxillary only by ligament.

The paired vomer is narrow.

The palatine bone and pterygoid are long and parallel to the axis of the skull, the latter diverging behind and extending to the quadrate or to the articular extremity of the mandible; the pterygoid is connected with the maxillary by the ectopterygoid or transverse bone, which may be very long, and the maxillary often emits a process towards the palatine, the latter bone being usually produced inwards and upwards towards the anterior extremity of the basisphenoid.

The quadrate is usually large and elongate, and attached to the cranium through the supratemporal (often regarded as the squamosal).

In rare cases, (Miodon, Polemon) the transverse bone is forked, and articulates with two branches of the maxilla.

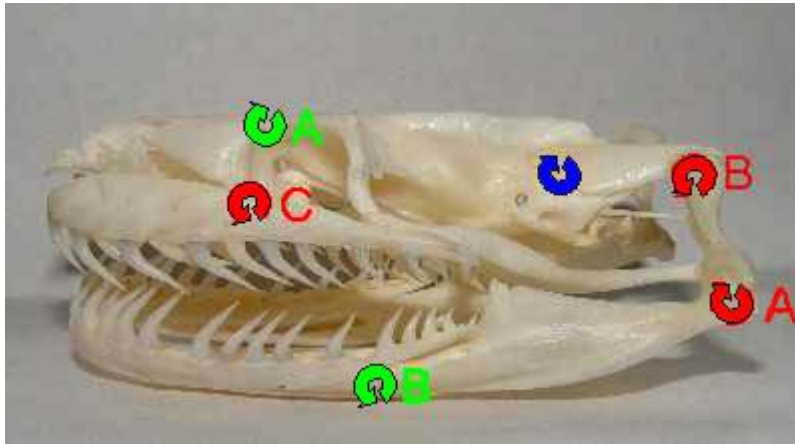
The quadrate and the maxillary and palatopterygoid arches are more or less movable to allow for the distension required by the passage of prey, often much exceeding the size of the mouth. For the same reason, the rami of the lower jaw, which consist of dentary, splenial, angular, and articular elements, with the addition of a coronoid in the boas and a few other small families, are connected at the symphysis by a very extensible elastic ligament.

The hyoid apparatus is reduced to a pair of cartilaginous filaments situated below the trachea, and united in front.

There are various modifications according to the genera. A large hole may be present between the frontal bones and the basisphenoid (*Psammophis*, *Coelopeltis*); the maxillary may be much abbreviated and movable vertically, as in the *Viperidae*; the pterygoids may taper and converge posteriorly, without any connection with the quadrate, as in the *Amblycephalidae*; the supratemporal may be much reduced, and wedged in between the adjacent bones of the cranium; the quadrate may be short or extremely large; the prefrontals may join in a median suture in front of the frontals; the dentary may be freely movable, and detached from the articular posteriorly.

The deviation from the normal type is much greater still when we consider the degraded wormlike members of the families *Typhlopidae* and *Glauconiidae*, in which the skull is very compact and the maxillary much reduced. In the former this bone is loosely attached to the lower aspect of the cranium; in the latter it borders the mouth, and is suturally joined to the premaxillary and the prefrontal. In both the transverse bone and the supratemporal are absent, but the coronoid element is present in the mandible.

Joints of the snake skull



Lateral view of the skull of a Burmese python, with visible kinetic joints labeled. Red = highly mobile, green = slightly mobile, blue = immobile.

Red A: the joint between the mandible and quadrate. It is analogous to the joint in mammal jaws.

Red B: the joint between the quadrate and the supratemporal. It is highly mobile in most directions, allowing a wider gape (i.e., the snake can open its mouth wider) and greater jaw flexibility.

Red C: the joint between the prefrontal and maxilla. It allows the maxilla to pivot in the plane of the photograph, and while it does not increase gape, it does facilitate the complex action by which the snake draws prey into its mouth.

Green A: the joint between the frontal bone and nasal bone. It allows the nose to upturn slightly, increasing gape and assisting in swallowing.

Green B: allows the lower jaws to bow outwards, further increasing the gape.

Blue: the joint between the supratemporal and parietal. Immobile, except for *Dasypeltis*.

Snake dentition

In most snakes, teeth are located on the dentary of the lower jaw, the maxilla, the palatine bone and the lateral pterygoid plate. The latter form an "inner row" of teeth that can move separately from the rest of the jaws and are used to help "walk" the jaws over prey. While most snakes are not hazardous to humans, several lineages have evolved venom which is typically delivered by specialized teeth called fangs located on the maxilla.

Most snakes can be placed into one of four groups, based on their teeth, which correlate strongly with venom and lineage.

Aglyph



An **aglyphous** snake. A Burmese python skull (*Python molurus*)

Aglyphous snakes (*lacking grooves*) have no specialized teeth; each tooth is similar in shape and often size. When teeth vary in size, as in some bird eaters, they do not vary in shape. Most aglyphous snakes are non-venomous, however some, like *Thamnophis*, are considered mildly venomous, but generally not harmful to humans. The feature is not a synapomorphy.

Opisthoglyph



An **opisthoglyphous** snake. A hognose snake skull (*Heterodon nasicus*)

Opisthoglyphous snakes (*rearward grooves*) possess weak venom injected by a pair of enlarged teeth at the back of the maxillae which normally angle backwards and are grooved to channel venom into the puncture. Since these fangs are not located at the front of the mouth this arrangement is vernacularly called *rear-fanged*. In order to

envenomate prey, an opisthoglyphous snake must move the prey into the rear of its mouth and then penetrate it with its fangs, presenting difficulties with large prey although they can quickly move smaller prey (or a human handler's finger) into position.

While the venom of most opisthoglyphous snakes is too weak to harm humans, sometimes this is not the case. Notably, herpetologists Karl Schmidt and Robert Mertens were killed by a boomslang and twig snake, respectively, after each underestimated the effects of the bite and failed to seek medical help. Opisthoglyphous snakes are found in family Colubridae.

Proteroglyph



A **proteroglyphous** snake. A king cobra skull (*Ophiophagus hannah*)

Proteroglyphous snakes (*forward grooved*) have shortened maxillae bearing few teeth except for a substantially enlarged fang pointing downwards and completely folded around the venom channel, forming a hollow needle. Because the fangs are only a fraction of an inch long in even the largest species these snakes must hang on, at least momentarily, as they inject their venom, the most toxic of all snakes. Some spitting cobras have modified fang tips allowing them to spray venom at an attacker's eyes. This form of dentition is unique to elapids.

Solenoglyph



A **solenoglyphous** snake. A rattlesnake skull (*Crotalus sp.*)

Solenoglyphous snakes (*pipe grooved*) have the most advanced venom delivery method of any snake. Each maxilla is reduced to a nub supporting a single hollow fang tooth. The fangs, which can be as long as half the length of the head, are folded against the roof of the mouth, pointing posteriorly. The skull has a series of interacting elements which ensure that the fangs rotate into biting position when the jaws open. Solenoglyphous snakes open their mouths almost 180 degrees, and the fangs swing into a position to allow them to penetrate deep into the prey. While solenoglyph venom is typically less toxic than that of proteroglyphs, this system allows them to deeply inject large quantities of venom. This form of dentition is unique to vipers.

Exceptions

A few snakes do not conform to these categories. Atractaspis is solenoglyphous but the fangs swing out sideways, allowing it to strike without opening its mouth, perhaps allowing it to hunt in small tunnels. Scolecophidia (blind burrowing snakes) typically have few teeth, often only in the upper jaw or lower jaw.

Taxonomic key of skull modifications

Modifications of the skull in the European genera:

- I. Quadrate articulating with the cranium, supratemporal absent; mandible much shorter than the skull, with coronoid bone; maxillary small, on lower aspect of cranium; pterygoids not extending to quadrate; nasals forming long sutures with the premaxillary, prefrontals, and frontal: *Typhlops*.
- II. Quadrate suspended from the supratemporal; mandible at least as long as the skull; pterygoids extending to quadrate or mandible.
 - A. Mandible with coronoid bone; nasals in sutural contact with frontals and prefrontals; transverse bone short, not projecting much beyond cranium; maxillary not half as long as mandible, which is not longer than skull (to occiput): *Eryx*.
 - B. No coronoid bone; nasals isolated.
 - 1. Maxillary elongate, not movable vertically.
 - a. Maxillary half as long as mandible.
 - Supratemporal half as long as skull, projecting far beyond cranium; mandible much longer than skull: *Tropidonotus*.
 - Supratemporal not half as long as skull, projecting far beyond cranium; mandible much longer than skull: *Zamenis*.
 - Supratemporal not half as long as skull, projecting but slightly beyond cranium; mandible much longer than skull: *Coluber*.
 - Supratemporal not half as long as skull, not projecting beyond cranium; mandible not longer than skull: *Coronella*, *Contia*.
 - b. Maxillary not half as long as mandible, which is longer than skull; supratemporal not half as long as skull, projecting beyond cranium.
 - Quadrate longer than supratemporal; maxillary much longer than quadrate, nearly straight in front of prefrontal; a large vacuity between the frontal bones and the basisphenoid: *Coelopeltis*.
 - Quadrate not longer than supratemporal; maxillary little longer than quadrate, strongly curved in front of prefrontal: *Macroprotodon*
 - Quadrate longer than supratemporal; maxillary little longer than quadrate, nearly straight in front of prefrontal: *Tarbophis*
 - 2. Maxillary much abbreviated and erectile; supratemporal not half as long as skull; mandible much longer than skull; basioccipital with a strong process.
 - Maxillary bone solid: *Vipera*.

- Maxillary bone hollow: *Ancistrodon*.
- The vertebrae number 130 to 500 - in the European forms 147 (*Vipera ursinii*) to 330 (*Coluber leopardinus*).

Vertebrae and ribs

The vertebral column consists of an atlas (composed of two vertebrae) without ribs; numerous precaudal vertebrae, all of which, except the first or first three, bear long, movable, curved ribs with a small posterior tubercle at the base, the last of these ribs sometimes forked; two to ten so-called lumbar vertebrae without ribs, but with bifurcate transverse processes (lymphapophyses) enclosing the lymphatic vessels; and a number of ribless caudal vertebrae with simple transverse processes. When bifid, the ribs or transverse processes have the branches regularly superposed.

The centra have the usual ball and socket joint, with the nearly hemispherical or transversely elliptic condyle at the back (procoelous vertebrae), while the neural arch is provided with additional articular surfaces in the form of pre- and post-zygapophyses, broad, flattened, and overlapping, and of a pair of anterior wedge-shaped processes called zygosphenes, fitting into a pair of corresponding concavities, zygantrum, just below the base of the neural spine. Thus the vertebrae of snakes articulate with each other by eight joints in addition to the cup-and-ball on the centrum, and interlock by parts reciprocally receiving and entering one another, like the mortise and tenon joinery. The precaudal vertebrae have a more or less high neural spine which, as a rare exception (*Xenopholis*), may be expanded and plate-like above, and short or moderately long transverse processes to which the ribs are attached by a single facet. The centra of the anterior vertebrae emit more or less developed descending processes, or haemapophyses, which are sometimes continued throughout, as in *Tropidonotus*, *Vipera*, and *Ancistrodon*, among European genera.

In the caudal region, elongate transverse processes take the place of ribs, and the haemapophyses are paired, one on each side of the haemal canal. In the rattlesnakes the seven or eight last vertebrae are enlarged and fused into one.

Vestigial limbs

No living snake shows any remains of the pectoral arch, but remains of the pelvis are found in:

- Boas and Pythons: a long ilium, attached to the lower branch of the first bifurcate transverse process of the lumbar vertebrae, bearing three short bones, the longest of which, regarded as the femur, terminates in a claw-like spur which, in males at least, usually appears externally on each side of the cloaca.
- Leptotyphlopidae: ilium, pubis, and ischium, and rudimentary femur, the ischium forming a ventral symphysis.
- Aniliidae
- Typhlopidae: a single bone on each side.

Chapter- 5

Frog

Frogs

Temporal range: Triassic–present



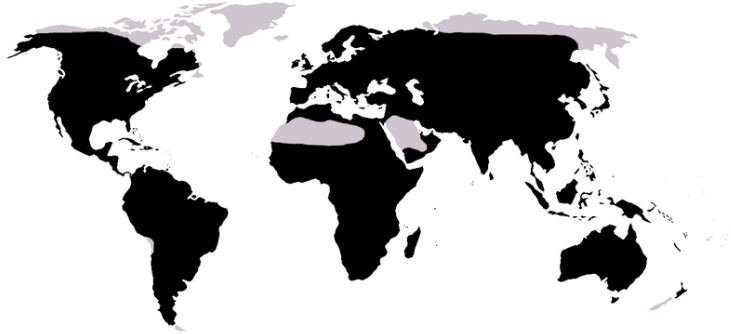
Australian Green Tree Frog (*Litoria caerulea*)

Scientific classification

| | |
|-----------|------------------------------|
| Kingdom: | Animalia |
| Phylum: | Chordata |
| Class: | Amphibia |
| Subclass: | Lissamphibia |
| Order: | Anura
Merrem, 1820 |

Suborders

Archaeobatrachia
Mesobatrachia
Neobatrachia



Native distribution of frogs (in black)

Frogs are amphibians in the order Anura (meaning "tail-less", from Greek *an-*, without + *oura*, tail), formerly referred to as *Salientia* (Latin *salere* (*salio*), "to jump"). Most frogs are characterized by a short body, webbed digits (fingers or toes), protruding eyes and the absence of a tail. Frogs are widely known as exceptional jumpers, and many of the anatomical characteristics of frogs, particularly their long, powerful legs, are adaptations to improve jumping performance. Due to their permeable skin, frogs are often semi-aquatic or inhabit humid areas, but move easily on land. They typically lay their eggs in puddles, ponds or lakes, and their larvae, called tadpoles, have gills and develop in water. Adult frogs follow a carnivorous diet, mostly of arthropods, annelids and gastropods. Frogs are most noticeable by their call, which can be widely heard during the night or day, mainly in their mating season.

The distribution of frogs ranges from tropic to subarctic regions, but most species are found in tropical rainforests. Consisting of more than 5,000 species described, they are among the most diverse groups of vertebrates. However, populations of certain frog species are declining significantly.

A popular distinction is often made between frogs and toads on the basis of their appearance, but this has no taxonomic basis. (Members of the anuran family Bufonidae are called true toads, but many species from other families are also called toads.) In addition to their ecological importance, frogs have many cultural roles, such as in literature, symbolism and religion, and they are also valued as food and as pets.

Etymology and terminology

The name frog derives from Old English *frogga*, (compare Old Norse *frauki*, German *Frosch*, older Dutch spelling *kikvorsch*), cognate with Sanskrit *plava* (frog), probably deriving from Proto-Indo-European *praw* = "to jump".

A distinction is often made between frogs and toads on the basis of their appearance, caused by the convergent adaptation among so-called toads to dry environments; however, this distinction has no taxonomic basis. The only family exclusively given the common name "toad" is Bufonidae, but many species from other families are also called "toads," and the species within the toad genus *Atelopus* are referred to as "harlequin frogs".

Taxonomy

The order *Anura* contains 4,810 species in 33 families, of which the Leptodactylidae (1100 spp.), Hylidae (800 spp.) and Ranidae (750 spp.) are the richest in species. About 88% of amphibian species are frogs.



European Fire-bellied Toad (*Bombina bombina*)



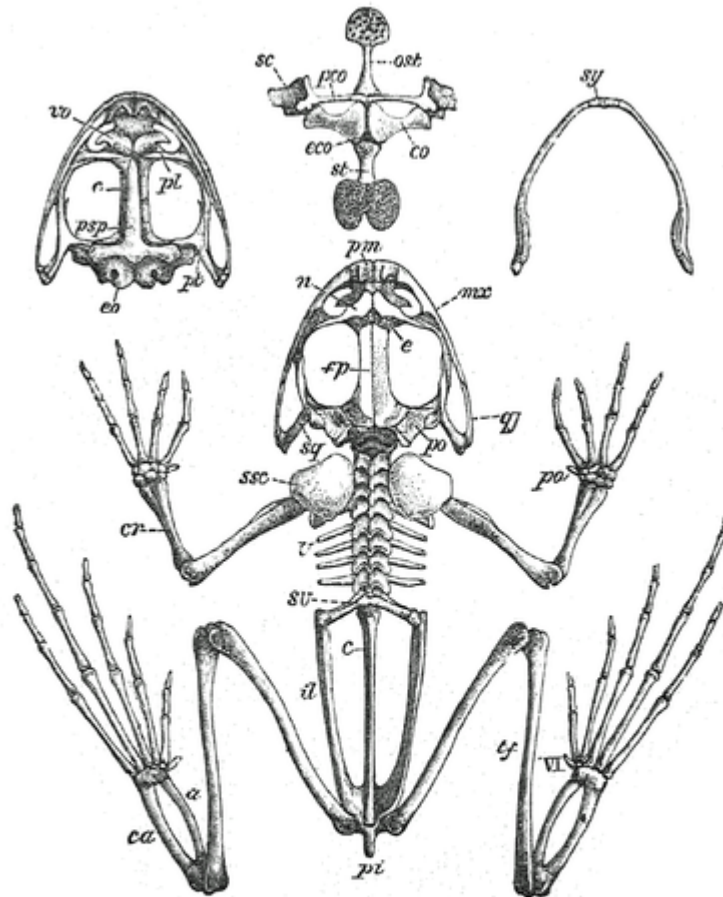
Young American bullfrog found in a stream in New Jersey

The use of the common names "frog" and "toad" has no taxonomic justification. From a taxonomic perspective, all members of the order Anura are frogs, but only members of the family Bufonidae are considered "true toads". The use of the term "frog" in common names usually refers to species that are aquatic or semi-aquatic with smooth and/or moist skins, and the term "toad" generally refers to species that tend to be terrestrial with dry, warty skin. An exception is the fire-bellied toad (*Bombina bombina*): while its skin is slightly warty, it prefers a watery habitat.

Frogs and toads are broadly classified into three suborders: Archaeobatrachia, which includes four families of primitive frogs; Mesobatrachia, which includes five families of more evolutionary intermediate frogs; and Neobatrachia, by far the largest group, which contains the remaining 24 families of "modern" frogs, including most common species throughout the world. Neobatrachia is further divided into the Hyloidea and Ranoidea. This classification is based on such morphological features as the number of vertebrae, the structure of the pectoral girdle, and the morphology of tadpoles. While this classification is largely accepted, relationships among families of frogs are still debated. Future studies of molecular genetics should soon provide further insights to the evolutionary relationships among anuran families.

Some species of anurans hybridise readily. For instance, the Edible Frog (*Rana esculenta*) is a hybrid of the Pool Frog (*R. lessonae*) and the Marsh Frog (*R. ridibunda*). *Bombina bombina* and *Bombina variegata* similarly form hybrids, although these are less fertile, giving rise to a hybrid zone.

Morphology and physiology



Skeleton of *Rana esculenta*. (Guide to Reptile Gallery B.M.)

| | | |
|---------------------|--------------------|----------------------------|
| a. Astragalus. | n. Nasal. | sc. Scapula. |
| c. Coccyx. | ost. Onosternum. | sq. Squamosal. |
| ca. Calcaneum. | pco. Præcoracoid. | ssc. Suprascapula. |
| co. Coracoid. | pl. Palatine. | st. Sternum. |
| cr. Radius-ulna. | pi. Pubis-ischium. | sv. Sacral vertebra. |
| e. Ethmoid. | pm. Præmaxillary. | sy. Symphyseal. |
| eco. Epicoracoid. | po. Prootic. | tf. Tibia-fibula. |
| eo. Exocephal. | po'. Pollex. | v. Dorsal vertebræ. |
| fp. Frontoparietal. | psp. Parasphenoid. | vo. Vomer. |
| il. Ilium. | pt. Pterygoid. | VI. Rudiment of sixth toe. |
| msc. Maxillary. | qj. Quadratojugal. | |

Skeleton of *Rana*

The morphology of frogs is unique among amphibians. Compared with the other two groups of amphibians, (salamanders and caecilians), frogs are unusual because they lack tails as adults and their legs are more suited to jumping than walking. The physiology of frogs is generally like that of other amphibians (and differs from other terrestrial

vertebrates) because oxygen can pass through their highly permeable skin. This unique feature allows frogs to "breathe" largely through their skin. Because the oxygen is dissolved in an aqueous film on the skin and passes from there to the blood, the skin must remain moist at all times; this makes frogs susceptible to many toxins in the environment, some of which can similarly dissolve in the layer of water and be passed into their bloodstream. This may be the cause of the decline in frog populations.

Many characteristics are not shared by all of the approximately 5,250 described frog species. However, some general characteristics distinguish them from other amphibians. Frogs are usually well suited to jumping, with long hind legs and elongated ankle bones. They have a short vertebral column, with no more than ten free vertebrae, followed by a fused tailbone (urostyle or coccyx), typically resulting in a tailless phenotype.

