004127.a0001 # Sauria (Lizards)

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Lizards are generally small fast-moving four-legged slender terrestrial animals. The group of 4880 species of lizards, however, contains some exceptions: the large predatory Komodo dragon, the marine Galapagos iguana, the gliding *Draco*, various limbless forms, and burrowers.

Introductory article

Article Contents

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004127.s0001 ## Introduction

004127.p0001 The Suborder Sauria, or Lacertilia, includes at least 4880 living species, easily the most diverse living group of reptiles. Lizards arose at least 175 Ma, in the Mid Jurassic, and they diversified into five or six main lines at that time. The snakes, Suborder Serpentes, or Ophidia, arose from lizard ancestors in the Early Cretaceous, some 120 Ma. The technical name for the lizard group, Sauria, was established in 1802, and so it precedes the name Lacertilia, given in 1842. **See also**: Reptilia (reptiles).

004127.s0002 ## Basic Design

004127.p0002 Lizards are generally small in size, the smallest being certain geckos, only 2–3 cm long, but range up to the giant predatory Komodo dragon, *Varanus komodoensis*, at 3 m long and 75 kg in weight when mature. Most lizards have small heads, long backs, relatively short legs and a long tail. There are many variations, however, on this basic design. Some skinks have large heads, plump bodies, short limbs and short tails. The burrowing amphisbaenians look like fat worms, with heads that are reduced to blunt battering rams and usually no limbs. Several other groups are limbless also. Some tree-climbers, like chamaeleons, have their fingers and toes arranged in sets of two opposing three, for improved grip. Other lizards have expanded ribs covered with flaps of skin that act as substantial gliding membranes.

004127.p0003 The lizard skull is specialized by being kinetic, that is, mobile. Lizard skulls contain extra joints in addition to the normal jaw joint (**Figure 1**). These are found between:

1. frontal and parietal in the skull roof, and a matching joint in the palate (the mesokinetic joints), that allows lizards to tip their snouts up and down;
2. braincase and skull (the metakinetic joints);
3. quadrate and squamosal, in the back of the cheek region, and pterygoid and lower jaw, in the palate (the streptostylic joints), to allow the skull to move backwards and forwards relative to the lower jaw.

When the jaws open (**Figure 1a**), the snout tips up and the quadrate bone is nearly horizontal. When the jaws close (**Figure 1b**), the snout tips down and the quadrate becomes more vertical. The pterygoideus muscle (**Figure 1c**) is an important component of this action. This muscle runs diagonally from the back of the lower jaw to a position well forwards on the pterygoid bone on the palate. When the pterygoideus contracts, the jaws close, but the snout is also pulled back, and the quadrate rocks into its vertical position. 004127.p0004

The kinetic skull mechanism allows lizards to open their mouths wider than expected, but also to manipulate their food efficiently. Normally, when an animal closes its jaws, pressure is exerted on a food item not only from above and below, but also from behind, since closing jaws are like closing blades of a pair of scissors. There is a risk that the food may be propelled out of the mouth. The kinetic lizard system means that pressure is exerted only onto the food, and not forwards (**Figure 1d**). 004127.p0005

Apart from skull kinesis, lizards share a number of further synapomorphies of the skull in comparison to other reptiles: the nasal bones are reduced, the squamosal bone is reduced or absent, the quadratojugal bone is absent, the lower temporal bar is incomplete, and the quadrate bone bears a deeply crescent-shaped excavation, or conch, which houses the ear drum. 004127.p0006

Lizards generally have slender bodies and long limbs and feet. The astragalus and calcaneum, the two main ankle bones are fused, and the fifth metatarsal (the top joint in the little toe) is L-shaped, features that perhaps give lizards more control over their foot actions during climbing. 004127.p0007

The primitive condition of lizards can be seen in the 'living fossil' *Sphenodon*, the tuatara, from New Zealand. *Sphenodon* belongs to a long-lived group, the sphenodontids, which arose in the Late Triassic, 230 Ma, and which were moderately diverse at that time, and in the Jurassic and Cretaceous included some marine forms. *Sphenodon* has a solid skull, with no hint of kinesis (**Figure 1e**). Instead, it retains the full rim of bone around both of the temporal 004127.p0008 openings in the skull. The lower temporal bar, composed of the jugal and quadratojugal, is complete, whereas in lizards, this bar and also the quadratojugal are absent.

