Serpentes (Snakes)

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Introductory article

Article Contents

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Snakes are a diverse group of long-bodied, limb-reduced reptiles closely related to lizards; together they are termed squamate reptiles. Primitive snakes with vestigial legs appear in the fossil record of the Cretaceous period (~90 Mya). Snakes have since been diversified rapidly, and now comprise ~3500 species that occupy terrestrial, subterranean, aboreal and aquatic niches. All snakes are predators, having highly mobile skulls and jaws that can often swallow prey much larger than their own diameter. Primitive snakes such as boas, pythons and blindsnakes lack venom fangs. Such fangs have evolved repeatedly within more advanced snakes, called the Colubroidea, which make up ~80% of the diversity of living snakes: front fangs in viperids (e.g. vipers and rattlesnakes), fixed front fangs in elapids (e.g. mambas and cobras) and rear fangs in many lineages of colubrids (e.g. boomslangs and twig snakes).

Basic Anatomy

Snakes (formal name: Serpentes), lizards and amphisbaenians together comprise the group of reptiles called squamates (formal name: Squamata). Snakes evolved when a lineage of lizards lost their limbs, greatly elongated their bodies and developed extremely flexible skulls and jaws (Wiens *et al*., 2006). Accordingly, the anatomy of a snake can be readily understood as that of a lizard with these modifications superimposed. The closest lizard relatives of snakes remain contentious, but the intersection of molecular and morphological data points towards anguimorphs, which include predaceous forms such as monitors and gila monsters (Lee, 2009). **See also**: Reptilia (Reptiles); Sauria (Lizards)

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Head

Unlike most lizards, all snakes lack movable eyelids; instead, the eyes are covered by a transparent scale. Unlike most lizards, they lack eardrums, and hear only low-frequency sounds, either directly through the quadrate bone or through the lower jaw. They have a long, retractable forked tongue used for chemoreception (see section General Ecology).

With their elongated shape, snakes have small heads relative to their body size, but almost invariably swallow prey whole; this problem is often circumvented by adaptations to increase the gape. The skull of snakes consists of a solid, bony braincase surrounded by mobile struts bearing the upper and lower jaws (Cundall and Irish, 2008). Snakes have much more mobility between skull bones (cranial kinesis) compared to lizards. The tooth-bearing bones of the upper jaw are all mobile. The lateral element (the maxilla) is used to capture prey during the initial strike; later, the elements in the roof of the mouth (palatines and pterygoid) ratchet the prey into the oesophagus during the swallowing phase (**Figure 1**). The lower jaws are also highly flexible. In primitive snakes, a joint within the left and right halves of the lower jaw allows them to bulge outwards during the swallowing of large prey, although the left and right jaws remain connected at the chin. In more advanced snakes, the left and right jaws can separate, further increasing the gape (Young, 1998). Contrary to popular belief, the hinge between the upper and lower jaws never dislocates.

Venom delivery systems are present in the upper jaws of many advanced snakes (Jackson, 2007; Vonk *et al*., 2008). These consist of fangs (enlarged teeth with grooves or canals for injecting venom) and venom glands (modified oral glands, similar to our salivary glands). There are four basic arrangements (**Figure 1**). Aglyphous snakes lack fangs and true venom glands; this arrangement is found in all primitive lineages such as boas, pythons, pipesnakes and blindsnakes, and is retained in many more advanced snakes (Colubroidea). Other advanced snakes have fangs and glands. Opisthoglyphous snakes have fixed fangs at the back of the jaws. Some colubrids (e.g. boomslangs and twig snakes) have this arrangement. Proteroglyphous snakes have fixed fangs at the front of the jaws. This characterises