Frogs range in size from 10 mm (0.39 in) (*Brachycephalus didactylus* of Brazil and *Eleutherodactylus iberia* of Cuba) to 300 mm (12 in) (goliath frog, *Conraua goliath*, of Cameroon). The skin hangs loosely on the body because of the lack of loose connective tissue. Skin texture varies: it can be smooth, warty or folded. Frogs have three eyelid membranes: one is transparent to protect the eyes underwater, and two vary from translucent to opaque. Frogs have a tympanum on each side of the head, which is involved in hearing and, in some species, is covered by skin. Most frogs have teeth, specifically pedicellate teeth in which the crown is separated from the root by fibrous tissue. Most only have teeth on the edge of the upper jaw (*maxillary teeth*) as well as *vomerine teeth* on the roof of their mouth. They do not have any teeth on their lower jaw, so they usually swallow their food whole. The teeth are mainly used to hold the prey and keep it in place till they can get a good grip on it and swallow their meal, assisted by retracting their eyes into their head. True toads lack any teeth at all, and some species (*Pyxicephalus*) which prey on relatively large organisms (including mice and other frogs) have cone shaped projections of bone, called odontoid processes, at the front of the lower jaw which function like teeth.

Feet and legs



Tyler's Tree Frog (*Litoria tyleri*) illustrates large toe pads and webbed feet



A bullfrog skeleton, showing elongate limb bones and extra joints. Red marks indicate bones which have been substantially elongated in frogs and joints which have become mobile. Blue indicates joints and bones which have not been modified or only somewhat elongated.

The structure of the feet and legs varies greatly among frog species, depending in part on whether they live primarily on the ground, in water, in trees, or in burrows. Frogs must be able to move quickly through their environment to catch prey and escape predators, and numerous adaptations help them do so.

Many frogs, especially those that live in water, have webbed toes. The degree to which the toes are webbed is directly proportional to the amount of time the species lives in the water. For example, the completely aquatic African dwarf frog (*Hymenochirus sp.*) has fully webbed toes, whereas the toes of White's tree frog (*Litoria caerulea*), an arboreal species, are only a half or a quarter webbed.

Arboreal frogs have "toe pads" to help grip vertical surfaces. These pads, located on the ends of the toes, do not work by suction. Rather, the surface of the pad consists of interlocking cells, with a small gap between adjacent cells. When the frog applies pressure to the toe pads, the interlocking cells grip irregularities on the substrate. The small gaps between the cells drain away all but a thin layer of moisture on the pad, and maintain a grip through capillarity. This allows the frog to grip smooth surfaces, and does not function when the pads are excessively wet.

In many arboreal frogs, a small "intercalary structure" in each toe increases the surface area touching the substrate. Furthermore, since hopping through trees can be dangerous, many arboreal frogs have hip joints that allow both hopping and walking. Some frogs that live high in trees even possess an elaborate degree of webbing between their toes, as do aquatic frogs. In these arboreal frogs, the webs allow the frogs to "parachute" or control their glide from one position in the canopy to another.

Ground-dwelling frogs generally lack the adaptations of aquatic and arboreal frogs. Most have smaller toe pads, if any, and little webbing. Some burrowing frogs have a toe extension—a metatarsal tubercle—that helps them to burrow. The hind legs of ground dwellers are more muscular than those of aqueous and tree-dwelling frogs.

Sometimes during the tadpole stage, one of the animal's rear leg stubs is eaten by a dragonfly nymph. In some of these cases, the full leg grows anyway, and in other cases, it does not, although the frog may still live out its normal lifespan with only three legs. Other times, a parasitic flatworm called *Riberoria trematodes* digs into the rear of a tadpole, where it rearranges the limb bud cells, which sometimes causes the frog to have extra legs.

Jumping



Rainforest Rocket Frog jumping

Frogs are generally recognized as exceptional jumpers, and the best jumper of all vertebrates. The Australian rocket frog, *Litoria nasuta*, can leap over 50 times its body length (5.5 cm), resulting in jumps of over 2 meters. The acceleration of the jump may be up to twice gravity. There are tremendous differences between species in jumping capability, but within a species, jump distance increases with increasing size, but relative jumping distance (body-lengths jumped) decreases.

While frog species can use a variety of locomotor modes (running, walking, gliding, swimming, and climbing), more are either proficient at jumping or descended from ancestors who were, with much of the musculo-skeletal morphology modified for this purpose. The tibia, fibula and tarsals have been fused into a single, strong bone, as have the radius and ulna in the forelimbs (which must absorb the impact of landing). The metatarsals have become elongated to add to the leg length and allow the frog to push against the ground for longer during a jump. The ilium has elongated and formed a mobile joint with the sacrum which, in specialist jumpers such as Ranids or Hylids, functions as an additional limb joint to further power the leaps. This elongation of the limbs results in the frog being able to apply force to the ground for longer during a jump, which in turn results in a longer, faster jump.

The muscular system has been similarly modified. The hind limbs of the ancestor of frogs presumably contained pairs of muscles which would act in opposition (one muscle to flex the knee, a different muscle to extend it), as is seen in most other limbed animals.

However, in modern frogs, almost all muscles have been modified to contribute to the action of jumping, with only a few small muscles remaining to bring the limb back to the starting position and maintain posture. The muscles have also been greatly enlarged, with the muscles involved in jumping accounting for over 17% of the total mass of the frog.

In some extremely capable jumpers, such as the cuban tree frog, the peak power exerted during a jump can exceed what muscle is capable of producing. Currently, it is hypothesized that frogs are storing muscular energy by stretching their tendons like springs, then triggering the release all at once, allowing the frog to increase the energy of its jump beyond the limits of muscle-powered acceleration. A similar mechanism has already been documented in locusts and grasshoppers.

Skin



Pouched Frog (*Assa darlingtoni*) camouflaged against leaf litter

Many frogs are able to absorb water and oxygen directly through the skin, especially around the pelvic area. However, the permeability of a frog's skin can also result in water loss. Some tree frogs reduce water loss with a waterproof layer of skin. Others have adapted behaviours to conserve water, including engaging in nocturnal activity and resting in a water-conserving position. This position involves the frog lying with its toes and fingers tucked under its body and chin, respectively, with no gap between the body and substrate. Some frog species will also rest in large groups, touching the skin of the neighbouring frog. This reduces the amount of skin exposed to the air or a dry surface, and thus reduces water loss. These adaptations only reduce water loss enough for a predominantly arboreal existence, and are not suitable for arid conditions.

Camouflage is a common defensive mechanism in frogs. Most camouflaged frogs are nocturnal, which adds to their ability to hide. Nocturnal frogs usually find the ideal camouflaged position during the day to sleep. Some frogs have the ability to change colour, but this is usually restricted to shades of one or two colours. For example, White's tree frog varies in shades of green and brown. Features such as warts and skin folds are usually found on ground-dwelling frogs, where a smooth skin would not disguise them effectively. Arboreal frogs usually have smooth skin, enabling them to disguise themselves as leaves.

Certain frogs change colour between night and day, as light and moisture stimulate the pigment cells and cause them to expand or contract.

Poison

Many frogs contain mild toxins that make them unpalatable to potential predators. For example, all toads have large poison glands—the parotoid glands—located behind the eyes, on the top of the head. Some frogs, such as some poison dart frogs, are especially toxic. The chemical makeup of toxins in frogs varies from irritants to hallucinogens, convulsants, nerve poisons, and vasoconstrictors. Many predators of frogs have adapted to tolerate high levels of these poisons. Others, including humans, may be severely affected.



Oophaga pumilio, a poison dart frog, contains numerous alkaloids which deter predators

Some frogs obtain poisons from the ants and other arthropods they eat; others, such as the Australian Corroboree Frogs (*Pseudophryne corroboree* and *Pseudophryne pengilleyi*), can manufacture an alkaloid not derived from their diet. Some native people of South America extract poison from the poison dart frogs and apply it to their darts for hunting, although few species are toxic enough to be used for this purpose. It was previously a misconception the poison was placed on arrows rather than darts. The common name of these frogs was thus changed from "poison arrow frog" to "poison dart frog" in the early 1980s. Poisonous frogs tend to advertise their toxicity with bright colours, an adaptive strategy known as aposematism. There are at least two non-poisonous species of frogs in tropical America (*Eleutherodactylus gaigei* and *Lithodytes lineatus*) that mimic the colouration of dart poison frogs' coloration for self-protection (Batesian mimicry).

Because frog toxins are extraordinarily diverse, they have raised the interest of biochemists as a "natural pharmacy". The alkaloid epibatidine, a painkiller 200 times more potent than morphine, is found in some species of poison dart frogs. Other chemicals isolated from the skin of frogs may offer resistance to HIV infection. Arrow and dart poisons are under active investigation for their potential as therapeutic drugs.

The skin secretions of some toads, such as the Colorado River toad and cane toad, contain bufotoxins, some of which, such as bufotenin, are psychoactive, and have therefore been used as recreational drugs. Typically, the skin secretions are dried and smoked. Skin licking is especially dangerous, and appears to constitute an urban myth.

Respiration and circulation

The skin of a frog is permeable to oxygen and carbon dioxide, as well as to water. There are a number of blood vessels near the surface of the skin. When a frog is underwater, oxygen is transmitted through the skin directly into the bloodstream. On land, adult frogs use their lungs to breathe. Their lungs are similar to those of humans, but the chest muscles are not involved in respiration, and there are no ribs or diaphragm to support breathing. Frogs breathe by taking air in through the nostrils (which often have valves which close when the frog is submerged), causing the throat to puff out, then compressing the floor of the mouth, which forces the air into the lungs. In August 2007 an aquatic frog named *Barbourula kalimantanensis* was discovered in a remote part of Indonesia. The Bornean Flat-headed Frog (*B. kalimantanensis*) is the first species of frog known to science without lungs.

Frogs are known for their three-chambered heart, which they share with all tetrapods except birds, crocodilians and mammals. In the three-chambered heart, oxygenated blood from the lungs and de-oxygenated blood from the respiring tissues enter by separate atria, and are directed via a spiral valve to the appropriate vessel—aorta for oxygenated blood and pulmonary artery for deoxygenated blood. This special structure is essential to keeping the mixing of the two types of blood to a minimum, which enables frogs to have higher metabolic rates, and to be more active than otherwise.

Some species of frog have remarkable adaptations that allow them to survive in oxygen deficient water. The lake titicaca frog (*Telmatobius culeus*) is one such species and to survive in the poorly oxygenated waters of Lake Titicaca it has incredibly wrinkly skin that increases its surface area to enhance gas exchange. This frog will also do 'push-ups' on the lake bed to increase the flow of water around its body.

Digestion and excretion

The frog's digestive system begins with the mouth. Frogs have teeth along their upper jaw called the maxillary teeth, which are used to grind food before swallowing. These teeth are very weak, and cannot be used to catch or harm agile prey. Instead, the frog uses its sticky tongue to catch food (such as flies or other insects). The food then moves through the esophagus into the stomach. The food then proceeds to the small intestine (duodenum and ileum) where most digestion occurs. Frogs carry pancreatic juice from the pancreas, and bile (produced by the liver) through the gallbladder from the liver to the small intestine, where the fluids digest the food and extract the nutrients. When the food passes into the large intestine, the water is reabsorbed and wastes are routed to the cloaca. All wastes exit the body through the cloaca and the cloacal vent.

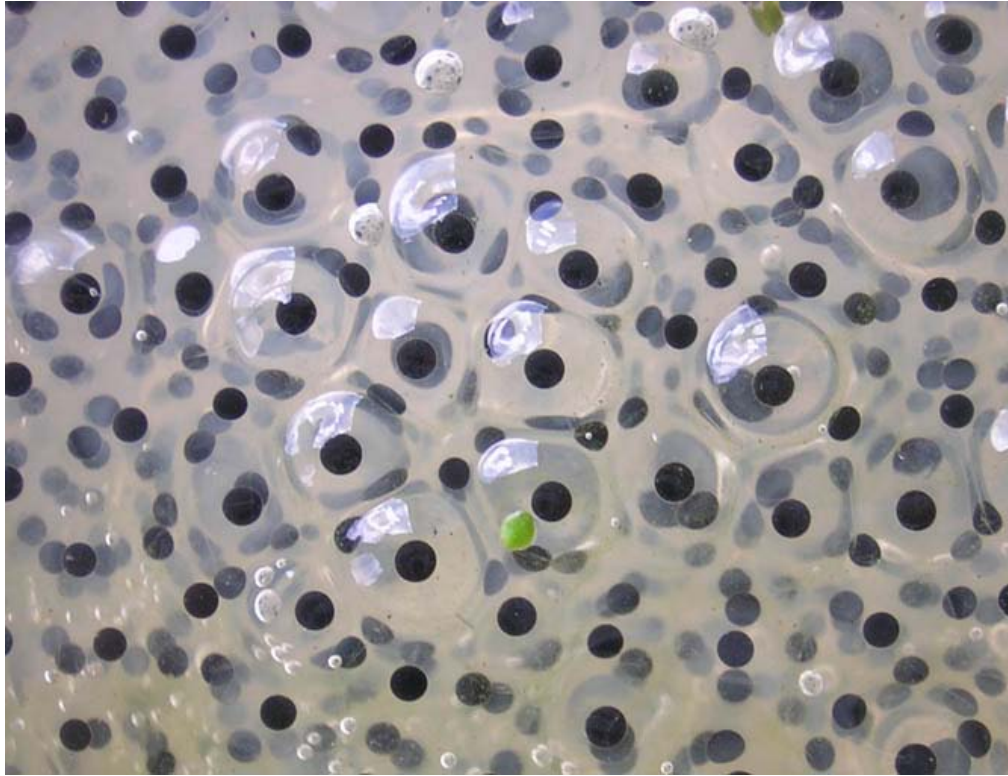
Nervous system

The frog has a highly developed nervous system which consists of a brain, spinal cord and nerves. Many parts of the frog's brain correspond with those of humans. The medulla oblongata regulates respiration, digestion, and other automatic functions. Muscular coordination and posture are controlled by the cerebellum. The relative size of the cerebrum of a frog is much smaller than that of a human. Frogs have ten cranial nerves (nerves which pass information from the outside directly to the brain) and ten pairs of spinal nerves (nerves which pass information from extremities to the brain through the spinal cord). By contrast, all amniotes (mammals, birds and reptiles) have twelve cranial nerves. Frogs do not have external ears; the eardrums (tympanic membranes) are directly exposed. As in all animals, the ear contains semicircular canals which help control balance and orientation. Due to their short cochlea, frogs use electrical tuning to expand their range of audible frequencies.

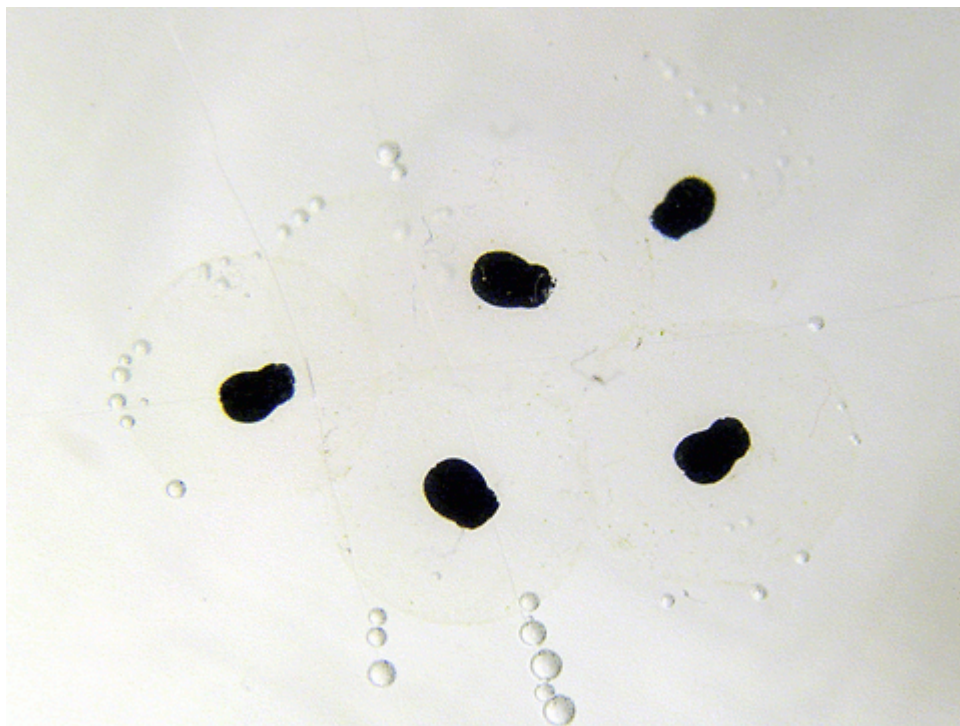
Natural history

The life cycle of frogs, like that of other amphibians, consists of four main stages: egg, tadpole, metamorphosis and adult. The reliance of frogs on an aquatic environment for the egg and tadpole stages gives rise to a variety of breeding behaviours that include the well-known mating calls used by the males of most species to attract females to the bodies of water that they have chosen for breeding. Some frogs also look after their eggs—and in some cases even the tadpoles—for some time after laying.

Life cycle



Frogspawn



Frogspawn development



Tadpole of Haswell's Froglet (*Paracrinia haswelli*)

The life cycle of a frog starts with an egg. A female generally lays gelatinous egg masses containing thousands of eggs, in water. Each anuran species lays eggs in a distinctive, identifiable manner. An example are the long strings of eggs laid by the common American toad. The eggs are highly vulnerable to predation, so frogs have evolved many techniques to ensure the survival of the next generation. In colder areas the embryo is black to absorb more heat from the sun, which speeds up the development. Most commonly, this involves synchronous reproduction. Many individuals will breed at the same time, overwhelming the actions of predators; the majority of the offspring will still die due to predation, but there is a greater chance some will survive. Another way in which some species avoid the predators and pathogens eggs are exposed to in ponds is to lay eggs on leaves above the pond, with a gelatinous coating designed to retain moisture. In these species the tadpoles drop into the water upon hatching. The eggs of some species laid out of water can detect vibrations of nearby predatory wasps or snakes, and will hatch early to avoid being eaten. Some species, such as the Cane Toad (*Bufo marinus*), lay poisonous eggs to minimise predation. While the length of the egg stage depends on the species and environmental conditions, aquatic eggs generally hatch within one week. Other species go through their whole larval phase inside the eggs or the mother, or they have direct development. Unlike salamanders and newts, frogs and toads never become sexually mature while still in their larval stage.

Eggs hatch and continue life as tadpoles (occasionally known as polliwogs), which typically have oval bodies and long, vertically flattened tails. At least one species (*Nannophrys ceylonensis*) has tadpoles that are semi-terrestrial and live among wet rocks, but as a general rule, free living larvae are fully aquatic. They lack eyelids and have a cartilaginous skeleton, a lateral line system, gills for respiration (external gills at first, internal gills later) and tails with dorsal and ventral folds of skin for swimming. From pretty early onward they develop a gill pouch that covers the gills and the front legs and also the lungs are developed in an early stage as an accessory breathing organ. Some

species which go through the metamorphosis inside the egg and hatch to small frogs never develop gills, instead there are specialised areas of skin that takes care of the respiration. Tadpoles also lack true teeth, but the jaws in most species usually have two elongate, parallel rows of small keratinized structures called keradonts in the upper jaw while the lower jaw has three rows of keradonts, surrounded by a horny beak, but the number of rows can be lower or absent, or much higher. Tadpoles are typically herbivorous, feeding mostly on algae, including diatoms filtered from the water through the gills. Some species are carnivorous at the tadpole stage, eating insects, smaller tadpoles, and fish. Cannibalism has been observed among tadpoles. Early developers who gain legs may be eaten by the others, so the late bloomers survive longer. This has been observed in England in the species *Rana temporaria* (common frog).

Tadpoles are highly vulnerable to predation by fish, newts, predatory diving beetles and birds such as kingfishers. Poisonous tadpoles are present in many species, such as Cane Toads. The tadpole stage may be as short as a week, or tadpoles may overwinter and metamorphose the following year in some species, such as the midwife toad (*Alytes obstetricans*) and the common spadefoot (*Pelobates fuscus*). In the Pipidae, with the exception for Hymenochirus, the tadpoles have paired anterior barbels which make them resemble small catfish.

With the exception of the base of the tail, where a few vertebral structures develop to give rise to the urostyle later in life, the tail lacks the completely solid, segmental, skeletal elements of cartilage or bony tissue that are so typical for other vertebrates, although it does contain a notochord

At the end of the tadpole stage, frogs undergo metamorphosis, in which they undergo a transition into the adult form. This metamorphosis last typically only 24 hours and consists of:



Larva of the common frog *Rana temporaria* a day before metamorphosis



Common frog - Metamorphosis stage. Notice the deformed jaws, large eyes and the remains of the gill pouch.



Young frog with tail remains after metamorphosis



Adult leopard frog

- The disappearance of the gill pouch, making the front legs visible.
- The transformation of the jaws into the big jaws of predatory frogs (most tadpoles are scraping of algae or are filter feeders)
- The transformation of the digestive system: the long spiral gut of the larva is being replaced by the typical short gut of a predator.
- An adaptation of the nervous system for stereoscopic vision, locomotion and feeding
- A quick growth and movement of the eyes to higher up the skull and the formation of eyelids.
- Formation of skin glands, thickening of the skin and loss of the lateral line system
- An eardrum is developed to lock the middle ear.