004127.s0003 Diversity

004127.p0009 Reptiles today number about 8200 species, of which lizards are by far the most diverse, with about 4880 species. Of the remainder, 2950 species are snakes, while turtles and crocodilians are much less diverse. The diversities of the major lizard groups are indicated in **Table 1**.

004127.p0010 Lizards are most diverse in the tropics. Moving away from the equator, diversity decreases, and large species become rarer and rarer. Some lizards live as far north as the Arctic Circle, and as far south as the southern tip of South America, and others above the treeline in temperate zones. With the exception of Antarctica, they have reached all continents and every oceanic island apart from New Zealand and Hawaii. **See also**: Geographical variation.

004127.s0004 Habits and Lifestyles

004127.p0011 Lizards show a great range of shapes and sizes (**Figure 2**), and their habits range from diving in the sea to gliding between trees, and from burrowing in the soil to stalking insects in the tree tops. The major groups of lizards are listed in **Table 1**, together with an outline of the habits and lifestyles of the major groups.

004127.p0012 The iguanas are often brightly coloured forms, with ornamental frills and throat fans. They are herbivores, mainly arboreal, and are found mainly in tropical South America. Large ground-dwelling iguanas live on islands in the Caribbean and on the Galapagos Islands, where their most striking representative is the marine iguana. This iguana, *Amblyrhynchus*, feeds on seaweed, which it gathers from the seabed at depths of 10 m or more. The agamids are another large group of modest-sized lizards, found in the Old World, and they live on the ground and in trees. Close relatives are the chamaeleons, tree-living lizards found mainly in Africa that feed on insects by flicking out an elongate tongue with lightning speed, and seizing the prey on its sticky end. Chamaeleons sit still in trees, gripping the branches with their unusual feet (two fingers opposing three in front, three opposing two behind) and their tails. Their eyes can swivel from side to side, and they can change colour to match the background; both these adaptations allow them to remain concealed until they are ready to strike.

004127.p0013 Geckos are small agile forms that are mainly nocturnal. Many of them have adhesive pads on their feet, made from ridged scales, and they can run about on the walls and ceilings of houses. They are found on all continents except Antarctica. Pygopodids, close relatives, lack their forelimbs and have reduced hindlimbs. They are found in Australia and New Guinea.

The amphisbaenians are sometimes classified as a separate Suborder from remaining lizards. However, cladistic analyses suggest they fall within the clade Lacertilia. Amphisbaenians, or 'worm lizards', are highly specialized burrowers. Their bodies are cylindrical, superficially like a large worm, and most have entirely lost their limbs. The eyes and ears are hidden under the skin, and the skull is modified into a short blunt object that is used to batter through the earth and form tunnels. Amphisbaenians live in tropical South America and Africa, and there is one species in Florida, USA. 004127.p0014

The scincomorphs include skinks, often long-bodied and short-tailed, with short limbs. There are nearly 2000 species and they are found on all continents except Antarctica. The European and Asian lacertids, close relatives, are also small, ground-living lizards that feed on insects and worms. The teiids, herbivorous lizards, are mainly small forms that inhabit the New World. The cordylids are small to medium-sized terrestrial lizards with heavy bony scutes beneath their scales. They are found in subSaharan Africa and on Madagascar. The xantusiids are tiny terrestrial lizards found in the New World. 004127.p0015

The anguimorphs are a diverse group of perhaps six families. They include the varanids, or monitor lizards, a widespread Old World tropical group of ground-dwelling predatory lizards. Varanids include the largest living lizard, the Komodo monitor, *V. komodoensis*, as well as other giant fossil forms including a range of extinct marine forms such as the Late Cretaceous mosasaurs, 3–10 m in length. The living anguids are small elongate forms, often limbless, and found in the America, Europe and Asia. They include the glass lizard, *Ophisaurus* and the slow worm, *Anguis*. The helodermatids include the Gila monster, a bulky lizard of desert regions of South-West North America, which is one of only two venomous lizards. Unlike snakes, it stores venom in its lower jaw. Other anguimorphs include the anniellids, a family of two species of small burrowers from North America; the xenosaurids, represented by two species in Mexico and one in China; and the lanthanotids, a single species of semiaquatic lizard from Borneo. 004127.p0016