The disappearance of the tail is somewhat later (occurs at higher thyroxin levels) and after the tail has been resorbed the animals are ready to leave the water. The material of the tail is being used for a quick growth of the legs. The disappearing of the larval structures is a regulated process called apoptosis tail.



Incident of frog cannibalism

After metamorphosis, young adults may leave the water and disperse into terrestrial habitats, or continue to live in the aquatic habitat as adults. Almost all species of frogs are carnivorous as adults, eating invertebrates such as arthropods, annelids and gastropods. A

few of the larger species may eat prey such as small mammals, fish and smaller frogs. Some frogs use their sticky tongues to catch fast-moving prey, while others capture their prey and force it into their mouths with their hands. However, there are a very few species of frogs that primarily eat plants. Adult frogs are themselves preyed upon by birds, large fish, snakes, otters, foxes, badgers, coatis, and other animals. Frogs are also eaten by people.

Frogs and toads can live for many years; though little is known about their life span in the wild, captive frogs and toads are recorded living up to 40 years.

Frogs from temperate climates hibernate through the winter, and 4 species are known to freeze during this time, most notably *Rana sylvatica*.

Reproduction of frogs

Once adult frogs reach maturity, they will assemble at a water source such as a pond or stream to breed. Many frogs return to the bodies of water where they were born, often resulting in annual migrations involving thousands of frogs. In continental Europe, a large proportion of migrating frogs used to die on roads, before special fences and tunnels were built for them.



Male and female Common toad (*Bufo bufo*) in amplexus



A Male and Female common toad in amplexus. The black strands are eggs released into open water minutes after birth.

Once at the breeding ground, male frogs call to attract a mate, collectively becoming a chorus of frogs. The call is unique to the species, and will attract females of that species. Some species have satellite males who do not call, but intercept females that are approaching a calling male.

The male and female frogs then undergo amplexus. This involves the male mounting the female and gripping her (sometimes with special nuptial pads) tightly. Fertilization is external: the egg and sperm meet outside of the body. The female releases her eggs, which the male frog covers with a sperm solution. The eggs then swell and develop a protective coating. The eggs are typically brown or black, with a clear, gelatin-like covering.

Most temperate species of frogs reproduce between late autumn and early spring. In the UK, most common frog populations produce frogspawn in February, although there is wide variation in timing. Water temperatures at this time of year are relatively low, typically between four and 10 degrees Celsius. Reproducing in these conditions helps the developing tadpoles because dissolved oxygen concentrations in the water are highest at cold temperatures. More importantly, reproducing early in the season ensures that

appropriate food is available to the developing frogs at the right time.

Parental care



Colour plate from Ernst Haeckel's 1904 *Kunstformen der Natur*, depicting frog species that include two examples of parental care.

Although care of offspring is poorly understood in frogs, it is estimated that up to 20% of amphibian species may care for their young in one way or another, and there is a great diversity of parental behaviours. Some species of poison dart frog lay eggs on the forest floor and protect them, guarding the eggs from predation and keeping them moist. The frog will urinate on them if they become too dry. After hatching, a parent (the sex depends upon the species) will move them, on its back, to a water-holding bromeliad.

The parent then feeds them by laying unfertilized eggs in the bromeliad until the young have metamorphosed. Other frogs carry the eggs and tadpoles on their hind legs or back (e.g. the midwife toads, *Alytes spp.*). Some frogs even protect their offspring inside their own bodies. The male Australian Pouched Frog (*Assa darlingtoni*) has pouches along its side in which the tadpoles reside until metamorphosis. The female Gastric-brooding Frogs (genus *Rheobatrachus*) from Australia, now probably extinct, swallows its tadpoles, which then develop in the stomach. To do this, the Gastric-brooding Frog must stop secreting stomach acid and suppress peristalsis (contractions of the stomach). Darwin's Frog (*Rhinoderma darwini*) from Chile puts the tadpoles in its vocal sac for development. Some species of frog will leave a 'babysitter' to watch over the frogspawn until it hatches.

The evolution of parental care in frogs is driven primarily by the size of the water body in which they breed. There is an inverse relationship between the level of parental care in a frog species and the degree of parental care they exhibit—frogs that breed in smaller water bodies tend to have more complex parental care behaviors. Water body size shows this strong relationship with parental care because it encompasses several important variables that interact to select for parental care: predation, desiccation, competition, and resource limitation. Because predation of eggs and larvae is high in large water bodies, a number of frog species evolved terrestrial oviposition. Once eggs are deposited on land, the desiccating terrestrial environment demands uniparental care in the form of egg hydration to ensure egg survival. The subsequent need to transport hatched tadpoles to a water source requires an even more intense form of uniparental care. In small water bodies where predators are mostly absent, such as phytotelmata (water-filled leaf axils or small woody cavities), inter-tadpole competition becomes the variable that constrains tadpole survival. Certain frogs species avoid this competition by evolving the use of smaller phytotelmata as tadpole deposition sites. However, while these smaller tadpole rearing sites are free of competition, they also lack nutrients. Because they do not have sufficient nutrients to support a tadpole without parental provisioning behavior, frog species that transitioned from the use of larger to smaller phytotelmata have evolved trophic (unfertilized) egg laying. In this complex form of biparental care, the female provides her offspring with nutritive eggs. While each of these variables select for different behaviors, they correlate with the size of a species' tadpole-rearing site and influence the degree of parental care displayed by a species.

Call



A male *Dendropsophus microcephalus* displaying its vocal sac during its call

Some frog calls are so loud, they can be heard up to a mile away. The call of a frog is unique to its species. Frogs call by passing air through the larynx in the throat. In most calling frogs, the sound is amplified by one or more vocal sacs, membranes of skin under the throat or on the corner of the mouth that distend during the amplification of the call. The field of neuroethology studies the neurocircuitry that underlies frog audition.

Some frogs lack vocal sacs, such as those from the genera *Heleioporus* and *Neobatrachus*, but these species can still produce a loud call. Their buccal cavity is enlarged and dome-shaped, acting as a resonance chamber that amplifies their call. Species of frog without vocal sacs and that do not have a loud call tend to inhabit areas close to flowing water. The noise of flowing water overpowers any call, so they must communicate by other means.

The main reason for calling is to allow males to attract a mate. Males call either individually or in a group called a chorus. Females of many frog species, for example *Polypedates leucomystax*, produce calls reciprocal to the males', which act as the catalyst for the enhancement of reproductive activity in a breeding colony. A male frog emits a release call when mounted by another male. Tropical species also have a rain call that they make on the basis of humidity cues prior to a rain shower. Many species also have a territorial call that is used to chase away other males. All of these calls are emitted with the mouth of the frog closed.

A distress call, emitted by some frogs when they are in danger, is produced with the mouth open, resulting in a higher-pitched call. The effectiveness of the call is unknown; however, it is suspected the call intrigues the predator until another animal is attracted, distracting them enough for its escape.

Many species of frog have deep calls, or croaks. The English onomatopoeic spelling is "ribbit". The croak of the American bullfrog (*Rana catesbiana*) is sometimes spelt "jug o' rum". Other examples are Ancient Greek *brekekekex koax koax* for probably *Rana ridibunda*, and the description in Rigveda 7:103.6 *gómāyur éko ajámāyur ékaḥ* = "one has a voice like a cow's, one has a voice like a goat's".

Distribution and conservation status



The Red-eyed Tree Frog (*Litoria chloris*) is a species of tree frog native to eastern Australia.

The habitat of frogs extends almost worldwide, but they do not occur in Antarctica and are not present on many oceanic islands. The greatest diversity of frogs occurs in the tropical areas of the world, where water is readily available, suiting frogs' requirements due to their skin. Some frogs inhabit arid areas such as deserts, where water may not be easily accessible, and rely on specific adaptations to survive. The Australian genus *Cyclorana* and the American genus *Pternohyla* will bury themselves underground, create a water-impervious cocoon and hibernate during dry periods. Once it rains, they emerge, find a temporary pond and breed. Egg and tadpole development is very fast in comparison to most other frogs so that breeding is complete before the pond dries up. Some frog species are adapted to a cold environment; for instance the wood frog, whose habitat extends north of the Arctic Circle, buries itself in the ground during winter when much of its body freezes.



Golden toad (*Bufo periglenes*) – last seen in 1989

Frog populations have declined dramatically since the 1950s: more than one third of species are believed to be threatened with extinction and more than 120 species are suspected to be extinct since the 1980s. Among these species are the golden toad of Costa Rica and the Gastric-brooding frogs of Australia. Habitat loss is a significant cause of frog population decline, as are pollutants, climate change, the introduction of non-indigenous predators/competitors, and emerging infectious diseases including chytridiomycosis. Many environmental scientists believe that amphibians, including frogs, are excellent biological indicators of broader ecosystem health because of their intermediate position in food webs, permeable skins, and typically biphasic life (aquatic larvae and terrestrial adults). It appears that it is the species with both aquatic eggs and

aquatic larvae that are most affected by the decline, while those with direct development are the most resistant.

A Canadian study conducted in 2006, suggested heavy traffic near frog habitats as a large threat to frog populations. In a few cases, captive breeding programs have been attempted to alleviate the pressure on frog populations, and these have proved successful. In 2007, it was reported the application of certain probiotic bacteria could protect amphibians from chytridiomycosis. One current project, The Panama Amphibian Rescue and Conservation Project, has subsequently been developed in order to rescue species at risk of chytridiomycosis in eastern Panama, and to develop field applications of this probiotic cure.

Zoos and aquariums around the world named 2008 the Year of the Frog, to draw attention to the conservation issues.

Evolution



A fossilized frog from the Czech Republic, possibly *Palaeobatrachus gigas*

Until the discovery of the Early Permian *Gerobatrachus hottoni* in 2008, a stem-batrachian with many salamander-like characteristics, the earliest known proto-frog was *Triadobatrachus massinoti*, from the 250 million year old early Triassic of Madagascar. The skull is frog-like, being broad with large eye sockets, but the fossil has features diverging from modern amphibia. These include a different ilium, a longer body with more vertebrae, and separate vertebrae in its tail (whereas in modern frogs, the tail vertebrae are fused, and known as the *urostyle* or *coccyx*). The tibia and fibula bones are unfused and separate, making it probable *Triadobatrachus* was not an efficient leaper.

Another fossil frog, *Prosalirus bitis*, was discovered in 1995. The remains were recovered from Arizona's Kayenta Formation, which dates back to the Early Jurassic epoch, somewhat younger than *Triadobatrachus*. Like *Triadobatrachus*, *Prosalirus* did not have greatly enlarged legs, but had the typical three-pronged pelvic structure. Unlike *Triadobatrachus*, *Prosalirus* had already lost nearly all of its tail and was well adapted for jumping.

The earliest known "true frog" is *Vieraella herbsti*, from the early Jurassic (188–213 million years ago). It is known only from the dorsal and ventral impressions of a single animal and was estimated to be 33 mm (1.3 in) from snout to vent. *Notobatrachus degiustoi* from the middle Jurassic is slightly younger, about 155–170 million years old. It is likely the evolution of modern *Anura* was completed by the Jurassic period. The main evolutionary changes involved the shortening of the body and the loss of the tail.

The earliest full fossil record of a modern frog is of *Sanyanlichan*, which lived 125 million years ago and had all modern frog features, but bore 9 presacral vertebrae instead of the 8 of modern frogs.

Frog fossils have been found on all continents except Antarctica, but biogeographic evidence suggests they inhabited Antarctica when it was warmer.

Uses in agriculture and research

Frogs are raised commercially for several purposes. Frogs are used as a food source; frog legs are a delicacy in China, France, the Philippines, the north of Greece and in many parts of the American South, especially Louisiana. Dead frogs are sometimes used for dissections in high school and university anatomy classes, often after being injected with coloured plastics to enhance the contrast between the organs. This practice has declined in recent years with the increasing concerns about animal welfare.

Frogs have served as important model organisms throughout the history of science. Eighteenth-century biologist Luigi Galvani discovered the link between electricity and the nervous system through studying frogs. The African clawed frog or platanna (*Xenopus laevis*) was first widely used in laboratories in pregnancy assays in the first half of the 20th century. When human chorionic gonadotropin, a hormone found in substantial quantities in the urine of pregnant women, is injected into a female *X. laevis*, it induces them to lay eggs. In 1952, Robert Briggs and Thomas J. King cloned a frog by somatic

cell nuclear transfer, the same technique later used to create Dolly the Sheep, their experiment was the first time successful nuclear transplantation had been accomplished in metazoans.

Frogs are used in cloning research and other branches of embryology because frogs are among the closest living relatives of man to lack egg shells characteristic of most other vertebrates, and therefore facilitate observations of early development. Although alternative pregnancy assays have been developed, biologists continue to use *Xenopus* as a model organism in developmental biology because it is easy to raise in captivity and has a large and easily manipulatable embryo. Recently, *X. laevis* is increasingly being displaced by its smaller relative *X. tropicalis*, which reaches its reproductive age in five months rather than one to two years (as in *X. laevis*), facilitating faster studies across generations. The genome sequence of *X. tropicalis* will probably be completed by 2015 at the latest.

Chapter- 6

Toad and Salamander

Toad

Toads



A common toad, *Bufo bufo*

Scientific classification

Kingdom: Animalia
Phylum: Chordata
Class: Amphibia
Anura
Order: Merrem, 1820

List of Anuran families

A **toad** is any of a number of species of amphibians in the order Anura characterized by dry, leathery skin, brown coloration, and wart-like parotoid glands. A distinction between frogs and toads, though common in popular culture, is not made in taxonomy, where toads are spread across families Bufonidae, Bombinatoridae, Discoglossidae, Pelobatidae, Rhinophrynidae, Scaphiopodidae, and Microhylidae. The characteristic features of toads are a result of convergent evolution in dry habitats. A group of toads is called a "Knot."

Toads cannot transmit warts to people through handling or skin contact. The bumps on a toad's skin help the animal blend into its environment visually by breaking up its outline. Also, the paratoid gland is often mistaken as 'warts'. They are present on healthy specimens and are not a result of infection.

Salamander

Salamanders

Temporal range: Jurassic–present



Spotted Salamander, *Ambystoma maculatum*

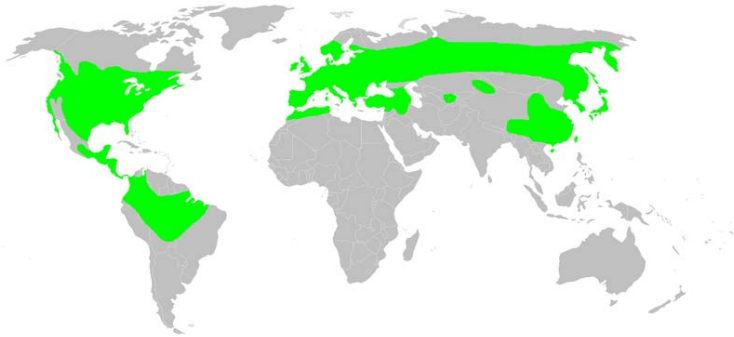
Scientific classification

Kingdom: Animalia
Phylum: Chordata

Class: Amphibia
Subclass: Lissamphibia
Order: **Caudata**
Scopoli, 1777

Suborders

Cryptobranchoidea
Salamandroidea
Sirenoidea



Native distribution of salamanders (in green)

Salamander is a common name of approximately 500 species of amphibians. They are typically characterized by their slender bodies, short noses, and long tails. All known fossils and extinct species fall under the order **Caudata**, while sometimes the extant species are grouped together as the **Urodela**. Most salamanders have four toes on their front legs and five on their rear legs. Their moist skin usually makes them reliant on habitats in or near water, or under some protection (e.g., moist ground), often in a wetland. Some salamander species are fully aquatic throughout life, some take to the water intermittently, and some are entirely terrestrial as adults. Unique among vertebrates, they are capable of regenerating lost limbs, as well as other body parts.

Characteristics

Mature salamanders generally have a primitive tetrapod body form similar to that of lizards, with slender bodies, long tails, and four limbs. However, like some lizards, many species of salamander have reduced or absent limbs, giving them a more eel-like appearance. Most species have limbs with four toes on the forelimbs, and five on the hind limbs, and lack claws. Salamanders are often brightly colored, either in both sexes throughout the year, or only in the males, especially during the breeding season. However, the species dwelling entirely underground are often white or pink, lacking any skin pigment.

Many salamanders are relatively small, but there are definite exceptions. They range in size from the minute salamanders, with a total length of 2.7 centimetres (1.1 in), including the tail, to the Chinese giant salamander which reaches 1.8 metres (5.9 ft) and weighs up to 65 kg (140 lb). Most, however, are between 10 centimetres (3.9 in) and

20 centimetres (7.9 in) in length. Salamanders regularly shed the outer layer of their skin (the epidermis) as they grow, and then eat the resulting slough.



A fire salamander in Mount Olympus National Park, Greece

Respiration differs among the different species of salamanders. Species that lack lungs respire through gills. In most cases, these are external gills, visible as tufts on either side of the head, although the amphiumas have internal gills and gill slits. Some salamanders that are terrestrial have lungs that are used in respiration, although these are simple and sac-like, unlike the more complex organs found in mammals. Many species, such as the olm, have both lungs and gills as adults.

Some terrestrial species lack both lungs and gills and perform gas exchange through their skin, a process known as cutaneous respiration in which the capillary beds are spread throughout the epidermis, and inside the mouth. Even some species with lungs can respire through the skin in this manner.

The skin of salamanders secretes mucus, which helps keep the animal moist when on dry land, and maintains their salt balance while in water, as well as providing a lubricant during swimming. Salamanders also secrete poison from glands in their skin, and some additionally have skin glands for secreting courtship pheromones.

Hunting is yet another unique aspect of salamanders. In the lungless salamanders, muscles surrounding the hyoid bone contract to create pressure and actually "shoot" the hyoid bone out of the mouth along with the tongue. The tip of the tongue is composed of a mucus which creates a sticky end to which the prey is captured. Muscles in the pelvic region are used in order to reel the tongue and the hyoid back to its original position.

Many of the highly aquatic species, however, have no muscles in the tongue, and do not use it for capturing prey, while most other species have a mobile tongue, but without the adaptations to the hyoid bone. Most species of salamander have small teeth in both the upper and lower jaws. Unlike frogs, even the larvae of salamanders possess these teeth.

To find their prey, salamanders use trichromatic color vision in the ultraviolet range based on two photoreceptor types maximally sensitive around 450 nm, 500 nm and 570 nm. Permanently subterranean salamanders have reduced eyes, which may even be covered by a layer of skin. The larvae, and the adults of some highly aquatic species, also have a lateral line organ, similar to that of fish, which can detect changes in water pressure. Salamanders have no external ear, and only a vestigial middle ear.

Salamanders will use tail autotomy to escape predators. Their tail will drop off and wriggle around for a little while, and the salamanders will either run away or stay still enough to not be noticed while the predator is distracted. Salamanders routinely regenerate complex tissues. Within only a few weeks of losing a piece of limb, a salamander perfectly reforms the missing structure.

Distribution

Salamanders split off from the other amphibians during the Mid to Late Permian, and initially were similar to modern members of the Cryptobranchoidea. Their resemblance to lizards is the result of symplesiomorphy, their common retention of the primitive tetrapod body plan, and they are no more closely related to lizards than they are to mammals – or to birds for that matter. Their nearest relatives are the frogs and toads, within Batrachia.

Caudates are found on all continents except for Australia, Antarctica, and most of Africa. One-third of the known salamander species are found in North America. The highest concentration of these is found in the Appalachian Mountains region. Species of salamander are numerous and found in most moist or arid habitats in the northern hemisphere. They usually live in or near brooks, creeks, ponds, and other moist locations.

Development

The life history of salamanders is similar to that of other amphibians such as frogs and toads. Most species fertilize the eggs internally, with the male depositing a sac of sperm in the female's cloaca. The most primitive salamanders – those grouped together as the Cryptobranchoidea – instead exhibit external fertilisation. The eggs are laid in a moist environment, often a pond, but sometimes moist soil, or inside bromeliads. Some species are ovoviviparous, with the female retaining the eggs inside her body until they hatch.

A larval stage follows in which the organism is fully aquatic or land dwelling, and possesses gills. Depending on species, the larval stage may or may not possess legs. The larval stage may last anything from days to years, depending on the species. Some species (such as Dunn's Salamander) exhibit no larval stage at all, with the young hatching as miniature versions of the adult.




Neoteny has been observed in all salamander families, in which an individual may retain gills into sexual maturity. This may be universally possible in all salamander species. More commonly, however, metamorphosis continues with the loss of gills, the growth (or increase in size) of legs, and the capability of the animal to function terrestrially.

Declining populations

A general decline in living amphibian species, caused by the fungal disease chytridiomycosis, has had a significant effect on the salamander as well. While researchers have not yet found a direct link between the fungus and the population decline, they do believe it has played a role. Researchers also cite deforestation and climate change as possible contributing factors. This is based on surveys conducted in Guatemala during the 1970s as well as recently. Especially affected were *Pseudoeurycea brunnata* and *Pseudoeurycea goebeli*, both of which were abundant during the 1970s.

Taxonomy

There are ten families belonging to the order Caudata, divided into three suborders. The clade Neocaudata is often used to separate Cryptobranchoidea and Salamandroidea from the Sirenoidea.

| Cryptobranchoidea
(Giant salamanders) | | | |
|--|---------------------|---|---|
| Family | Common Names | Example Species | Example Photo |
| Cryptobranchidae | Giant salamanders | Hellbender
(<i>Cryptobranchus alleganiensis</i>) |  |
| Hynobiidae | Asiatic salamanders | Hida Salamander
(<i>Hynobius kimurae</i>) |  |
| Salamandroidea
(Advanced salamanders) | | | |
| Ambystomatidae | Mole salamanders | Marbled Salamander
(<i>Ambystoma opacum</i>) |  |

Amphiumidae Amphiumas or Congo eels Two-toed Amphiuma (*Amphiuma means*)



Dicamptodontidae Pacific giant salamanders Pacific Giant Salamander (*Dicamptodon tenebrosus*)



Plethodontidae Lungless salamanders Red Back Salamander (*Plethodon cinereus*)



Proteidae Mudpuppies and olms olm (*Proteus anguinus*)



Rhyacotritonidae Torrent salamanders Southern Torrent Salamander (*Rhyacotriton variegatus*)



Salamandridae Newts and true salamanders Alpine Newt (*Triturus alpestris*)



Sirenoidea (Sirens)

Sirenidae Sirens Greater Siren (*Siren lacertina*)



Implications of limb regeneration as applied to humans

Salamanders' limb regeneration has been the focus of significant interest among scientists. A theory persists in the scientific community that such regeneration could be artificially recreated in humans using stem cells. Axolotls have been highlighted for research.

Chapter- 7

Newt

Newts



Smooth newt (*Lissotriton vulgaris*)

Scientific classification

| | |
|-------------|----------------------|
| Kingdom: | Animalia |
| Phylum: | Chordata |
| Subphylum: | Vertebrata |
| Superclass: | Tetrapoda |
| Class: | Amphibia |
| Subclass: | Lissamphibia |
| Order: | Caudata |
| Family: | Salamandridae |
| Subfamily: | Pleurodelinae |

A **newt** is an amphibian of the Salamandridae family, although not all aquatic salamanders are considered newts. Newts are classified in the subfamily **Pleurodelinae** of the family Salamandridae, and are found in North America, Europe and Asia. Newts metamorphose through three distinct developmental life stages: aquatic larva, terrestrial

juvenile (called an **eft**), and adult. Adult newts have lizard-like bodies and may be either fully aquatic, living permanently in the water, or semi-aquatic, living terrestrially but returning to the water each year to breed.

Characteristics



A red-spotted newt (eft stage) showing bright aposematic colouration to warn predators of its highly toxic skin.

Like all members of the order Caudata, newts are characterised by a frog-like body with four equal sized limbs and a distinct tail. Aquatic larvae have true teeth on both upper and lower jaws, and external gills. They have the ability to regenerate limbs, eyes, spinal cords, hearts, intestines, and upper and lower jaws. The cells at the site of the injury have the ability to de-differentiate, reproduce rapidly, and differentiate again to create a new limb or organ. One theory is that the de-differentiated cells are related to tumour cells since chemicals which produce tumours in other animals will produce additional limbs in newts.

Development



Newt larva (species not identified) part-way through metamorphosis.

The main breeding season for newts is between the months of June and July. After courtship rituals of varying complexity, which take place in ponds or slow moving streams, the male newt transfers a spermatophore which is taken up by the female. Fertilised eggs are laid singly and are usually attached to aquatic plants. This distinguishes them from the free-floating eggs of frogs or toads, that are laid in clumps or in strings. Plant leaves are usually folded over and adhered to the eggs to protect them. The tadpoles, which resemble fish fry but are distinguished by their feathery external gills, hatch out in about three weeks. After hatching they eat algae, small invertebrates or other tadpoles.

During the next few months the tadpoles undergo metamorphosis, during which they develop legs, and the gills are absorbed and replaced by air-breathing lungs. Some species, such as the North American newts, also become more brightly coloured during this phase. Once fully metamorphosed they leave the water and live a terrestrial life, when they are known as "efts". Only when the eft reaches adulthood will the North American species return to live in water, rarely venturing back onto the land. Conversely, most European species live their adult lives on land and only visit water to breed.

Toxicity

Many newts produce toxins in their skin secretions as a defense mechanism against predators. *Taricha* newts of western North America are particularly toxic. The Rough-skinned newt *Taricha granulosa* of the Pacific Northwest produces more than enough tetrodotoxin to kill an adult human, and some Native Americans of the Pacific Northwest used the toxin to poison their enemies. More recently, a 29-year-old man in Coos Bay, Oregon, who had been drinking heavily, swallowed a rough-skin newt for a dare; he died later that day despite hospital treatment.

Most newts can be safely handled, provided that the toxins they produce are not ingested or allowed to come in contact with mucous membranes, or breaks in the skin. After

handling, proper hand-washing techniques should be followed due to the risk from the toxins they produce and bacteria they carry, such as salmonella. It is, however, illegal to handle or disturb Great Crested Newts in the UK without a licence.

Systematics

About two thirds of all species of the family Salamandridae are commonly called "newts", comprising the following genera:

- *Calotriton*, Spanish brook newts
- *Cynops*, firebelly newts
- *Echinotriton*, spiny newts
- *Lissotriton*, small bodied newts
- *Mesotriton*, Alpine newts
- *Neurergus*, spotted newts
- *Notophthalmus*, Eastern newts
- *Ommatotriton*, banded newts
- *Pachytriton*, paddle-tail newts
- *Paramesotriton*, warty newts
- *Pleurodeles*, ribbed newts
- *Taricha*, Pacific newts
- *Triturus*, crested newts
- *Tylototriton*, crocodile newts

The term "newt" has traditionally been seen as an exclusively functional term for salamanders living in water, and not a systematic unit. The relationship between the genera has been uncertain, although it has been suggested that they constitute a natural systematic unit and newer molecular analyses tend to support this position. Newts only appear in one subfamily of salamanders, the Pleurodelinae (of the family Salamandridae), however, *Salamandrina* and *Euproctus*, which are sometimes listed as Pleurodelinae, are not newts. Whether these are basal to the subfamily (and thus the sister group of the newt group) or derived, making the newts an evolutionary grade (an "incomplete" systematic unit, where not all branches of the family tree belong to the group) is currently not known.

Distribution

The three common European genera are the crested newts (*Triturus* spp.), the smooth and palmate newts (*Lissotriton* spp.) and the banded Newts (*Ommatotriton* spp.). Other species present in Europe are the Iberian ribbed newt (*Pleurodeles waltl*), which is the largest of the European newts, the pyrenean brook newt (*Calotriton* sp.); the European brook newt (*Euproctus* sp.) and the Alpine newt (*Mesotriton alpestris*).

In North America, there are the Eastern newts (*Notophthalmus* spp.), of which the red-spotted newt (*Notophthalmus viridescens*) is the most abundant species, but it is limited to the area east of the Rocky Mountains. The three species of coastal or Western newts

are the red-bellied newt, the California newt, and the rough-skinned newt, all of which belong to the genus *Taricha*, which is confined to the area west of the Rockies.

In Southeast Asia and Japan, species commonly encountered in the pet trade include the fire belly newts (*Cynops* spp.), the paddletail newts (*Pachytriton* spp.), the crocodile newts (*Tylototriton* spp.), and the warty newts (*Paramesotriton* spp.). In the Middle East there are the spotted newts (*Neurergus* spp.).

Conservation status

Newt populations have fallen across the world because of pollution or destruction of their breeding sites and terrestrial habitats, and countries such as the USA and the UK have taken steps to halt their decline. In the UK, they are protected under the Wildlife and Countryside Act 1981 and the *Habitat Regulations Act 1994*. It is illegal to catch, possess or handle Great Crested Newts without a licence, and it is also illegal to cause them harm or death, or to disturb their habitat in any way. The IUCN Red List categorises the species as 'lower risk' Although the other UK species, the smooth newt and palmate newt are not listed, the sale of either species is prohibited under the Wildlife and Countryside Act, 1981.

In Europe, nine newts are listed as "strictly protected fauna species" under appendix II of the Convention on the Conservation of European Wildlife and Natural Habitats:

- *Euproctus asper*
- *Euproctus montanus*
- *Euproctus platycephalus*
- *Triturus carnifex*
- *Triturus cristatus*
- *Triturus dobrogicus*
- *Triturus italicus*
- *Triturus karelinii*
- *Triturus montandoni*

The remaining European species are listed as "protected fauna species" under appendix III.

Etymology

The etymology for this term has gone through a complex twist of old Middle English variations. The oldest form of the name is *eft*, which is still used for newly metamorphosed specimens, but according to the *Oxford English Dictionary* it changed for unknown reasons first to *euft* and then to *ewt*. For some time it remained as *an ewt*, but the "n" from the indefinite article *an* shifted to form *a newt*. The sexually mature stage was also called an *ewte*, with similar etymology roots linking an *ewte*, *newt*, "euft", and *eft*: "small lizard-like animal".

Chapter- 8

Caecilian

Caecilians
Temporal range: 170–0 Ma
Lower Jurassic – Recent



Dermophis mexicanus

Scientific classification

| | |
|----------|------------------------------------|
| Kingdom: | Animalia |
| Phylum: | Chordata |
| Class: | Amphibia |
| Order: | Gymnophiona
Müller, 1832 |

Families

Rhinatreumatidae
Ichthyophiidae
Uraeotyphlidae
Scolecomorphidae
Typhlonectidae
Caeciliidae



Distribution of caecilians (in green)

The **caecilians** are an order (**Gymnophiona**) of amphibians that superficially resemble earthworms or snakes. They mostly live hidden in the ground, which makes them one of the least known orders of amphibians. All extant caecilians and their closest fossil relatives are grouped as the clade Apoda.

Description

Caecilians completely lack limbs, making the smaller species resemble worms, while the larger species with lengths up to 1.5 m (4 ft 11 in) resemble snakes. The tail is short or absent, and the cloaca is near the end of the body.

Their skin is smooth and usually dark-matte, but some species have colorful skins. Inside the skin are calcite scales. Because of these scales, the caecilians were once thought to be related to the fossil Stegocephalia, but they are now believed to be a secondary development, and the two groups are most likely unrelated. The skin also has numerous ring-shaped folds, or annuli, that partially encircle the body, giving them a segmented appearance. Like other living amphibians, the skin contains glands that secrete a toxin to deter predators. The skin secretions of *Siphonops paulensis* have been shown to have hemolytic properties.

Caecilians' vision is limited to dark-light perception, and their anatomy is highly adapted for a burrowing lifestyle. They have a strong skull, with a pointed snout used to force their way through soil or mud. In most species, the number of bones in the skull are reduced and fused together, and the mouth is recessed under the head. Their muscles are adapted to pushing their way through the ground, with the skeleton and deep muscles acting as a piston inside the skin and outer muscles. This allows the animal to anchor its hind end in position, and force the head forwards, and then pull the rest of the body up to reach it in waves. In water or very loose mud, caecilians instead swim in an eel-like fashion. Caecilians in the family Typhlonectidae are aquatic as well as being the largest of their kind. The representatives of this family have a fleshy fin running along the rear section of their body, which enhances propulsion in water.

All but the most primitive caecilians have two sets of muscles for closing the jaw, compared with the single pair found in other creatures. These are more highly developed

in the most efficient burrowers among the caecilians, and appear to help keep the skull and jaw rigid.

Adapting to their underground life, the eyes are small and covered by skin for protection, which has led to the misconception that they are blind. This is not strictly true, although their sight is limited to simple dark-light perception. All caecilians possess a pair of tentacles, located between their eyes and nostrils. These are probably used for a second olfactory capability, in addition to the normal sense of smell based in the nose.

Except for two lungless species — *Atretochoana eiselti* and *Caecilita iwokrama* — all caecilians have lungs, but also use the skin or the mouth for oxygen absorption. Often the left lung is much smaller than the right one, an adaptation to body shape that is also found in snakes.

Distribution

Caecilians are found in wet tropical regions of Southeast Asia, India and Sri Lanka, parts of East and West Africa, the Seychelles islands in the Indian Ocean and in northern and eastern South America. In Africa caecilians are found from Guinea-Bissau (*Geotrypetes*) to Southern Malawi (*Scolecormorphus*), with an unconfirmed record from eastern Zimbabwe. They have not been recorded from the extensive areas of tropical forest in central Africa. In South America they extend through subtropical eastern Brazil well into temperate northern Argentina. They can be seen as far south as Buenos Aires, when they are carried by the flood waters of the Parana River coming from farther north. The northernmost distribution is of the species *Ichthyophis sikkimensis* of Northern India. *Ichthyophis* is also found in South China and North Vietnam. In Southeast Asia, they do not cross Wallace's Line, and they are not found in Australia or the islands in between.

Reproduction

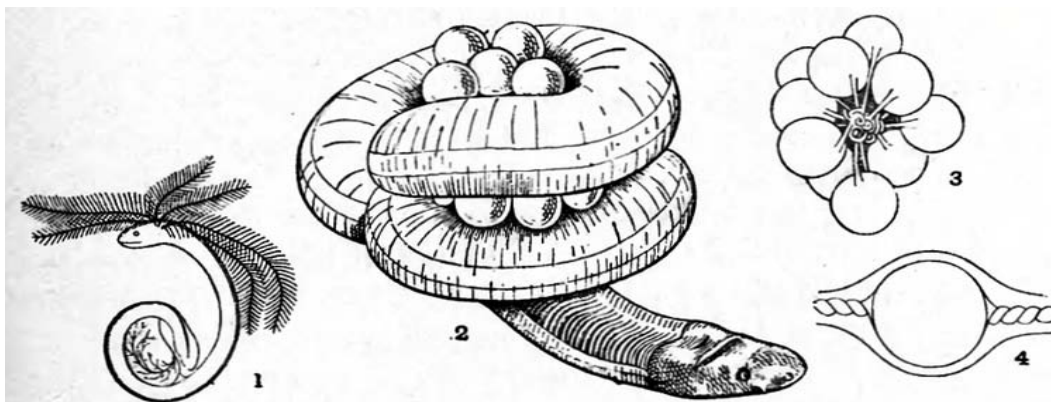


FIG. 15.—*Ichthyophis glutinosa* × 1. (After P. and F. Sarasin.) 1, A nearly ripe embryo, with gills, tail-fin, and still with a considerable amount of yolk ; 2, female guarding her eggs, coiled up in a hole underground ; 3, a bunch of newly laid eggs ; 4, a single egg, enlarged, schematised to show the twisted albuminous strings or chalazae within the outer membrane, which surrounds the white of the egg.

Maternal care in *Ichthyophis*

Caecilians are the only order of amphibians that use internal insemination exclusively (although the tailed frog in the U.S. does use a tail-like appendage for internal insemination in its fast flowing water environment). The male caecilians have a penis-like organ, the phallodeum, which is inserted into the cloaca of the female for 2 to 3 hours. About 25% of the species are oviparous (egg-laying); the eggs are guarded by the female. For some species the young caecilians are already metamorphosed when they hatch; others hatch as larvae. The larvae are not fully aquatic, but spend the daytime in the soil near the water.

75% of the species are viviparous, meaning that they give birth to already developed offspring. The fetus is fed inside the female with cells of the oviduct, which they eat with special scraping teeth.

The egg laying species *Boulengerula taitanus* feeds its young by developing an outer layer of skin, high in fat and other nutrients, which the young peel off with similar teeth. This allows them to grow by up to ten times their own weight in a week. The skin is consumed every three days, the time it takes for a new layer to grow, and the young have only been observed to eat it at night. It was formerly thought that the juveniles subsisted only on a liquid secretion from their mother.

Some larvae, such as those of *Typhlonectes*, are born with enormous external gills which are shed almost immediately. *Ichthyophis* is oviparous and known to show maternal care, with the mother guarding the eggs until they hatch.

Diet

The diet of caecilians is not well-known. Mature caecilians seem to feed mostly on insects and other invertebrates found in the habitat of the respective species. The stomach contents of 14 specimens of *Afrocaecilia taitana* consisted of mostly undefinable organic material and plant remains. Where identifiable remains were most abundant, they were found to be termite heads. While it was suggested that the undefinable organic material shows that the caecilians eat detritus, others believe these are in fact the remains of earthworms. Caecilians in captivity can be easily fed with earthworms, and worms are also common in the habitat of many caecilian species.

Etymology

The name *caecilian* derives from the Latin word *caecus*, meaning "blind", referring to the small or sometimes non-existent eyes. The name dates back to the taxonomic name of the first species described by Carolus Linnaeus, which he gave the name *Caecilia tentaculata*. The taxonomic name of the order derives from the Greek words γυμνος (*gymnos*, naked) and οφίς (*ophis*, snake), as the caecilians were originally thought to be related to snakes.

Taxonomy

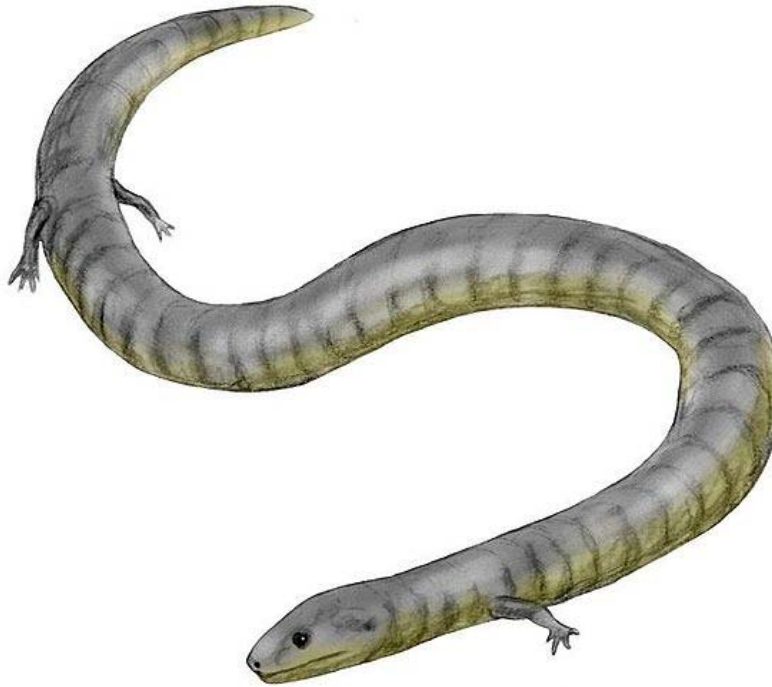


Caecilian from the San Antonio Zoo

Until recently caecilians were divided into 6 families. In 2006 Daryl Frost of the American Museum of Natural History, along with 18 co-authors from around the world, published a major revision of amphibian classification. Based on parsimony analysis of DNA sequence data, Frost and co-authors found that some named groups of caecilians were nested within other such groups and should be subsumed into these, resulting in the current concept of three scientific families of caecilians. Although the taxonomic changes suggested in this work are somewhat controversial this controversy does not involve the changes to caecilian classification, which largely corroborated results from previous studies. Many described species are identified on the basis of a single specimen. It is almost certain that not all species have been described yet and also that some currently accepted species may be lumped together in future reclassifications.

- Beaked Caecilians (Rhinatreumatidae) - 2 genera, 9 species, South America
- Fish Caecilians (Ichthyophiidae) - 3 genera, 44 species, Indo-Burma and Sundaland (including species formerly placed in Uraeotyphlidae)
- Common Caecilians (Caeciliidae) - 33 genera, 118 species, Africa, South America, Indo-Burma and Seychelles (including species formerly placed in Scolecomorphidae and Typhlonectidae)

Evolution

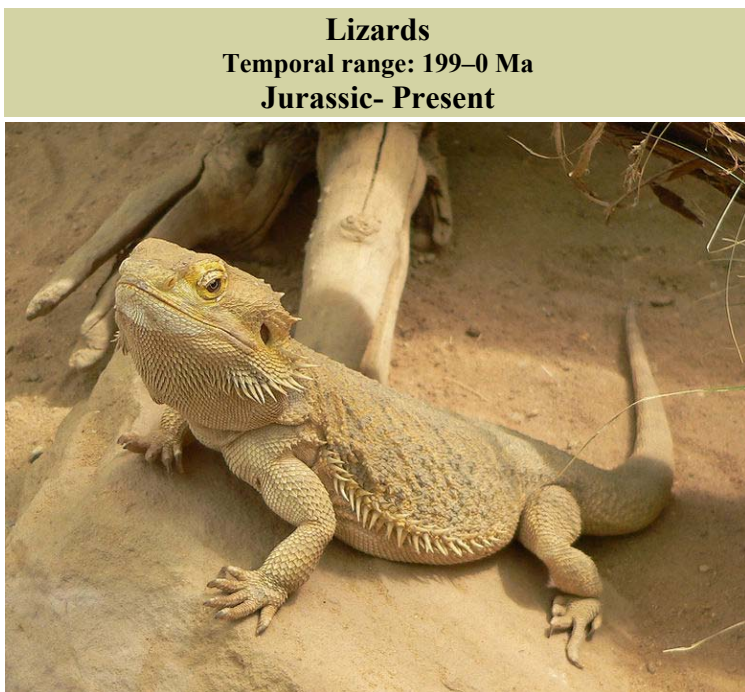


Eocaecilia, the earliest known caecilian

Little is known of the evolutionary history of the caecilians, which have left a sparse fossil record. The first fossil, a vertebra dated to the Paleocene, wasn't discovered until 1972. The earliest fossil known comes from the Jurassic period; its primitive genus, *Eocaecilia*, had small limbs and well-developed eyes. In their 2008 description of the fossil batrachian *Gerobatrachus* in 2008 Anderson and co-authors suggested that caecilians arose from the Lepospondyl group of ancestral tetrapods, and may be more closely related to amniotes than to frogs and salamanders, which arose from Temnospondyl ancestors. Divergent origins of caecilians and other living amphibians may help explain the discrepancy between fossil dates for the origins of modern amphibia, which suggest Permian origins, and the much earlier dates, in the Carboniferous, predicted by molecular clock studies of DNA sequences. Most morphological and molecular studies of living amphibians, however, support monophyly for caecilians, frogs and salamanders.