Lizards are all ectotherms, in other words, animals that do not have direct internal, physiological, control of their body temperatures. Lizards use behavioural means to control their body temperatures. When the sun rises, they crawl out of their hiding places and bask on a rock. They absorb heat by direct radiation from the sun, but also by conduction through the rock, and by reflection from surrounding rocks. When it has absorbed enough heat to become active, a lizard goes about its business, until the air temperature becomes too high in the middle of the day. Then, it may shelter in a dark spot until air temperatures cool down. At night, as body heat is lost, the lizard becomes inactive. 004127.p0017

004127.p0018 Lizards can operate efficiently over a range of body temperatures as much as 4–10°C, unlike birds and mammals, which must maintain a constant body temperature within 1–2°C. The rate of heat absorption and loss can be controlled by varying the orientation of the body to the sun, the body shape, the body colour, and the rate of blood flow in peripheral regions of the body. These mechanisms allow lizards to divorce themselves from changes in the temperature of the air to a great extent: active lizards living above the timberline in temperate regions may be 30°C warmer than air temperature.

004127.p0019 Lizards are well adapted to conserving water, and this allows them to live in arid regions, both hot and cold. Indeed, lizards are the most successful desert-dwelling vertebrates. Their water conservation strategies depend on three attributes.

1. They have low metabolic rates, as a result of their ectothermy; a lizard generally eats 1/10th or 1/15th of the amount of food required by a mammal of the same size.
2. They excrete nitrogenous waste as semisolid uric acid and salts, instead of as urea as in mammals, which must be dissolved in water to be passed as urine.
3. Many lizards have additional pathways of salt secretion via salt glands in the nasal region; salt is excreted and is then expelled by sneezing or shaking the head.

004127.s0005 ## Life Histories

004127.p0020 Many lizards engage in premating rituals. Species-specific signals are given by specialized crests, throat pouches and other structures that may be brightly coloured, and, which are expanded and waved about during display activity. The display activities may involve specific movements – species of *Anolis* lizards on Costa Rica raise their bodies on their forelimbs, bob their heads, and expand and contract the throat pouch in particular ways unique to each species. The site chosen for display is also indicative of species.

004127.p0021 Most lizards lay eggs (ovipary), often elongate and with leathery shells, instead of hard mineralized shells. Lizards lay from 1–2 to 60 eggs in a clutch. The nest is usually abandoned, and when the young hatch they must fend for themselves immediately. This leads to a high mortality rate among juveniles, with only 15–40% reaching sexual maturity, depending on the species and environmental conditions.

004127.p0022 Some have suppressed egg-laying, and produce live young (vivipary), a habit seen also in some snakes. However, this form of live-bearing is different from that of placental mammals in that the mother lizard or snake retains the eggs inside until hatching time. This habit evolved many times, perhaps on 45 occasions, and it is seen most in lizards and snakes that live in colder areas, so the mother can bask in the sun to keep the eggs warm.

Lizards grow to adult size rapidly, and sexual maturity is 004127.p0023
reached within 1–3 years, but this figure has been determined in only a tiny number of lizard species in the wild. Lizards typically have rather short lives. Survivorship to first breeding is often in the range 10–50% of juveniles, and survivorship to second breeding is similarly 10–50%. In most species, individual lizards are unlikely to survive for more than 1–2 years in all. Larger lizards grow more slowly. The Komodo dragon, *V. komodoensis*, probably reaches sexual maturity at an age of 4–6 years when about 1.5 m long. It is estimated that the largest Komodo dragons, at 3.5 m long, are about 20 years old, perhaps the maximum age attained by any lizard. Problems in determining these figures are that wild lizards must be marked and recaught year after year to follow their progress, and figures from zoos are hard to compare, since captive animals may be protected and fed in ways that allow them to live much longer than any animal in the wild.

Fossil History 004127.s0006

The first lepidosaurs, members of the broader group that 004127.p0024
includes lizards, are the sphenodontids of the Late Triassic. These small- to medium-sized herbivorous and insectivorous forms are similar to the living tuatara, *Sphenodon* (**Figure 1e**), and probably indicate what the ancestor of lizards was like.