Chapter- 9

Lizard



Central bearded dragon, *Pogona vitticeps*

Scientific classification

| | |
|-------------|-------------------------------------|
| Kingdom: | Animalia |
| Phylum: | Chordata |
| Superclass: | Tetrapoda |
| Class: | Reptilia |
| Order: | Squamata |
| Suborder: | Lacertilia*
Günther, 1867 |

Lizards are a widespread group of squamate reptiles, with nearly 3800 species, ranging across all continents except Antarctica as well as most oceanic island chains. The group,

traditionally recognized as the suborder **Lacertilia**, is defined as all extant members of the Lepidosauria (reptiles with overlapping scales), which are neither sphenodonts (i.e., *tuatara*) nor snakes. While the snakes are recognized as falling phylogenetically within the anguimorph lizards from which they evolved, the sphenodonts are the sister group to the squamates, the larger monophyletic group, which includes both the lizards and the snakes.

Lizards typically have limbs and external ears, while snakes lack both these characteristics. However, because they are defined negatively as excluding snakes, lizards have no unique distinguishing characteristic as a group. Lizards and snakes share a movable quadrate bone, distinguishing them from the sphenodonts, which have a more primitive and solid diapsid skull. Many lizards can detach their tails to escape from predators, an act called autotomy, but this ability is not shared by all lizards. Vision, including color vision, is particularly well developed in most lizards, and most communicate with body language or bright colors on their bodies as well as with pheromones.

The adult length of species within the suborder ranges from a few centimetres for some chameleons and geckos to nearly three metres (9 feet, 6 inches) in the case of the largest living varanid lizard, the Komodo Dragon. Some extinct varanids reached great size. The extinct aquatic mosasaurs reached 17 metres, and the giant monitor *Megalania prisca* is estimated to have reached perhaps seven metres.

Physiology

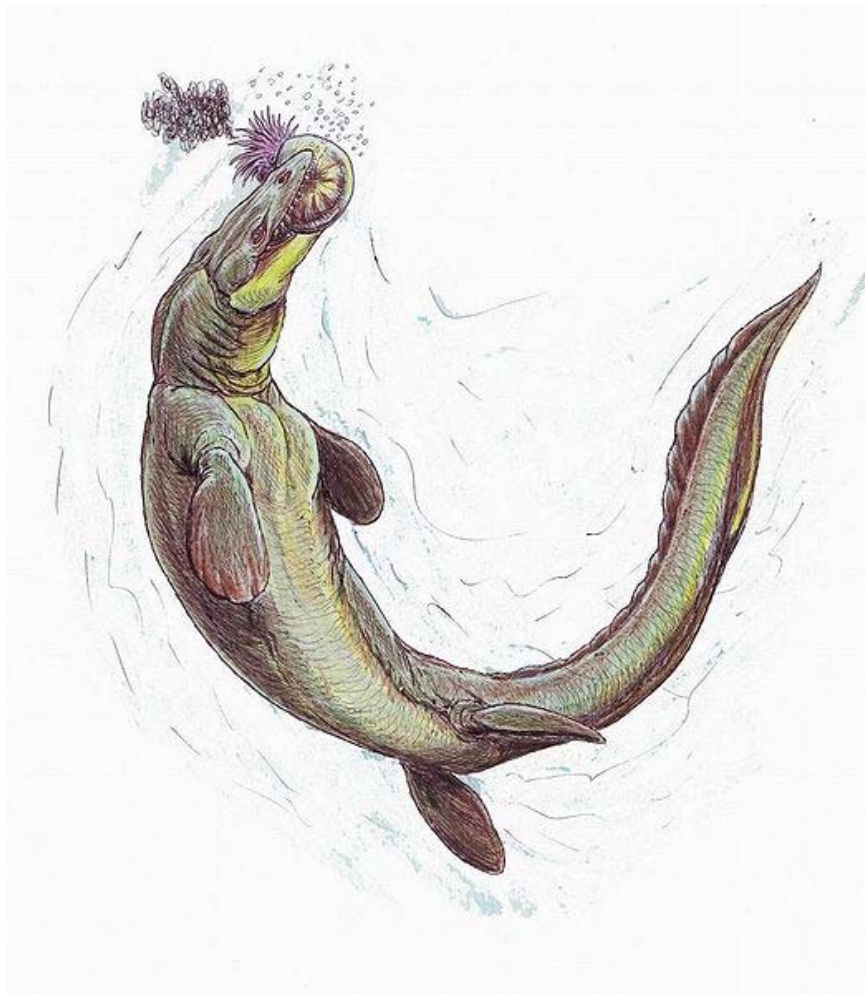


Feral Jackson's Chameleon from a population introduced to Hawaii in the 1970s

Sight is very important for most lizards, both for locating prey and for communication, and, as such, many lizards have highly acute color vision. Most lizards rely heavily on body language, using specific postures, gestures, and movements to define territory, resolve disputes, and entice mates. Some species of lizard also utilize bright colors, such as the iridescent patches on the belly of *Sceloporus*. These colors would be highly visible to predators, so are often hidden on the underside or between scales and only revealed when necessary.

The particular innovation in this respect is the dewlap, a brightly colored patch of skin on the throat, usually hidden between scales. When a display is needed, the lizards erect the hyoid bone of their throat, resulting in a large vertical flap of brightly colored skin beneath the head which can be then used for communication. Anoles are particularly famous for this display, with each species having specific colors, including patterns only visible under ultraviolet (UV) light, as lizards can often see UV.

Evolution and relationships



Fossil mosasaur *Prognathodon*, a varanoid

The retention of the basic 'reptilian' amniote body form by lizards makes it tempting to assume any similar animal, alive or extinct, is also a lizard. However, this is not the case, and lizards as squamates are part of a well-defined group.

The earliest amniotes were superficially lizard-like, but had solid, box-like skulls, with openings only for eyes, nostrils, termed the anapsid condition. Turtles retain this skull form. Early anapsids later gave rise to two new groups with additional holes in the skull to make room for and anchor larger jaw muscles. The Synapsids, with a single fenestra, gave rise to the superficially lizard-like Pelycosaurs, which include *Dimetrodon* and the Therapsids, including the Cynodonts, from which the modern mammals would evolve.

The Diapsids, possessing one temporal fenestra before the eye and one behind it, continued to diversify. One branch, the Archosaurs, retained the basic Diapsid skull, and gave rise to a bewildering array of animals, most famous being the crocodylians, the pterosaurs, the dinosaurs and their descendants, birds. The Ichthyosaurs and Plesiosaurs radiated from the same basal Diapsid group.

The smaller Lepidosaur branch, which would give rise to the lizards, began to reduce the skull bones, making the skull lighter and more flexible. The modern *Tuatara* retains the basic Lepidosaur skull, distinguishing it from true lizards in spite of superficial similarities. Squamates, including snakes and all true lizards, further lightened the skull by eliminating the lower margin of the lower skull opening.

Although squamate fossils first appear in the early Jurassic, mitochondrial phylogenetics suggests that they evolved in the late Permian. Most evolutionary relationships within the squamates are not yet completely worked out, with the relationship of snakes to other groups being most problematic. From morphological data, Iguanid lizards have been thought to have diverged from other squamates very early, but recent molecular phylogenies, both from mitochondrial and nuclear DNA, do not support this early divergence. Because snakes have a faster molecular clock than other squamates, and there are few early snake and snake ancestor fossils, it is difficult to resolve the relationship between snakes and other squamate groups.

Lizard diversification

Within the **Lacertilia** are found four generally recognized suborders, Iguania, Gekkota, Amphisbaenia and Autarchoglossa, with the "blind skinks" in the family Dibamidae having an uncertain position. While traditionally excluded from the lizards, the snakes are usually classified as a clade with a similar subordinal rank.

Iguania



Anoles mating, Gainesville, FL

The suborder Iguania, found in Africa, south Asia, Australia, the New World, and with iguanas colonizing the islands of the west Pacific, form the sister group to the remainder of the squamata. They are largely arboreal, and have primitively fleshy, non-prehensile tongues, some even have scales, but this condition is obviously highly modified in the chameleons. This clade includes the following families:

- Family Agamidae – Agamid Lizards, Old World Arboreal Lizards
- Family Chamaeleonidae – Chameleons
- Family Corytophanidae – Helmet Lizards
- Family Crotaphytidae – Collared Lizards, Leopard Lizards
- Family Hoplocercidae – Dwarf and Spiny Tail Iguanas
- Family Iguanidae – American Arboreal Lizards, Chuckwallas, Iguanas, Iguanids
- Family Opluridae – Malagasy Iguanas

- Family Phrynosomatidae – North American Spiny Lizards
- Family Polychrotidae – Anoles and kin
- Family Tropicuridae – Tropicurid Lizards

Gekkota

Active hunters, the Gekkota includes three families comprising the distinctive cosmopolitan geckos and the legless flap-footed lizards of Australia and New Zealand. Like snakes, the flap-footed lizards and most geckos lack eyelids. Unlike snakes, they use their tongues to clean their often highly developed eyes. While gecko feet have unique surfaces that allow them to cling to glass and run on ceilings, the flapfoot has lost its limbs. The three families of this suborder are:

- Family Eublepharidae – 'Eyelid' Geckos
- Family Gekkonidae – Geckos
- Family Pygopodidae – Flap-footed Lizards

Relationship with humans



Komodo dragons on Rinca



Green iguanas (*Iguana iguana*), are popular exotic pets

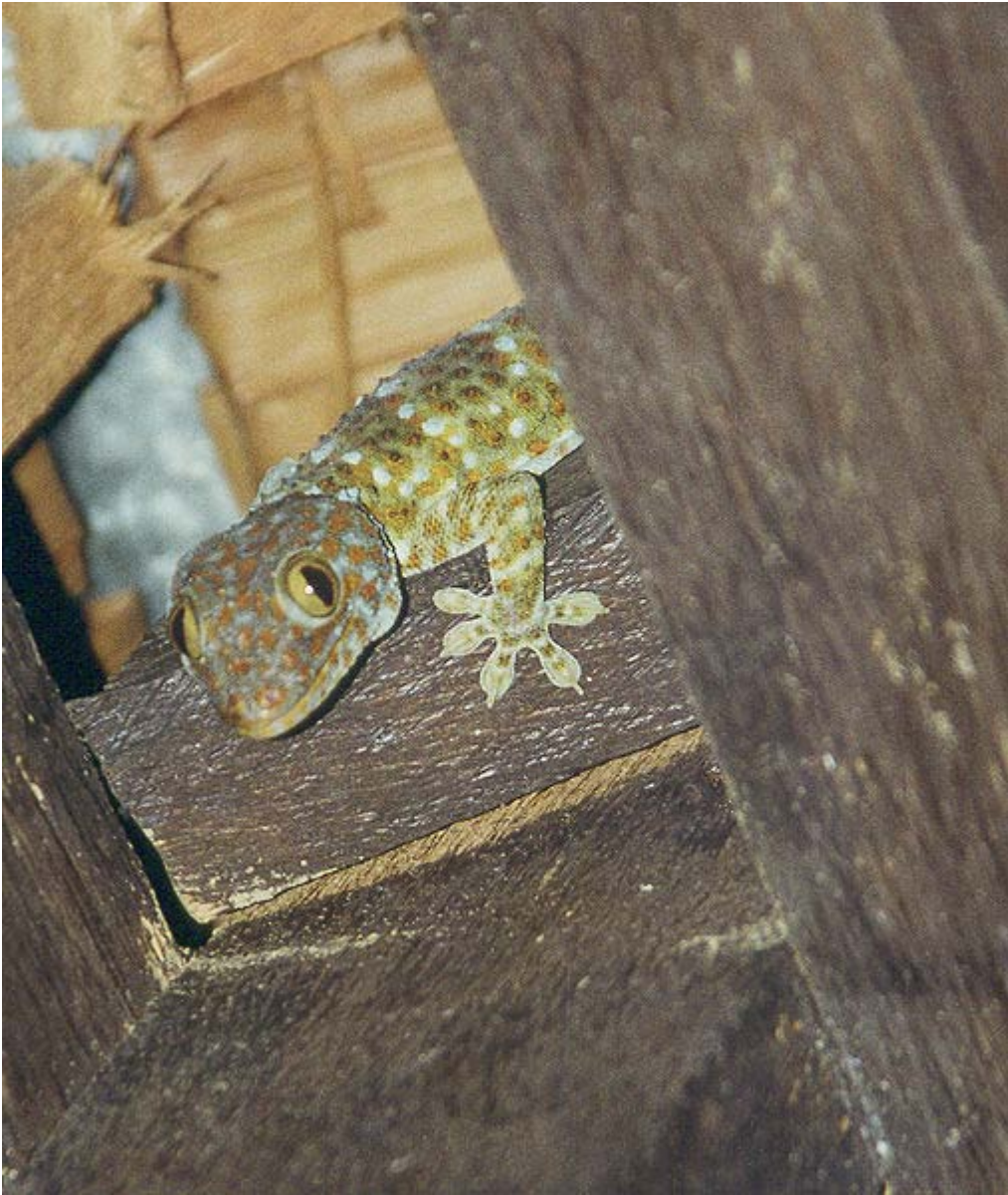
Most lizard species are harmless to humans. Only the very largest lizard species pose threat of death; the Komodo dragon, for example, has been known to stalk, attack, and, on occasion, kill humans. An eight-year-old Indonesian boy died from blood loss after an attack in 2007. The venom of the Gila monster and beaded lizard is not usually deadly but they can inflict extremely painful bites due to powerful jaws.

Numerous species of lizard are kept as pets.

Lizard symbolism plays important though rarely predominant roles in some cultures (e.g., Tarrotarro in Australian Aboriginal mythology). The Moche people of ancient Peru worshiped animals and often depicted lizards in their art. According to a popular legend in Maharashtra, a Common Indian Monitor, with ropes attached, was used to scale the walls of the Sinhagad fort in the Battle of Sinhagad.

Green Iguanas are eaten in Central America and Uromastyx in Africa. In North Africa, Uromastyx are considered *dhaab* or 'fish of the desert' and eaten by nomadic tribes.

Classification



Gekko gecko in Thailand



Underside of a Thorny devil, an agamid, Western Australia



Close-up of the head of the legless fossorial amphisbaenid *Rhineura*



The Eastern blue-tongued lizard, a scincomorph



The venomous Gila monster, *Heloderma s. suspectum*



Burton's legless lizard, a pygopodid lizard found in Australia and New Guinea

Suborder Lacertilia (Sauria) - (Lizards)

- Family †Bavarisauridae
- Family †Eichstaettisauridae
- Infraorder Iguania
 - Family †Arretosauridae
 - Family †Euposauridae
 - Family Corytophanidae (casquehead lizards)
 - Family Iguanidae (iguanas and spinytail iguanas)
 - Family Phrynosomatidae (earless, spiny, tree, side-blotched and horned lizards)
 - Family Polychrotidae (anoles)
 - Family Leiosauridae
 - Family Tropiduridae (neotropical ground lizards)
 - Family Liolaemidae
 - Family Leiocephalidae
 - Family Crotaphytidae (collared and leopard lizards)
 - Family Opluridae (Madagascar iguanids)
 - Family Hoplocercidae (wood lizards, clubtails)
 - Family †Priscagamidae
 - Family Agamidae (agamas)
 - Family Chamaeleonidae (chameleons)
- Infraorder Gekkota
 - Family Gekkonidae (geckos)
 - Family Pygopodidae (legless lizards)
 - Family Dibamidae (blind lizards)
- Infraorder Scincomorpha
 - Family †Paramacellodidae
 - Family †Slavoiidae
 - Family Scincidae (skinks)
 - Family Cordylidae (spinytail lizards)
 - Family Gerrhosauridae (plated lizards)
 - Family Xantusiidae (night lizards)
 - Family Lacertidae (wall lizards or true lizards)
 - Family †Mongolochamopidae
 - Family Teiidae (tegu and whiptails)
 - Family Gymnophthalmidae (spectacled lizards)
- Infraorder Diploglossa
 - Family Anguidae (glass lizards)
 - Family Anniellidae (American legless lizards)
 - Family Xenosauridae (knob-scaled lizards)
- Infraorder Platynota (Varanoidea)
 - Family Varanidae (monitor lizards)
 - Family Lanthanotidae (earless monitor lizards)
 - Family Helodermatidae (gila monsters & beaded lizards)
 - Family †Mosasauridae (marine lizards)

Chapter- 10

Amphisbaenia and Diamondback Terrapin

Amphisbaenia

Worm lizards

Temporal range: Cretaceous - Recent



Scientific classification

| | |
|-----------|-----------------------------------|
| Kingdom: | Animalia |
| Phylum: | Chordata |
| Class: | Reptilia |
| Order: | Squamata |
| Suborder: | Amphisbaenia
Gray, 1844 |

Families

Amphisbaenidae
Bipedidae
Rhineuridae
Trogonophidae



black: range of Amphisbaenia

The **Amphisbaenia** are a usually legless suborder of squamates closely related to lizards and snakes. As many species possess a pink body coloration and scales arranged in rings, they have a superficial resemblance to earthworms. They are very poorly understood, due to their burrowing lifestyle and general rarity. Most species are found in Africa and South America, with a few in other parts of the world. Little is known of them outside of their anatomy, and even that is difficult to study due to the mechanics of dissecting something so small. Most species are less than 6 inches (150 mm) long.

Description



Close-up of the head of Rhineura

Despite a superficial resemblance to some primitive snakes, amphisbaenians have many unique features that distinguish them from other reptiles. Internally, their right lung is reduced in size to fit their narrow bodies, whereas in snakes, it is always the left lung. Their skeletal structure and skin are also different from those of other squamates.

The head is stout, not set off from the neck, and either rounded, sloped, or sloped with a ridge down the middle. Most of the skull is solid bone, and they have a distinctive single median tooth in the upper jaw. They have no outer ears, and the eyes are deeply recessed and covered with skin and scales. The body is elongated, and the tail truncates in a manner that vaguely resembles the head. Their name is derived from Amphisbaena, a mythical serpent with a head at each end. The four species of ajolote are unusual in having a pair of forelimbs, but all limbless species have some remnants of the pelvic and pectoral girdles embedded within the body musculature.

The skin of amphisbaenians is only loosely attached to the body, and they move using an accordion-like motion, in which the skin moves and the body seemingly just drags along behind it. Uniquely, they are also able to perform this motion in reverse just as effectively.

Amphisbaenians are carnivorous, able to tear chunks out of larger prey with their powerful, interlocking teeth. Like lizards, some species are able to shed their tail (autotomy). Most species lay eggs, although at least some are known to be viviparous.

The white worm lizard (*Amphisbaena alba*) is often found in association with leaf cutter ants. It is thought this reptile forages in the ant's deep galleries where the insects deposit their waste. The larvae of certain large beetles live in these galleries and it is these the reptile preys on.

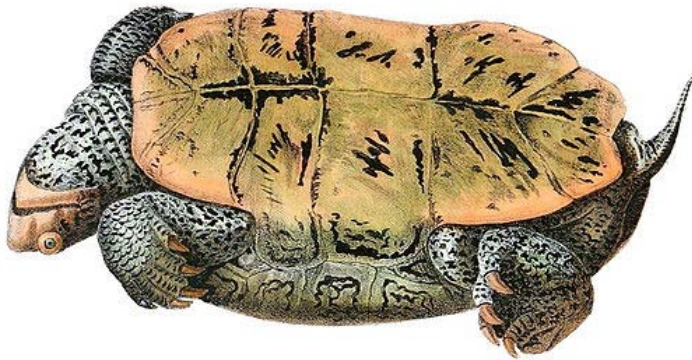
Families

Order: **Squamata**

- Suborder: **AMPHISBAENIA**
 - Family: Amphisbaenidae - Gray, 1865 -- Amphisbaenids, tropical worm lizards
 - Family: Bipedidae - Taylor, 1951 -- Ajolotes
 - Family: Rhineuridae - Vanzolini, 1951 -- North American worm lizards
 - Family: Trogonophidae - Gray, 1865 -- Palearctic worm lizards

Diamondback terrapin

Diamondback terrapin



Conservation status



Near Threatened (IUCN 2.3)

Scientific classification

| | |
|--------------|---------------------------------|
| Kingdom: | Animalia |
| Phylum: | Chordata |
| Class: | Reptilia |
| Subclass: | Anapsida |
| Order: | Testudines |
| Suborder: | Cryptodira |
| Superfamily: | Testudinoidea |
| Family: | Emyidae |
| Subfamily: | Deirochelyinae |
| Genus: | <i>Malaclemys</i>
Gray, 1844 |

Species: *M. terrapin*

Binomial name

Malaclemys terrapin

Schoepf, 1793

Synonyms

Emys Concentrica

Testudo concentrata

Testudo ocellata

Testudo terrapin

The **diamondback terrapin** (*Malaclemys terrapin*) or simply **terrapin**, is a species of turtle native to the brackish coastal swamps of the eastern and southern United States. It belongs to the monotypic genus, *Malaclemys*.

The name "terrapin" is derived from the Algonquian word *torope*. It is unambiguously applied to *Malaclemys terrapin* in both British English and American English. The name originally was used by early European settlers in North America to describe these brackish-water turtles that inhabited neither freshwater habitats nor the sea. It retains this exclusive use in American English. In British English, however, other semi-aquatic turtle species, such as the red-eared slider, might be called a terrapin.

Description



A picture of the terrapin, showing the diamond pattern

The species is named for the diamond pattern on top of its shell, but the overall pattern and coloration varies greatly by species. Its shell coloring can vary from browns to greys, and its body color can be grey, brown, yellow, or white. All have a unique pattern of wiggly, black markings or spots on their body and head. The species is sexually dimorphic in that the males grow to approximately 5 inches, while the females grow to an average of around 7.5 inches, though they are capable of growing larger. The largest female on record was just over 9 inches in length. Specimens from regions that are consistently warmer in temperature tend to be larger than those from cooler, more northern areas.

Distribution

The diamondback terrapin is found in a large range in the eastern and southern United States, from as far north as Cape Cod, Massachusetts to the southern tip of Florida and around the Gulf Coast to Texas.

Life cycle

Adult diamondback terrapins mate in the early spring, and clutches of 8–12 eggs are laid in sand dunes in the early summer. They hatch in late summer or early fall. Maturity in males is reached in 2–3 years at around 4.5 inches in length; it takes longer for females: 6–7 years at a length of around 6.75 inches.

Diet

Diamondback terrapins live on a diet of mollusks, fiddler crabs, and occasionally small fish.

Status

The diamondback terrapin is the state reptile of the U.S. state of Maryland and is the official mascot of the University of Maryland, College Park (the Maryland Terrapins or "Terps" for short). The species was once considered a delicacy to eat and was hunted almost to extinction. Due to this it is listed as an endangered species in Rhode Island, is considered a threatened species in Massachusetts, and is considered a "species of concern" in Georgia, Delaware, Alabama, Louisiana, North Carolina, and Virginia, but it holds no federal status.



Diamondback terrapin, *Malaclemys terrapin*

Historic uses

Terrapins were so plentiful in the 18th century that Maryland slaves protested the excessive use of this food source as their main protein. Late in the 19th century, demand for turtle soup claimed a harvest of 89,150 pounds from Chesapeake Bay in one year. In 1899, terrapin was offered on the dinner menu of Delmonico's Restaurant in New York as the third most expensive item on the extensive menu. A patron could request either Maryland or Baltimore terrapin at a price of \$2.50. Although demand was high, over capture was so high by 1920, the harvest of terrapins reached only 823 pounds for the year.

Diamondback terrapins and people

On July 8, 2009, flights at John F. Kennedy Airport in New York City were delayed for up to one and a half hours as 78 diamondback terrapins had invaded one of the runways. The turtles, which according to airport authorities were believed to have entered the runway in order to mate, were removed and released back into the wild. Given the time of year, it appears more likely, these were female turtles looking to deposit eggs.

According to the FAA National Wildlife Strike Database, a total of 18 strikes between diamondback terrapins and civil aircraft were reported in the US from 1990 to 2007, none of which caused damage to the aircraft.

Chapter- 11

Tortoise

Tortoises



A Galápagos tortoise (*Chelonoidis nigra*)

Scientific classification

| | |
|--------------|----------------------------------|
| Kingdom: | Animalia |
| Phylum: | Chordata |
| Class: | Reptilia |
| Order: | Testudines |
| Superfamily: | Testudinoidea |
| Family: | Testudinidae
Gray 1825 |

Tortoises (Testudinidae) or **land turtles** are a family of land-dwelling reptiles of the order of turtles (Testudines). Like their marine cousins, the sea turtles, tortoises are shielded from predators by a shell. The top part of the shell is the carapace, the underside is the plastron, and the two are connected by the bridge. The tortoise has both an endoskeleton and an exoskeleton. Tortoises can vary in size from a few centimeters to

two meters. Tortoises are usually diurnal animals with tendencies to be crepuscular depending on the ambient temperatures. They are generally reclusive animals.

Use of the term "tortoise"



Adult male tortoise, South Africa

Although the word "tortoise" is used by biologists in reference to the family *Testudinidae* only, in common usage it is used to describe many land-dwelling turtles. The inclusiveness of the term depends on the variety of English being used.

- British English normally describes these reptiles as "tortoises" if they live on land.
- American English tends to use the word "tortoise" for land-dwelling species, including members of *Testudinidae*, as well as other species such as box tortoises, though use of "turtle" by default is as common.
- Australian English uses "tortoise" for terrestrial species, including semi-aquatic species that live near ponds and streams. Traditionally a "tortoise" has feet (including webbed feet) while a "turtle" has flippers.

Biology

Birth



Young tortoise

Female tortoises dig nesting burrows in which they lay from one to thirty eggs. Egg laying typically occurs at night, after which the mother tortoise covers her clutch with sand, soil, and organic material. The eggs are left unattended, and depending on the species, take from 60 to 120 days to incubate. The size of the egg depends on the size of the mother and can be estimated by examining the width of the cloacal opening between the carapace and plastron. The plastron of a female tortoise often has a noticeable V-shaped notch below the tail which facilitates passing the eggs. Upon completion of the incubation period, a fully-formed hatchling uses an egg tooth to break out of its shell. It digs to the surface of the nest and begins a life of survival on its own. Hatchlings are born with an embryonic egg sac which serves as a source of nutrition for the first 3 to 7 days until they have the strength and mobility to find food. Juvenile tortoises often require a different balance of nutrients than adults, and therefore may eat foods which a more mature tortoise would not. For example, it is common that the young of a strictly herbivorous species will consume worms or insect larvae for additional protein.

Lifespan



Desert Tortoise in Rainbow Basin near Barstow, California

There are many old wives tales about the age of turtles and tortoises, one of which being that the age of a tortoise can be deduced by counting the number of concentric rings on its carapace, much like the cross-section of a tree. This is not true, since the growth of a tortoise depends highly on the accessibility of food and water. A tortoise that has access to plenty of forage (or is regularly fed by its owner) will grow faster than a Desert Tortoise that goes days without eating.

Tortoises generally have lifespans comparable with those of human beings, and some individuals are known to have lived longer than 150 years. Because of this, they symbolize longevity in some cultures, such as China. The oldest tortoise ever recorded, and one of the oldest individual animals ever recorded, was **Tu'i Malila**, which was presented to the Tongan royal family by the British explorer Captain Cook shortly after its birth in 1777. Tui Malila remained in the care of the Tongan royal family until its death by natural causes on May 19, 1965. This means that upon its death, Tui Malila was 188 years old. The record for the longest-lived vertebrate is exceeded only by one other, a koi named **Hanako** whose death on July 17, 1977 ended a 226 year life span.

The Alipore Zoo in India was the home to **Adwaita**, which zoo officials claimed was the oldest living animal until its death on March 23, 2006. Adwaita (sometimes spelled with

two d's) was an Aldabra Giant Tortoise brought to India by Lord Wellesley who handed it over to the Alipur Zoological Gardens in 1875 when the zoo was set up. Zoo officials state they have documentation showing that Adwaita was at least 130 years old, but claim that he was over 250 years old (although this has not been scientifically verified). Adwaita was said to be the pet of Robert Clive.

Harriet, was a resident at the Australia Zoo in Queensland from 1987 to her death in 2006, it was believed that she was brought to England by Charles Darwin aboard the Beagle and then on to Australia by John Clements Wickham. Harriet died on June 23, 2006, just shy of her 176th birthday.

Timothy, a spur-thighed tortoise, lived to be approximately 165 years old. For 38 years she was carried as a mascot aboard various ships in Britain's Royal Navy. Then in 1892, at age 53 she retired to the grounds of Powderham Castle in Devon. Up to the time of her passing in 2004 she was believed to be the UK's oldest resident.

According to articles published by the Daily Mail and the Times in December 2008, **Jonathan**, a Seychelles Giant tortoise living on the island of St Helena may be as old as 176 or 178 years. If this is true, he could be the current oldest living animal on Earth.

Sexual dimorphism

Many species of tortoises are sexually dimorphic, though the differences between males and females vary from species to species. In some species, males have a longer, more protruding neck plate than their female counterparts, while in others the claws are longer on the females. In most tortoise species, the female tends to be larger than the male. Some believe that males grow quicker, while the female grows slower but larger. The male also has a plastron that is curved inwards to aid reproduction. The easiest way to determine the sex of a tortoise is to look at the tail. The females, as a general rule have a smaller tail which is dropped down whereas the males have a much longer tail which is usually pulled up and to the side of the rear shell.

General information

Giant tortoises move very slowly on dry land, at only 0.17 miles per hour (0.27 km/h).

Diet



A baby tortoise feeding on lettuce

Most land based tortoises are herbivores, feeding on grazing grasses, weeds, leafy greens, flowers, and some fruits. Pet tortoises typically require a diet based on wild grasses, weeds and certain flowers. Certain species occasionally consume worms or insects, but too much protein is detrimental as it can cause shell deformation and other medical problems. Cat or dog foods should not be fed to tortoises, as these do not contain the proper balance of nutrients for a reptile; in particular, they are too high in protein. Additionally, it should not be assumed that all captive tortoises can be fed on the same diet. As different tortoise species vary greatly in their nutritional requirements it is essential to thoroughly research the dietary needs of your individual tortoise. Commercial tortoise pellets should not be offered as despite their claims they are not formulated to meet the nutritional needs of any type of tortoise. Large pellets have been known to rupture the oesophagus which begins the onset of choking and can cause a slow painful death. The best approach to determining the proper diet is to consult a qualified veterinarian specialising in chelonian care.

Taxonomy

The following species list largely follows Rhodin et al., 2010, this is a work in progress.

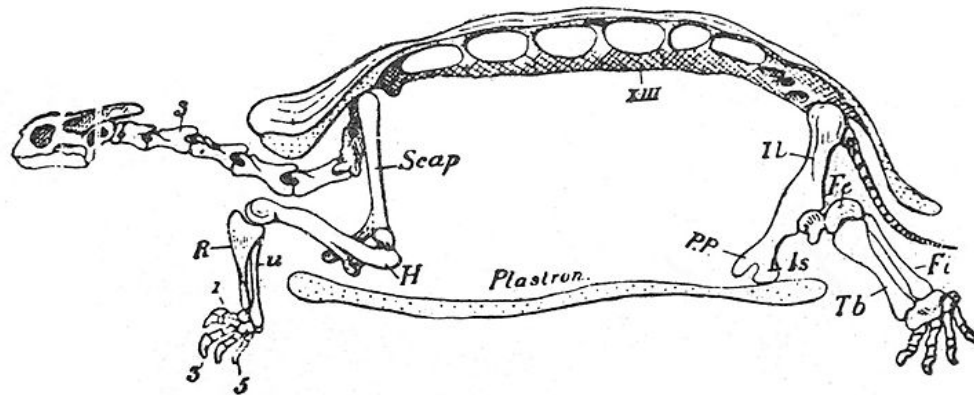


Diagram of skeleton of *Testudo*. (After Gadow. By kind permission of Messrs. Macmillan.)

| | |
|----------------------------------|--|
| <i>Fe.</i> Femur, foreshortened. | <i>Tb.</i> Tibia. |
| <i>Fi.</i> Fibula. | <i>U.</i> Ulna. |
| <i>H.</i> Humerus. | <i>3.</i> Third cervical vertebra. |
| <i>Il.</i> Ilium. | <i>1, 3, 5.</i> First, third, and fifth fingers. |
| <i>Is.</i> Ischium. | <i>xiii.</i> Thirteenth (fifth thoracic) vertebra. |
| <i>P.P.</i> Pubis. | |
| <i>R.</i> Radius. | |
| <i>Scap.</i> Scapula. | |

Skeleton of a tortoise



Fossil of the extinct *Ergilemys insolitus*



Achilemys cassouleti, the most primitive testudine

Family Testudinidae Batsch 1788

Subfamily Testudininae

- ***Aldabrachelys***
 - *Aldabrachelys gigantea gigantea*, Aldabra Giant Tortoise, common synonyms *Geochelone gigantea*, *Dipsochelys gigantea*
 - *Aldabrachelys gigantea arnoldi*, Arnold's Giant Tortoise,
 - *Aldabrachelys gigantea daudinii* (Extinct)
 - *Aldabrachelys gigantea hololissa*, Seychelles giant tortoise
 - *Aldabrachelys abrupta* (Extinct)
 - *Aldabrachelys grandidieri* (Extinct)

- ***Astrochelys*** Gray, 1873
 - *Astrochelys radiata*, Radiated Tortoise
 - *Astrochelys yniphora*, Angulated Tortoise, Madagascan (Plowshare) Tortoise

- ***Chelonoidis*** Fitzinger, 1835.

- *Chelonoidis carbonaria*, Red-Footed Tortoise
- *Chelonoidis chilensis*, Chaco or Chilean Tortoise
- *Chelonoidis denticulata*, Yellow-Footed Tortoise
- *Chelonoidis nigra*, Galápagos Giant Tortoise
- *Chelonoidis petersi*, Chaco tortoise
- ***Chersina***
 - *Chersina angulata*, Bowsprit Tortoise
- ***Colossochelys***
 - *Colossochelys atlas*, Atlas tortoise, (Extinct)
- ***Cylindraspis*** (All species Extinct) Following Austin and Arnold, 2001.
 - *Cylindraspis indica*, synonym *Cylindraspis borbonica*
 - *Cylindraspis inepta*
 - *Cylindraspis peltastes*
 - *Cylindraspis triserrata*
 - *Cylindraspis vosmaeri*
- ***Geochelone***
 - *Geochelone elegans*, Indian Star Tortoise
 - *Geochelone platynota*, Burmese Star Tortoise
 - *Geochelone sulcata*, African Spurred Tortoise (Sulcata Tortoise)
- †***Hadrianus***
 - *Hadrianus corsoni* (syn. *H. octonarius*)
 - *Hadrianus robustus*
 - *Hadrianus schucherti*
 - *Hadrianus utahensis*
- ***Homopus***
 - *Homopus aerolatus*, Parrot-Beaked Cape Tortoise
 - *Homopus boulengeri*, Boulenger's Cape Tortoise
 - *Homopus femoralis*, Karroo Cape Tortoise
 - *Homopus signatus*, Speckled Cape Tortoise, Speckled Padloper
 - *Homopus bergeri*, Berger's Cape Tortoise, Nama padloper, synonym *Homopus solus*
- ***Indotestudo***
 - *Indotestudo elongata*, Elongated Tortoise
 - *Indotestudo forstenii*, Travancore Tortoise, Forsten's Tortoise
 - *Indotestudo travancorica*, Travancore Tortoise
- ***Kinixys***
 - *Kinixys belliana*, Bell's Hinge-Backed Tortoise
 - *Kinixys erosa*, Serrated Hinge-Backed Tortoise

- *Kinixys homeana*, Home's Hinge-Backed Tortoise
- *Kinixys lobatsiana*, Lobatse Hingeback Tortoise
- *Kinixys natalensis*, Natal Hinge-Backed Tortoise
- *Kinixys spekii*, Speke's Hingeback Tortoise
- **Malacochersus**
 - *Malacochersus tornieri*, Pancake Tortoise
- **Psammobates**
 - *Psammobates geometricus*, Geometric Tortoise
 - *Psammobates oculifer*, Serrated Star Tortoise
 - *Psammobates tentorius*, African Tent Tortoise
- **Pyxis**
 - *Pyxis arachnoides*, Madagascan Spider Tortoise
 - *Pyxis planicauda*, Madagascan Flat-Tailed Tortoise
- **Stigmochelys** Gray, 1873
 - *Stigmochelys pardalis*, Leopard Tortoise
- **Testudo**
 - *Testudo graeca*, Greek Tortoise (Spur-Thighed Tortoise)
 - *Testudo hermanni*, Herman's Tortoise
 - *Testudo horsfieldii*, Russian Tortoise (Horsfield's Tortoise, or Central Asian Tortoise)
 - *Testudo kleinmanni*, Egyptian Tortoise, incl. Negev Tortoise
 - *Testudo marginata*, Marginated Tortoise

Subfamily Xerobatinae Agassiz, L. 1857.

- **Gopherus**
 - *Gopherus agassizii*, Desert Tortoise
 - *Gopherus berlandieri*, Texas Tortoise
 - *Gopherus flavomarginatus*, Bolson Tortoise
 - *Gopherus polyphemus*, Gopher Tortoise
- **Manouria**
 - *Manouria emys*, Brown Tortoise (Mountain Tortoise)
 - *Manouria impressa*, Impressed Tortoise
- **Stylemys** (Genus extinct)
 - *Stylemys botti*
 - *Stylemys calaverensis*
 - *Stylemys canetotiana*
 - *Stylemys capax*
 - *Stylemys conspecta*
 - *Stylemys copei*
 - *Stylemys emiliae*

- *Stylemys frizaciana*
- *Stylemys karakolensis*
- *Stylemys nebrascensis* (syn. *S. amphithorax*)
- *Stylemys neglectus*
- *Stylemys oregonensis*
- *Stylemys pygmaea*
- *Stylemys uintensis*
- *Stylemys undabuna*

In religion



The bas-relief from Angkor Wat, Cambodia, shows Samudra manthan-Vishnu in the centre, his turtle avatar Kurma below, asuras and devas to left and right.

In Hinduism, **Kurma** (Sanskrit: कूर्म) was the second avatar of Vishnu. Like the Matsya Avatara also belongs to the Satya Yuga. Vishnu took the form of a half-man half-tortoise, the lower half being a tortoise. He is normally shown as having four arms. He sat on the bottom of the ocean after the Great Flood. A mountain was placed on his back by the other gods so that they could churn the sea and find the ancient treasures of the Vedic peoples. Tortoise shells were used by ancient Chinese as Oracle Bones to make predictions.



A baby *Testudo marginata* emerges from its egg



A baby tortoise, less than a day old



Testudo graeca iberica, *Testudo hermanni boettgeri*, *Testudo hermanni hermanni*, *Testudo marginata sarda*



A young (3.5 years) Sulcata Tortoise *Geochelone sulcata*



A young, 20 year old Tanzanian Leopard Tortoise feeding on grass



Aldabra Giant Tortoise *Geochelone gigantea*



App 22 year old Leopard Tortoise



An African Spurred Tortoise from the Oakland Zoo



Pair of tortoises mate in a zoo



A boy rides tortoise at a zoo

Chapter- 12

Crocodylia

Crocodylians

Temporal range: Cretaceous - Recent, 84–0 Ma



Nile crocodiles (*Crocodylus niloticus*)

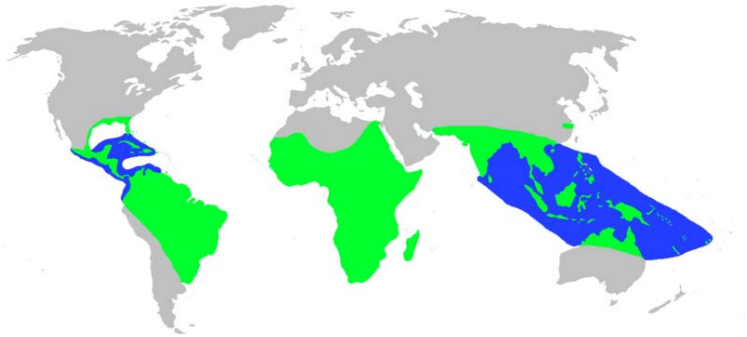
Scientific classification

| | |
|-------------|---------------------------------|
| Kingdom: | Animalia |
| Phylum: | Chordata |
| Class: | Reptilia |
| (unranked): | Metasuchia |
| (unranked): | Neosuchia |
| (unranked): | Eusuchia |
| Order: | Crocodylia
Owen, 1842 |

Families

- Gavialidae
- Alligatoridae

- Crocodylidae



Marine and freshwater ranges of crocodilians

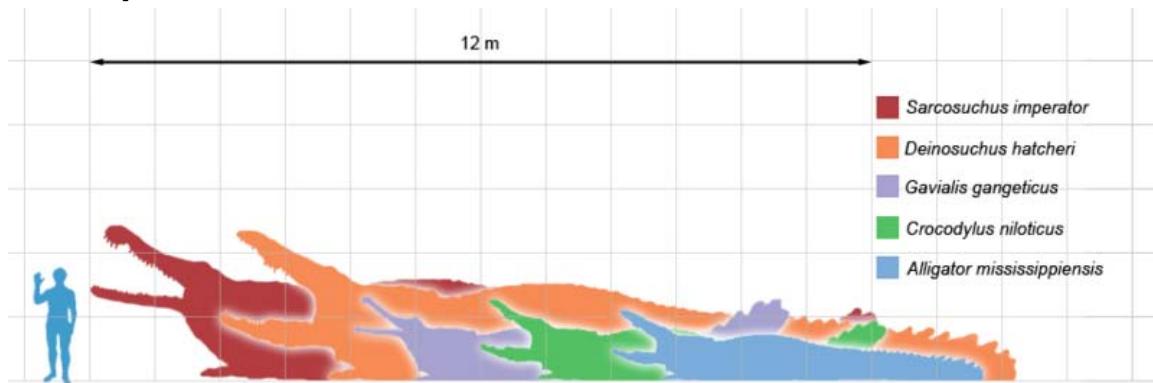
Crocodylia (or **Crocodylia**) is an order of large reptiles that appeared about 84 million years ago in the late Cretaceous Period (Campanian stage). They are the closest living relatives of birds, as the two groups are the only known survivors of the Archosauria. Members of the crocodylian total group, the clade Crurotarsi, appeared about 220 million years ago in the Triassic Period and exhibited a wide diversity of forms during the Mesozoic Era.