The oldest fossils of unequivocal lizards date from the 004127.p0025
Mid Jurassic of England and Scotland, and they include fragmentary remains of a possible gekkotan, an anguimorph, and several scincomorphs. These three groups radiated further in the Late Jurassic, and more complete fossils are known from North America and Europe from a number of locations.

The other lizard groups, Iguania and Amphisbaenia, as 004127.p0026
well as the snakes, must have originated in the Late Jurassic, because of the nature of the phylogenetic tree, but fossils are not known until later. The oldest iguanian is an agamid from the Late Cretaceous of Mongolia. The fossil record of amphisbaenians is limited, consisting only of isolated vertebrae from the Palaeocene and Eocene of North America and France. The first snake fossils date from the Early Cretaceous. Several lizard groups radiated in the Late Cretaceous, not least the Late Cretaceous dolichosaurs and mosasaurs, both relatives of varanids, and both highly successful marine predators, but which became extinct at the end of the Cretaceous.

004127.s0007 Phylogeny

004127.p0027 Snakes and lizards, as well as the tuatara, the sole surviving sphenodontid, are grouped together in the Order Squamata. The phylogeny of the lizards is debated, mainly on the basis of morphological data, which offer a number of possible resolutions of the phylogeny. Particularly problematic are the placements of amphisbaenians and of snakes. New character information, new fossils and new information from molecular sequencing may resolve the patterns. **See also**: Serpentes (snakes).

004127.p0028 One view (**Figure 3**) is that Iguania are the basal lizards. The remaining groups, termed collectively Scleroglossa, all share a keratinized (horn-covered) tongue and other features of the skull. Within Scleroglossa, the Gekkota may be the outgroup of the remaining four infraorders, but this is not clear, and Amphisbaenia and Serpentes may fit somewhere near this point in the cladogram. Serpentes was traditionally placed here, but new evidence from fossils suggests that snakes may be related more closely to the mosasaurs and other fossil aquatic groups, hence Varanoidea. The Anguimorpha and Scincomorpha seem to pair off as the clade Autarchoglossa, based on the shared possession of no contact between the jugal and squamosal bones, and other features.

004127.s0008 Conclusion

004127.p0029 Lizards are a highly successful vertebrate group, slightly more diverse than mammals. Most lizards are 50–300 mm long, long-tailed, agile and adapted to arid conditions. However, there are many exceptions, and the group is more diverse in habits and lifestyles than is often assumed. Lizards occupy all parts of the world except the polar regions, they live on the ground, in trees, and some live a partially marine existence. Lizards feed on plants, insects and larger prey. Lizards range in size from 20 mm to 3 m. Several lizard groups independently have lost their limbs (mainly to permit burrowing), others have evolved a kind of vivipary (live birth), some can glide, and two species are poisonous.

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Glossary

Clade#A monophyletic group; one that has a single ancestor and includes all descendants of that ancestor.

Ectothermy#'Cold-bloodedness'; the condition in which an animal does not control its body temperature by internal means.

Kinesis#Mobility (of a skull, typically) about particular joints.

Monophyletic#A group that has a single ancestor and includes all descendants of that ancestor; a clade.

Ovipary#The production of young from eggs that are laid.

Paraphyletic#A group that has a single ancestor, but does not include all descendants of that ancestor (like Sauria, which includes Serpentes).