The correct vernacular term for this group is "**crocodilians**" and it includes the alligator, crocodile, gharial and caiman families. The term 'crocodiles' is sometimes incorrectly used to refer to alligators and caiman, or even their distant prehistoric relatives, "marine crocodiles".

Spelling

The group is often spelled 'Crocodylia' for consistency with the genus *Crocodylus* (Laurenti, 1768). However, Richard Owen used the -i- spelling when he published the name in 1842, so it is generally preferred in the scientific literature. The -i- spelling is also a more accurate Latinization of the Greek κροκόδειλος (*crocodeilos*, literally "pebble-worm", referring to the texture and shape of the animal). However, the y-spelling is increasingly common, especially in the context of phylogeny-based names in which Crocodylia is limited to the crown group.

Description



Size comparison of the largest recorded examples (typical sizes in many cases are much smaller) of several crocodilian species (two of them of prehistoric times) and a prehistoric pholidosaurid with a human.

The smallest species of crocodilian is the Cuvier's Dwarf Caiman and the largest is the Saltwater Crocodile. The basic crocodilian body plan is a very successful one; modern species closely resemble their Cretaceous ancestors of 84 million years ago. Mammals, too, have adapted to this body plan at least once in history. One ancestral whale family, the Ambulocetidae, were aquatic predators living in rivers and lakes, and they filled an ecological niche similar to the crocodilians. Much earlier, before the age of reptiles, Amphibians like *Prionosuchus* and *Platyoposaurus* were the first animals to adopt this body plan and niche.

Crocodilians have a flexible semi-erect (semi-sprawled) posture. They can walk in low, sprawled "belly walk," or hold their legs more directly underneath them to perform the "high walk." Most other reptiles can only walk in a sprawled position, and chameleons are the only modern non-avian reptiles with a more erect posture than crocodilians. The semi-erect posture makes it possible for some species to gallop on land if necessary. An Australian species can reach a speed of over 16 km/h while galloping on an irregular forest floor. Crocodilian ancestors, fast-moving terrestrial predators like the rauisuchians, actually had a fully erect posture, indicating that the sprawling and semi-erect posture of crocodilians evolved after they adapted to as semi-aquatic ambush predators. Their ankle bones, or tarsi are highly modified. Modern crocodilian locomotion is not a primitive trait, but a specialization for their semi-aquatic lifestyle.

Teeth and jaws

All crocodilians have, like *Homo sapiens* (humans), thecodont dentition (teeth set in bony sockets) but unlike mammals, they replace their teeth throughout life (though not in 'extreme' old-age). Juvenile crocodilians replace teeth with larger ones at a rate as high as 1 new tooth per socket every month. After reaching adult size in a few years, however, tooth replacement rates can slow to two years and even longer. Very old members of some species have been seen in an almost "edentulous" (toothless) state, after teeth have

been broken and replacement slowed or ceased. The result of this is that a single crocodile can go through at least 3,000 teeth in its lifetime. Each tooth is hollow, and the new one is growing inside the old. In this way, a new tooth is ready once the old is lost.



From the left: Heads of the Indian gharial (*Gavialis gangeticus*), American Alligator (*Alligator mississippiensis*), and an American Crocodile (*Crocodylus acutus*).

Crocodylians have a secondary bony palate that enables them to breathe when partially submerged, even if the mouth is full of water. Their internal nostrils open in the back of their throat, where a special part of the tongue called the "palatal valve" closes off their respiratory system when they are underwater. This way they can open their mouths underwater without choking. Most reptiles lack a secondary palate, but some skinks (family Scincidae) have evolved a bony secondary palate too, to varying degrees.

Crocodiles and gharials have modified salivary glands on their tongue (salt glands), which are used for excreting excess salt ions from their body. Alligators and caimans have them too, but here they are non-functioning. This indicates that at some point the common origin of the Crocodylia were adapted to saline/marine environments. This also explains their wide distribution across the continents (i.e. marine dispersal). Species like the saltwater crocodile (*C. porosus*) can survive protracted periods of time in the sea, and can hunt prey within this environment.

Crocodylians are often seen lying with their mouths open, a behavior called gaping. One of its functions is probably to cool them down, but since they also do this at night and when it is raining, it is possible that gaping has a social function as well.

Internal organs

Crocodylians lack a vomeronasal organ (except in the embryonic stage) and a urinary bladder.

Like mammals and birds and unlike other reptiles, crocodiles have a four-chambered heart. While the four-chambered heart is traditionally characteristic of endotherms, it is thought that the ectothermic crocodylia have a four-chambered heart because of an

endothermic ancestry, originating in the archosaurs or in an earlier predecessor. When crocodilian ancestors transitioned back to aquatic ectothermy, it was advantageous for them to have a heart more akin to the normally three- or five-chambered heart found in most ectotherms. In order for their four-chambered heart to function more like the ectothermic heart, they adopted a mechanism for shunting blood in an alternative pathway through the heart. The right ventricle has two arteries leaving it; a pulmonary artery, which goes to the lungs, and the left aortic arch, which goes to the body, or systemic circulation. There is also a hole, the foramen of Panizza, between the left and right aortic arches. Because the left aortic arch goes directly to the gut, the shunting of oxygen depleted blood which is high in CO₂ may serve to aid in creating stomach acid to assist in digesting bones from its prey. Their blood has been shown to have strong antibacterial properties.

Crocodylians have lungs with alveoli. They have a unique muscle called the diaphragmaticus that attaches to the liver and viscera and acts as a piston to assist in breathing. The diaphragmaticus is not homologous to the diaphragm of mammals and the proto-diaphragm of tegu lizards. Like other amniotes, crocodilian breathing uses muscles between the ribs to both increase and decrease thoracic volume. In addition, expiration is accomplished by contracting muscles to move the liver towards the head to rotate the pubic bones to decrease abdominal volume. Inspiration involves contraction of the diaphragmaticus muscle to push organs to the back of the body and other muscles to make space for these organs. In crocodilians, expiration is mostly passive (involves little muscle contraction) during rest while inspiration always involves muscle contraction. Because many of these ventilatory muscles are used for maneuverability in water, and because the muscles were originally used for locomotion, it is possible that these muscles became ventilatory muscles after they evolved to move air around in the lungs for maneuverability.

Crocodylians are known to swallow stones, gastroliths ("stomach-stones"), which act as a ballast in addition to aiding post-digestion processing of their prey. The crocodylian stomach is divided into two chambers; the first one is described as being powerful and muscular, like a bird gizzard. This is where the gastroliths are found. The other stomach has the most acidic digestive system of any animal, and it can digest mostly everything from their prey; bones, feathers, and horns.

The sex of developing crocodilians is determined by the incubation temperature of the eggs. This means crocodilians do not have genetic sex determination, but instead have a form of environmental sex determination which is based upon the temperature embryos are subjected to early in their development.

Sensory organs



West African dwarf crocodile from the forests of West and West Central Africa

Like all non-avian reptiles, crocodilians have a relatively small brain, but it is more advanced than in other reptiles. Among other things they have true cerebral cortexes.

As in many other aquatic or amphibious tetrapods, the eyes, ears, and nostrils are all located on the same plane. They see well during the day and may even have color vision, plus the eyes have a vertical, cat-like pupil which also gives them excellent night vision. The iris is silvery and a light reflecting layer of tapetum behind the retina greatly increases their ability to see in weak light and also makes their eyes appear to glow in the dark when a light is pointed at them. A third transparent eyelid, the nictitating membrane, protects their eyes underwater. However, they cannot focus under water, meaning other senses are more important when submerged.

While birds and most reptiles have a ring of bones around each eye which supports the eyeball (the sclerotic ring), the crocodiles lack these bones, just like mammals and snakes. The eardrums are located behind the eyes and are covered by a movable flap of skin. This flap closes, along with the nostrils and eyes, when they dive, preventing water from entering their external head openings. The middle ear cavity has a complex of bony air-filled passages and a branching eustachian tube. There is also a small muscle (which

is also seen in geckos) next to or upon the stapes, the stapedius, which probably functions in the same way as the mammalian stapedius muscle does, damping strong vibrations.

The upper and lower jaws are covered with sensory pits, visible as small, black speckles on the skin, the crocodilian version of the lateral organ seen in fish and many amphibians, though arising from a completely different origin. These pigmented nodules encase bundles of nerve fibers that respond to the slightest disturbance in surface water, detecting vibrations and small pressure changes in water, making it possible for them to detect prey, danger, and intruders even in total darkness. These sense organs are known as DPRs (Dermal Pressure Receptors). While alligators and caimans only have them on their jaws, crocodiles have similar organs on almost every scale on their body. The function of the DPRs on the jaws are clear, but it is still not quite clear what the organs on the rest of the body in crocodiles actually do. They are probably doing the same as the organs on their jaws, but it seems as if they can do more than that, like assisting in chemical reception or even salinity detection.

Skin and skeleton

The skin is covered with scales composed of the protein keratin (the same protein that forms hooves, horns, feathers, hair, claws, and nails in other tetrapods), which are shed individually. On the head the skin is actually fused to the bones of the skull. There are small plates of bone, called osteoderms or scutes, under the scales. Like the scales comprising the shell of a turtle, or the cross-section of a tree trunk, crocodile osteoderms have annual growth rings, and by counting them it is possible to tell their age. Osteoderms are found especially on the back, and in some species also on the belly. The rows of scutes cover the crocodile's body from head to tail, forming a tough protective armor. Beneath the scales and osteoderms is another layer of armor, both strong and flexible and built of rows of bony overlapping shingles called osteoscutes, which are embedded in the animal's back tissue. The blood-rich bumpy scales seen on their backs act as solar panels.

Their spool-shaped vertebrae in their ancestors went from being biconcave to having a concave front and a convex back in the modern forms. This made the vertebral column more flexible and strong.

They possess ribs of dermal origin restricted to the sides of the ventral body wall. The collar bone (clavicle) is absent.

Differences between alligators and crocodiles



Crocodiles are generally much lighter in color than alligators

While alligators (and caimans) are often confused with crocodiles, they belong to two quite separate taxonomic families.

The most obvious external differences are visible in the head—alligators and caimans have wider and shorter heads, and a more U-shaped than V-shaped snout. The alligator's upper jaw is wider than its lower jaw, and the teeth in the lower jaw fit into small depressions in the upper jaw. The upper and lower jaws of the crocodiles are the same width, and teeth in the lower jaw fall along the edge or outside the upper jaw when the mouth is closed. When the crocodile's mouth is closed, the large fourth tooth in the lower jaw fits into a constriction in the upper jaw. For hard-to-distinguish specimens, the protruding tooth is the most reliable feature to define a species. However, in captivity, alligators and caimans may show jaw deformities which result in lower teeth protruding.

Alligators lack the jagged fringe which appears on the hind legs and feet of the crocodile and have the toes of the hind feet webbed, not more than halfway to the tips. Alligators strongly prefer freshwater, while crocodiles can better tolerate seawater due to specialized glands for filtering out salt. However, both taxa can survive in either.

Both species of alligator also tend to be darker in color than crocodiles—often nearly black (but color is very dependent on water quality). Algae-laden waters produce greener skin, while tannic acid from overhanging trees can produce often darker skin.

When cleaning alligator pools, some zookeepers can tread on alligators without eliciting a response, though crocodiles almost invariably react aggressively and are for the most part more aggressive in their natural habitat.

Evolution and classification

Eusuchia, a modern clade which includes the crown group Crocodylia, first appeared in the Lower Cretaceous of Europe. *Isisfordia duncani* lived approximately 95 to 98 million years ago, during the Cenomanian epoch of the Upper Cretaceous. *Isisfordia* is the second oldest known eusuchian, and the earliest crocodylomorph yet found in Australia. Eusuchians underwent a mass radiation during the Late Cretaceous and the Paleogene, in which they evolved into numerous forms, such as semi-aquatic dinosaur-eating species (*Deinosuchus*); hooved, terrestrial carnivores (*Pristichampsus*), and 'hatchet'-shaped skulled forms (*Baru*).

Extant taxonomy

- Family Gavialidae
 - Genus *Tomistoma*
 - False gharial (*Tomistoma schlegelii*)
 - Genus *Gavialis*
 - Gharial (*Gavialis gangeticus*)
- Family Alligatoridae
 - Genus *Alligator*
 - American Alligator (*Alligator mississippiensis*)
 - Chinese Alligator (*Alligator sinensis*)
 - Genus *Paleosuchus*
 - Cuvier's Dwarf Caiman (*Paleosuchus palpebrosus*)
 - Smooth-fronted Caiman (*Paleosuchus trigonatus*)
 - Genus *Caiman*
 - Yacare Caiman (*Caiman yacare*)
 - Spectacled Caiman (*Caiman crocodilus*)
 - Broad-snouted Caiman (*Caiman latirostris*)
 - Genus *Melanosuchus*
 - Black Caiman (*Melanosuchus niger*)
- Family Crocodylidae
 - Genus *Crocodylus*
 - American crocodile (*Crocodylus acutus*)
 - Slender-snouted crocodile (*Crocodylus cataphractus*)
 - Orinoco crocodile (*Crocodylus intermedius*)
 - Freshwater crocodile (*Crocodylus johnsoni*)
 - Philippine crocodile (*Crocodylus mindorensis*)

- Morelet's crocodile (*Crocodylus moreletii*)
- Nile crocodile (*Crocodylus niloticus*)
- New Guinea crocodile (*Crocodylus novaeguineae*)
- Mugger crocodile (*Crocodylus palustris*)
- Saltwater crocodile (*Crocodylus porosus*)
- Cuban crocodile (*Crocodylus rhombifer*)
- Siamese crocodile (*Crocodylus siamensis*)
- Genus *Osteolaemus*
 - Dwarf crocodile (*Osteolaemus tetraspis*)

Taxonomy

- Superorder Crocodylomorpha
 - **Order Crocodilia**
 - Superfamily Gavialoidea
 - Family Gavialidae: gharials & false gharials
 - Superfamily Alligatoroidea
 - Family Alligatoridae
 - Subfamily Alligatorinae: alligators
 - Subfamily Caimaninae: caimans
 - Family †Diplocynodontidae
 - Superfamily Crocodyloidea
 - Family Crocodylidae
 - Subfamily Crocodylinae: crocodiles
 - Subfamily †Mekosuchinae

Chapter- 13

Tuatara

Tuatara



Male tuatara

Conservation status



Vulnerable (IUCN 2.3)

Scientific classification

| | |
|------------|------------------|
| Kingdom: | Animalia |
| Phylum: | Chordata |
| Subphylum: | Vertebrata |
| Class: | Reptilia |
| Order: | Sphenodontia |
| Family: | Sphenodontidae |
| Genus: | <i>Sphenodon</i> |

Gray, 1831

Species

- *Sphenodon guntheri* – (Buller, 1877)
- *Sphenodon punctatus* – (Gray, 1842)
- *Sphenodon diversum* – Colenso, 1885 †



dark red: range (North Island, New Zealand)

The **tuatara** is a reptile endemic to New Zealand which, though it resembles most lizards, is actually part of a distinct lineage, order Sphenodontia. The two species of tuatara are the only surviving members of its order, which flourished around 200 million years ago. Their most recent common ancestor with any other extant group is with the squamates (lizards and snakes). For this reason, tuatara are of great interest in the study of the evolution of lizards and snakes, and for the reconstruction of the appearance and habits of the earliest diapsids (the group that also includes birds, dinosaurs, and crocodiles).

Tuatara are greenish brown, and measure up to 80 cm (31 in) from head to tail-tip and weigh up to 1.3 kilograms (2.9 lb) with a spiny crest along the back, especially pronounced in males. Their dentition, in which two rows of teeth in the upper jaw overlap one row on the lower jaw, is unique among living species. They are further unusual in having a pronounced photo-receptive eye dubbed the "third eye", whose current function is a subject of ongoing research but is thought to be involved in setting circadian and seasonal cycles. They are able to hear although no external ear is present, and have a number of unique features in their skeleton, some of them apparently evolutionarily retained from fish. Although tuatara are sometimes called "living fossils", recent taxonomic and molecular work has shown that they have changed significantly since the Mesozoic era.

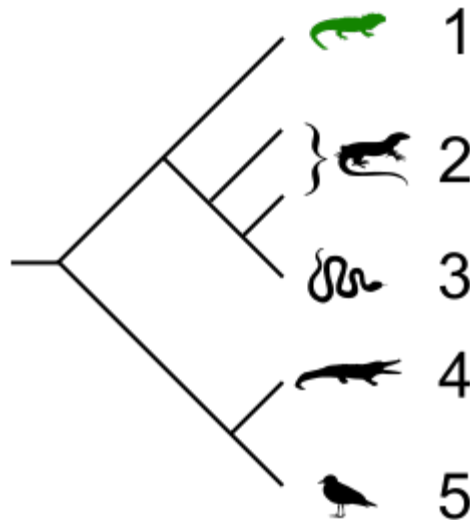
The name "tuatara" derives from the Māori language, and means "peaks on the back". As with many other Māori loanwords, the plural form is now generally the same as the singular in formal New Zealand English usage. "Tuataras" remains common in less formal speech, particularly among older speakers. The tuatara has been classified as an endangered species since 1895 (the second species, *S. guntheri*, was not recognised until 1989). Tuatara, like many of New Zealand's native animals, are threatened by habitat loss and introduced predators like the Polynesian Rat (*Rattus exulans*). They were extinct on

the mainland, with the remaining populations confined to 32 offshore islands, until the first mainland release into the heavily fenced and monitored Karori Sanctuary in 2005.

During routine maintenance work at Karori Sanctuary in late 2008, a tuatara nest was uncovered, with a hatchling found the following autumn. This is thought to be the first case of tuatara successfully breeding on the New Zealand mainland in over 200 years, outside of captive rearing facilities.

Taxonomy and evolution

Tuatara, and their sister group Squamata (which includes lizards, snakes and amphisbaenians), belong to the superorder Lepidosauria, the only surviving taxon within Lepidosauromorpha. Squamates and tuatara both show caudal autotomy (loss of the tail-tip when threatened), and have a transverse cloacal slit. The origin of the tuatara probably lies close to the split between the Lepidosauromorpha and the Archosauromorpha. Though tuatara resemble lizards, the similarity is superficial, because the family has several characteristics unique among reptiles. The typical lizard shape is very common for the early amniotes; the oldest known fossil of a reptile, the *Hylonomus*, resembles a modern lizard.



Cladogram showing relationships of extant members of the Sauria. Numbered items are:

- 1. Tuatara
- 2. Lizards
- 3. Snakes
- 4. Crocodiles
- 5. Birds

"Lizards" are paraphyletic. Branch lengths do not indicate divergence times.

Tuatara were originally classified as lizards in 1831 when the British Museum received a skull. The genus remained misclassified until 1867, when Albert Günther of the British

Museum noted features similar to birds, turtles, and crocodiles. He proposed the order Rhynchocephalia (meaning "beak head") for the tuatara and its fossil relatives. Now, most authors prefer to use the more exclusive order name of Sphenodontia for the tuatara and its closest living relatives.

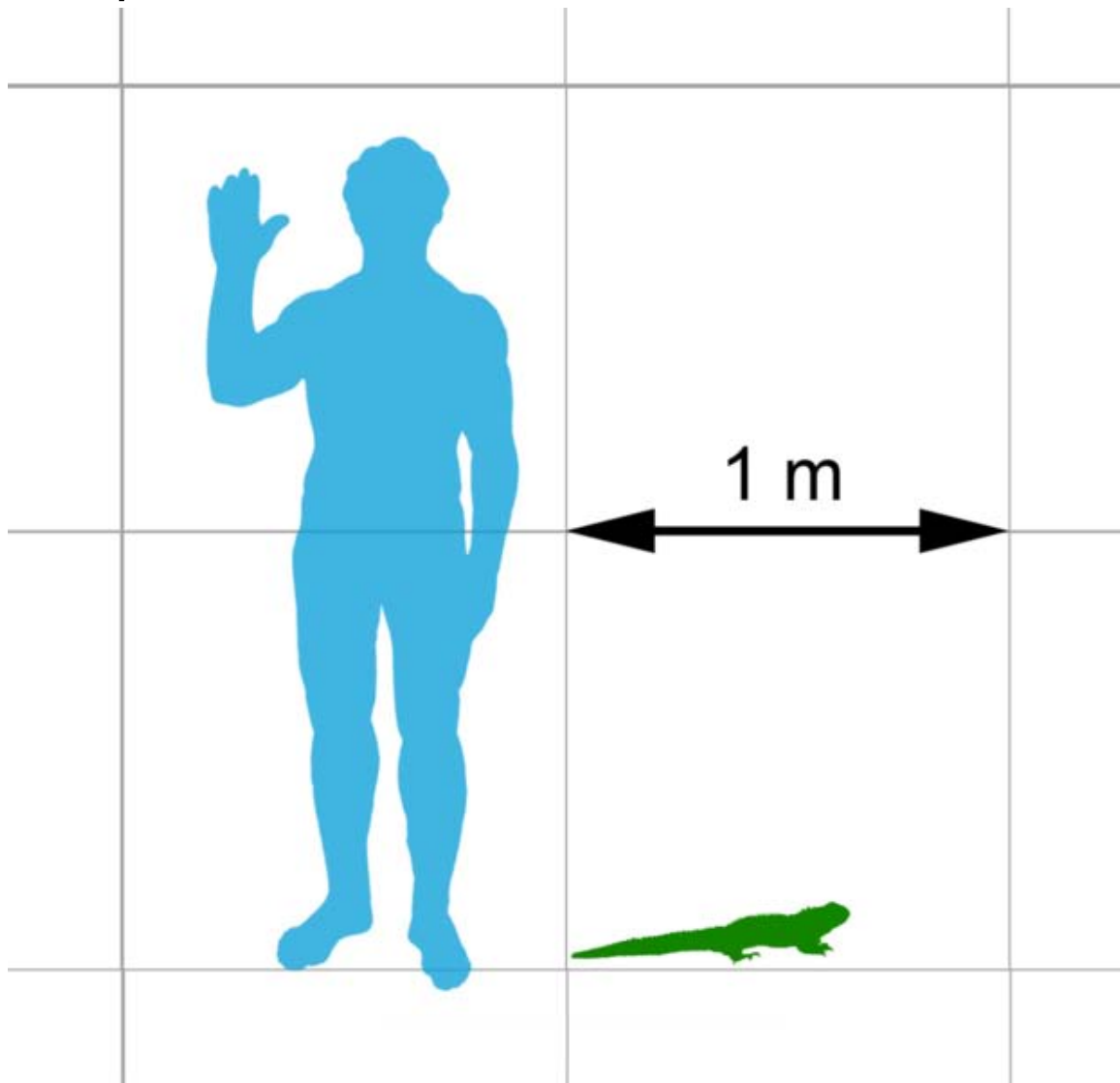
Many disparately related species were subsequently added to the Rhynchocephalia, resulting in what taxonomists call a "wastebasket taxon". Williston proposed the Sphenodontia to include only tuatara and their closest fossil relatives in 1925. *Sphenodon* is derived from the Greek for "wedge" (*σφηνος/sphenos*) and "tooth" (*δόντι/odon(t)*).

Tuatara have been referred to as living fossils, which means their group retains many basal characteristics from around the time of the squamate – rhynchocephalian split (220 MYA). However, taxonomic work on Sphenodontia has shown that this group has undergone a variety of changes throughout the Mesozoic, and a recent molecular study showed that their rate of molecular evolution is faster than of any other animal so far examined. Many of the niches occupied by lizards today were then held by sphenodontians. There was even a successful group of aquatic sphenodontians known as pleurosaurs, which differed markedly from living tuatara. Tuatara show cold weather adaptations that allow them to thrive on the islands of New Zealand; these adaptations may be unique to tuatara since their sphenodontian ancestors lived in the much warmer climates of the Mesozoic.

Species

There are two extant species: *Sphenodon punctatus* and the much rarer *Sphenodon guntheri*, or Brothers Island tuatara, which is confined to North Brother Island in Cook Strait. The species name *punctatus* is Latin for "spotted", and *guntheri* refers to Albert Günther. *S. punctatus* was named when only one species was known, and its name is misleading, since both species can have spots. The Brother's Island tuatara (*S. guntheri*) has olive brown skin with yellowish patches, while the colour of the other species, (*S. punctatus*), ranges from olive green through grey to dark pink or brick red, often mottled, and always with white spots. In addition, *S. guntheri* is considerably smaller. A third, extinct species of *Sphenodon* was identified in November 1885 by William Colenso, who was sent an incomplete sub-fossil specimen from a local coal mine. Colenso named the new species *S. diversum*. *Sphenodon punctatus* is further divided into two subspecies: the Cook Strait tuatara (unnamed subspecies), which lives on other islands in and near Cook Strait, and the northern tuatara (*Sphenodon punctatus punctatus*), which lives on the Bay of Plenty, and some islands further north. A 2009 paper reexamined the genetic bases used to distinguish the two species of tuatara, and concluded that they only represent geographic variants, and only one species should be recognized.

Description

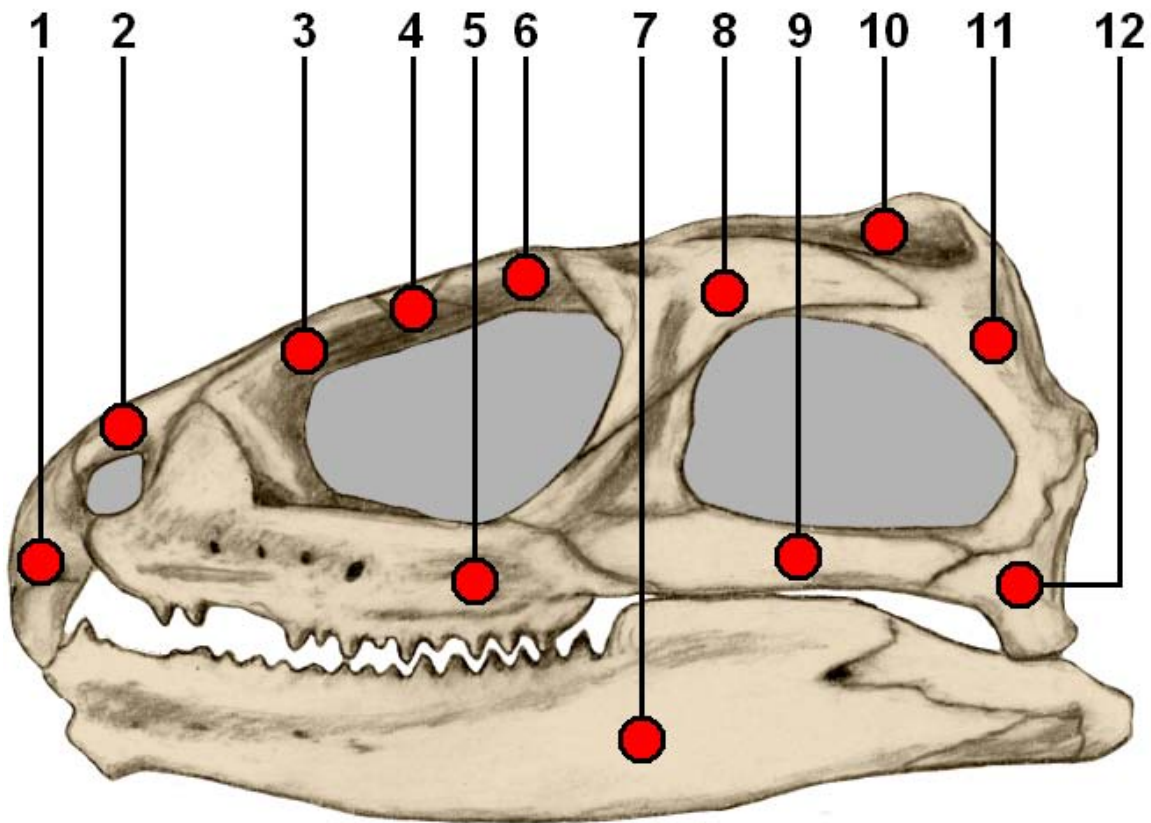


Size comparison of male *S. punctatus* and human

The tuatara is considered the most unspecialised living amniote; the brain and mode of locomotion resemble that of amphibians and the heart is more primitive than that of any other reptile. Their lungs have a single chamber and lack bronchi. Both species are sexually dimorphic, males being larger. Adult *S. punctatus* males measure 61 cm (24 in) in length and females 45 cm (18 in). The San Diego Zoo even cites a length of up to 80 cm (31 in). Males weigh up to 1 kg (2.2 lb), and females up to 0.5 kg (1.1 lb). Brother's Island tuatara are slightly smaller, weighing up to 660 g (1.3 lb).

The tuatara's greenish brown colour matches its environment, and can change over its lifetime. Tuatara shed their skin at least once per year as adults, and three or four times a year as juveniles. Tuatara sexes differ in more than size. The spiny crest on a tuatara's

back, made of triangular soft folds of skin, is larger in males, and can be stiffened for display. The male abdomen is narrower than the female's.



Skull of a tuatara, showing the complete temporal arches, and individual bones:

- 1 = premaxilla
- 2 = nasal
- 3 = prefrontal
- 4 = frontal
- 5 = maxilla
- 6 = postfrontal
- 7 = dentary
- 8 = postorbital
- 9 = jugal
- 10 = parietal
- 11 = squamosal
- 12 = quadrate

Skull

In the course of evolution, the skull has been modified in most diapsids from the original version evident in the fossil record. However, all the original features are preserved in that of the tuatara; it has two openings (*temporal fenestra*) on each side of the skull, with complete arches. In addition, the upper jaw is firmly attached to the skull. This makes for

a very rigid, inflexible construction. Testudines (turtle and tortoise) skulls with their single temporal fenestra are widely considered to be the most primitive among amniotes, though there is evidence they may have lost the temporal holes rather than never having had them.

The tip of the upper jaw is beak-like and separated from the remainder of the jaw by a notch. There is a single row of teeth in the lower jaw and a double row in the upper, with the bottom row fitting perfectly between the two upper rows when the mouth is closed. This specific tooth arrangement is not seen in any other reptile; although most snakes have a double row of teeth in their upper jaw, their arrangement and function is different from the tuatara's. The jaws, joined by ligament, chew with backwards and forwards movements combined with a shearing up and down action. The force of the bite is suitable for shearing chitin and bone. The tuatara's teeth are not replaced, since they are not separate structures like real teeth, but sharp projections of the jaw bone. As their teeth wear down, older tuatara have to switch to softer prey such as earthworms, larvae, and slugs, and eventually have to chew their food between smooth jaw bones.

Sensory organs

The eyes can focus independently, and are specialized with a duplex retina that contains two types of visual cells for both day and night vision, and a tapetum lucidum which reflects on to the retina to enhance vision in the dark. There is also a third eyelid on each eye, the nictitating membrane.

The tuatara has a third eye on the top of its head called the parietal eye. It has its own lens, cornea, retina with rod-like structures, and degenerated nerve connection to the brain, suggesting it evolved from a real eye. The parietal eye is only visible in hatchlings, which have a translucent patch at the top centre of the skull. After four to six months it becomes covered with opaque scales and pigment. Its purpose is unknown, but it may be useful in absorbing ultraviolet rays to manufacture vitamin D, as well as to determine light/dark cycles, and help with thermoregulation. Of all extant tetrapods, the parietal eye is most pronounced in the tuatara. The parietal eye is part of the pineal complex, another part of which is the pineal gland, which in tuatara secretes melatonin at night. It has been shown that some salamanders use their pineal body to perceive polarised light, and thus determine the position of the sun, even under cloud cover, aiding navigation.

Together with turtles, the tuatara has the most primitive hearing organs among the amniotes. There is no eardrum and no earhole, and the middle ear cavity is filled with loose tissue, mostly adipose (fatty) tissue. The stapes comes into contact with the quadrate (which is immovable) as well as the hyoid and squamosal. The hair cells are unspecialized, innervated by both afferent and efferent nerve fibres, and respond only to low frequencies. Even though the hearing organs are poorly developed and primitive with no visible external ears, they can still show a frequency response from 100–800 Hz, with peak sensitivity of 40 dB at 200 Hz.

Spine and ribs

The tuatara spine is made up of hour-glass shaped amphicoelous vertebrae, concave both before and behind. This is the usual condition of fish vertebrae and some amphibians, but is unique to tuatara within the amniotes.

The tuatara has gastralia, rib-like bones also called gastric or abdominal ribs, the presumed ancestral trait of diapsids. They are found in some lizards, where they are mostly made of cartilage, as well as crocodiles and the tuatara, and are not attached to the spine or thoracic ribs. The true ribs are small projections, with small, hooked bones, called uncinata processes, found on the rear of each rib. This feature is also present in birds. The tuatara is the only living tetrapod with well developed gastralia and uncinata processes.

In the early tetrapods, the gastralia and ribs with uncinata processes, together with bony elements such as bony plates in the skin (osteoderms) and clavicles (collar bone), would have formed a sort of exo-skeleton around the body, protecting the belly and helped to hold in the guts and inner organs. These anatomical details most likely evolved from structures involved in locomotion even before the vertebrates ventured onto land. The gastralia may have been involved in the breathing process in early amphibians and reptiles. The pelvis and shoulder girdles are arranged differently to those of lizards, as is the case with other parts of the internal anatomy and its scales.

Tail and back

The spiny plates on the back and tail of the tuatara resemble those of a crocodile more than a lizard, but has the latter reptile's ability to break off when caught by a predator, and then regenerate. The tail and back are covered with spiny plates that, too, resemble modern crocodiles more than they do those of a lizard.

Behaviour

Adult tuatara are terrestrial and nocturnal reptiles, though they will often bask in the sun to warm their bodies. Hatchlings hide under logs and stones, and are diurnal, likely because adults are cannibalistic. Tuatara thrive in temperatures much lower than those tolerated by most reptiles, and hibernate during winter. They remain active at temperatures as low as 5 °C (41 °F), while temperatures over 28 °C (82 °F) are generally fatal. The optimal body temperature for the tuatara is from 16 to 21 °C (61 to 70 °F), the lowest of any reptile. The body temperature of tuatara is lower than that of other reptiles ranging from 5.2–11.2 °C (41–52 °F) over a day, whereas most reptiles have body temperatures around 20 °C (68 °F). The low body temperature results in a slower metabolism.

Burrowing seabirds such as petrels, prions, and shearwaters share the tuatara's island habitat during the bird's nesting season. The tuatara use the bird's burrows for shelter when available, or dig their own. The seabirds' guano helps to maintain invertebrate

populations that tuatara predominantly prey on; including beetles, crickets, and spiders. Their diet also consists of frogs, lizards, and bird's eggs and chicks. The eggs and young of seabirds that are seasonally available as food for tuatara may provide beneficial fatty acids. Tuatara of both sexes defend territories, and will threaten and eventually bite intruders. The bite can cause serious injury. Tuatara will bite when approached, and will not let go easily.

Reproduction



A male tuatara named Henry, living at the Southland Museum and Art Gallery, is still reproductively active at 111 years of age.

Tuatara reproduce very slowly, taking ten to twenty years to reach sexual maturity. Mating occurs in midsummer; females mate and lay eggs once every four years. During courtship, a male makes his skin darker, raises his crests, and parades toward the female. He slowly walks in circles around the female with stiffened legs. The female will either submit, and allow the male to mount her, or retreat to her burrow. Males do not have a penis; they reproduce by the male lifting the tail of the female and placing his vent over hers. The sperm is then transferred into the female, much like the mating process in birds.



Tuatara juvenile (*Sphenodon punctatus*)

Tuatara eggs have a soft, parchment-like shell. It takes the females between one and three years to provide eggs with yolk, and up to seven months to form the shell. It then takes between 12 and 15 months from copulation to hatching. This means reproduction occurs at two- to five-year intervals, the slowest in any reptile. Wild tuatara are known to be still reproducing at about 60 years of age—"Henry", a 111-year-old tuatara at Southland Museum in Invercargill, New Zealand, became a father (possibly for the first time) on 23 January 2009.

The sex of a hatchling depends on the temperature of the egg, with warmer eggs tending to produce male tuatara, and cooler eggs producing females. Eggs incubated at 21 °C (70 °F) have an equal chance of being male or female. However, at 22 °C (72 °F), 80% are likely to be males, and at 20 °C (68 °F), 80% are likely to be females; at 18 °C (64 °F) all hatchlings will be females. There is some evidence that sex determination in tuatara is determined by both genetic and environmental factors.

Tuatara probably have the slowest growth rates of any reptile, continuing to grow larger for the first 35 years of their lives. The average lifespan is about 60 years, but they can live to be well over 100 years old. Some experts believe that captive tuatara could live as long as 200 years.

Conservation



Current distribution of tuatara (in black). Circles represent the North Island tuatara, squares the Brothers Island tuatara. Symbols may represent up to seven islands.

Distribution and threats

Tuatara were long confined to 32 offshore islands free of mammals. The islands are difficult to get to, and are colonised by few animal species, indicating that some animals absent from these islands may have caused tuatara to disappear from the mainland. However, kiore (Polynesian rats) had recently established on several of the islands, and tuatara were persisting, but not breeding, on these islands. Additionally, tuatara were much rarer on the rat-inhabited islands.

The recent discovery of a tuatara hatchling on the New Zealand mainland indicates that attempts to reestablish a breeding population on the mainland have had some success. The total population of tuatara of all species and subspecies is estimated to be greater than 60,000, but less than 100,000.

Eradication of rats

Tuatara were removed from Stanley, Red Mercury and Cuvier Islands in 1990 and 1991, and maintained in captivity to allow Polynesian rats to be eradicated on those islands. All three populations bred in captivity, and after successful eradication of the rats, all individuals including the new juveniles were returned to their islands of origin. In the 1991/92 season, Little Barrier Island was found to hold only eight tuatara, which were taken into *in situ* captivity, where females produced 42 eggs, which were incubated at Victoria University. The resulting offspring were subsequently held in an enclosure on the island, then released into the wild in 2006 after rats were eradicated there.

In the Hen and Chicken Islands, Pacific rats were eradicated on Whatupuke in 1993, Lady Alice Island in 1994, and Coppermine Island in 1997. Following this program, juveniles have once again been seen on the latter three islands. In contrast, rats persist on Hen Island of the same group, and no juvenile tuatara had been seen there as of 2001. In the Alderman Islands, Middle Chain Island holds no tuatara, but it is considered possible for rats to swim between Middle Chain and other islands that do hold tuatara, and the rats were eradicated in 1992 to prevent this. Another rodent eradication was carried out on the Rangitoto Islands east of D'Urville Island, to prepare for the release of 432 Cook Strait tuatara juveniles in 2004, which were being raised at Victoria University as of 2001.



Tuatara at the Karori Sanctuary are given coloured markings on the head for identification.

Brothers Island tuatara

Sphenodon guntheri is present naturally on one small island with a population of approximately 400. In 1995, 50 juvenile and 18 adult Brothers Island tuatara were moved to Titi Island in Cook Strait, and their establishment monitored. Two years later, more than half of the animals had been re-sighted and all but one had gained weight. In 1998, 34 juveniles from captive breeding and 20 wild caught adults were similarly transferred to Mātū/Somes Island, a more publicly accessible location within Wellington Harbour. The captive juveniles were from induced layings from wild females.

In late October 2007, it was announced that 50 tuatara collected as eggs from North Brother Island and hatched at Victoria University were being released onto Long Island in the outer Marlborough Sounds. The animals had been cared for at Wellington Zoo for the last five years and have been kept in secret in a specially built enclosure at the zoo, off display.

Northern tuatara

Sphenodon punctatus naturally occurs on 29 islands and its population is estimated to be over 60,000 individuals. In 1996, 32 adult northern tuatara were moved from Moutoki Island to Moutohora. The carrying capacity of Moutohora is estimated at 8500 individuals, and the island could allow public viewing of wild tuatara. In 2003, sixty northern tuatara were introduced to Tiritiri Matangi Island from Middle Island in the Mercury group. They are occasionally seen sunbathing by visitors to the island.

A mainland release of *S. punctatus* occurred in 2005 in the heavily fenced and monitored Karori Sanctuary. The second mainland release took place in October 2007, when a further 130 were transferred from Stephens Island to the Karori Sanctuary. In early 2009 the first recorded wild-born offspring were observed.

Captive breeding

There are several tuatara breeding programmes within New Zealand. Southland Museum and Art Gallery in Invercargill, was the first to have a tuatara breeding programme; they breed *Sphenodon punctatus*. Hamilton Zoo and Wellington Zoo also breed tuatara for release into the wild. The Victoria University of Wellington maintains a research programme into the captive breeding of tuatara, and the Pukaha Mount Bruce Wildlife Centre keeps a pair and a juvenile. The WildNZ Trust has a tuatara breeding enclosure at Ruawai. On 28 January 2009, the 11th of 11 eggs belonging to tuataras Henry and Mildred hatched. This rare occurrence came after Henry had surgery to remove a cancerous tumor that was inhibiting both his ability and desire to breed.