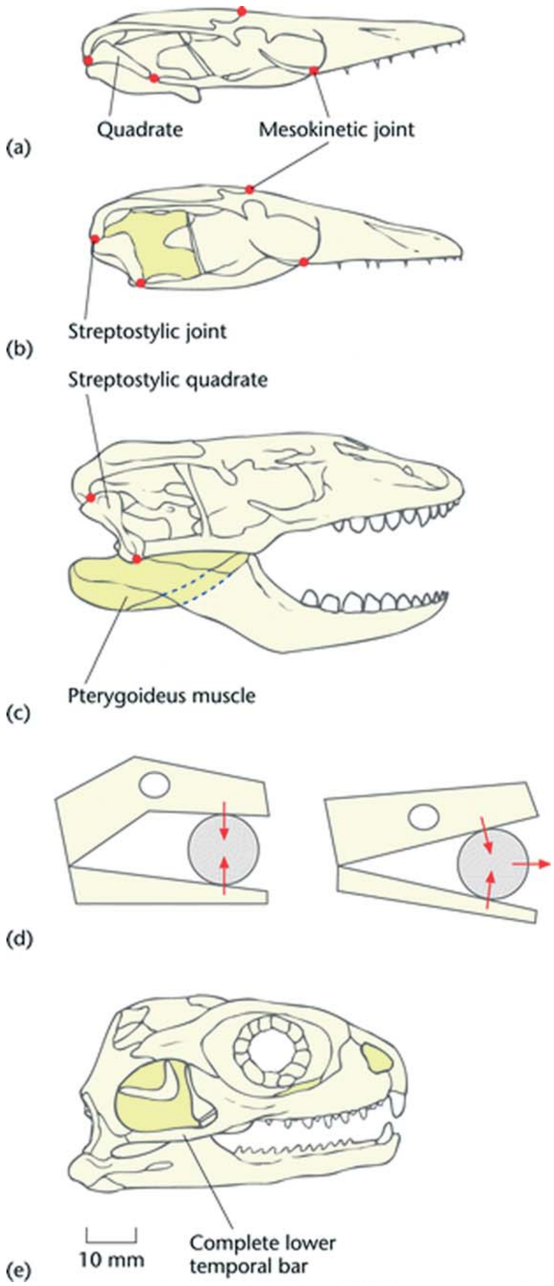
Phylogenetic#Relating to phylogeny (patterns of evolution and relationships).

Synapomorphy#A shared derived character; in cladistics, a character that defines a clade.

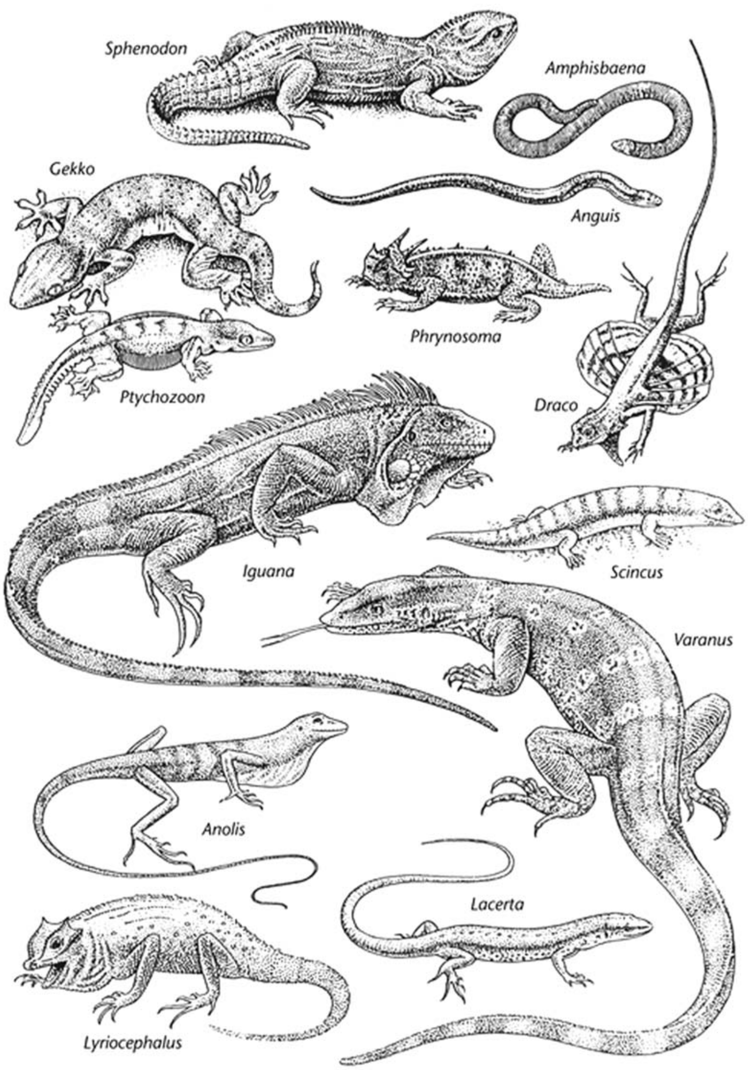
Vivipary#The production of live young directly from the mother's body, either by retention of eggs until hatching (in reptiles) or through a placenta (mammals).

004127.t0001 **Table 1** Classification of lizards, a consensus view based on the latest cladistic analyses (from Benton, 2004). Approximate diversity of the infraorders is indicated

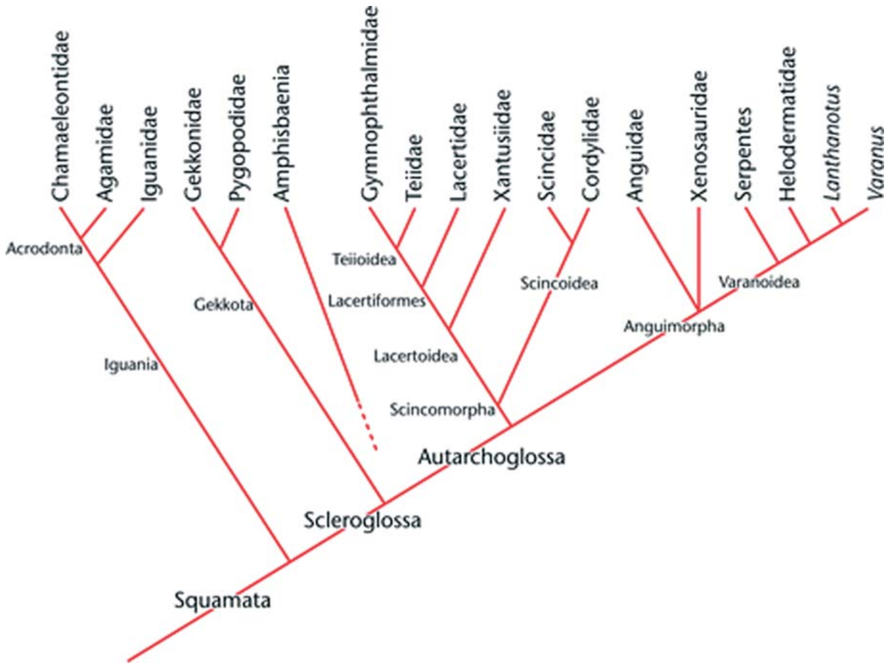
Order Squamata	
Suborder Lacertilia (= Sauria)	
Infraorder Iguania	1445 species
Family	
Iguanidae	
Agamidae	
Chamaeleonidae	
Infraorder Gekkota	1200 species
Family	
Gekkonidae	
Pygopodidae	
Infraorder Amphisbaenia	165 species
Family	
Amphisbaenidae	
Rhineuridae	
Bipedidae	
Trogonophidae	
Infraorder Scincomorpha	1950 species
Family	
Scincidae	
Lacertidae	
Xantusiidae	
Teiidae	
Gymnophthalmidae	
Cordylidae	
Infraorder Anguimorpha	120 species
Family	
Anguidae	
Anniellidae	
Xenosauridae	
Helodermatidae	
Lanthanotidae	
Varanidae	
Suborder Serpentes	



004127.f0001 **Figure 1** Lizard jaw mechanics: skull of *Varanus*, showing the skull flexed (a) up and (b) down; (c) lizard skull with the jaws open, and the streptostylic quadrate swung back, so that the pterygoideus jaw muscles have their maximum effect; (d) diagrams of lizard skulls showing the advantages of kinesis in holding a food particle (left), which would otherwise be forced out by the bite in a nonmobile skull (right). (e) Skull of the tuatara *Sphenodon*. Based on various sources in Benton (2004).



004127.f0002 **Figure 2** The diversity of modern lizards. Reproduced from Young, JZ (1981). *The Life of Vertebrates.* Oxford: Clarendon Press. With permission of Oxford University Press.



004127.f0003 **Figure 3** Cladogram of lizard relationships, based on data in Estes *et al.* (1988). Lizard relationships are highly contentious, and this cladogram is a 'conservative' estimate.