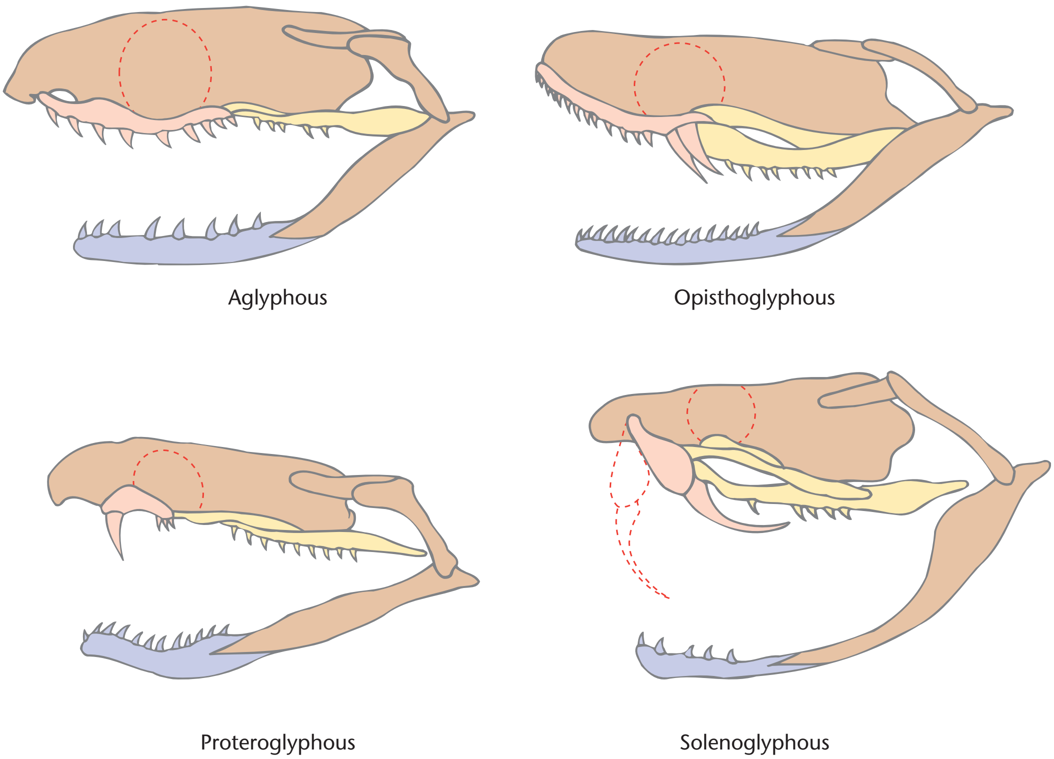

Figure 1 The four major jaw systems found in snakes. The marginal element on the upper jaw is shown in pink, the elements on the roof of the mouth are shown in yellow and the lower jaw element is shown in blue.

elapids (e.g. cobras and mambas) and their descendants, the sea snakes. Solenoglyphous snakes have mobile fangs that are only erected while striking. As the fangs can be folded away when not in use, they can be very large. Viperids (e.g. vipers, adders and rattlesnakes) have this arrangement. **See also**: Venoms

Body

Snakes are one of many tetrapod lineages which have evolved limblessness: all snakes lack a pectoral girdle and forelimbs, and most lack a pelvis and hindlimbs. However, living pythons retain tiny but externally visible hindlimbs, which are larger in males and used in courtship; some fossil snakes possess even larger limbs (see section Fossil History). The snake body is always long and flexible, although its shape may vary from rather stout (as in adders) to extremely thin (as in twig snakes). There are numerous vertebrae, usually between 120 and 600, most bearing a pair of ribs. There are extra articulatory points (zygosphenes and zygantra) between adjacent vertebrae, resulting in increased strength of the otherwise long and potentially weak vertebral column. The muscles of the body wall are very well developed and complex, permitting both great flexibility and precise local control of body movement, useful for both locomotion (e.g. arboreal forms) and feeding (constrictors). The tail is usually much shorter than that in lizards, being no more than about one-quarter of the total length.

Most of the organs of typical reptiles such as lizards are present, but their form has been modified to fit into a long slender body (Gans and Gaunt, 1998; **Figure 2**). The paired kidneys and reproductive organs (testes and ovaries) are arranged not side by side but one behind the other. The liver is not a roundish mass, but is elongate. There is only a single, large elongate lung (the other being vestigial or absent), instead of the paired arrangement found in other reptiles. Many other elongate, limb-reduced lizard groups (e.g. amphisbaenians) show similar adaptations.

As in lizards, males have paired copulatory organs called hemipenes (singular: hemipenis). These are normally ensheathed within the tail, but one is everted during copulation. Each hemipenis is a forked structure often covered with small spines. **See also**: Reproduction in Reptiles and Birds

Diversity

Snakes are one of the most rapidly diversifying groups of vertebrates. There are $\sim$3500 living species, mostly belonging to the superfamily Colubroidea. Molecular and morphological data have greatly clarified relationships

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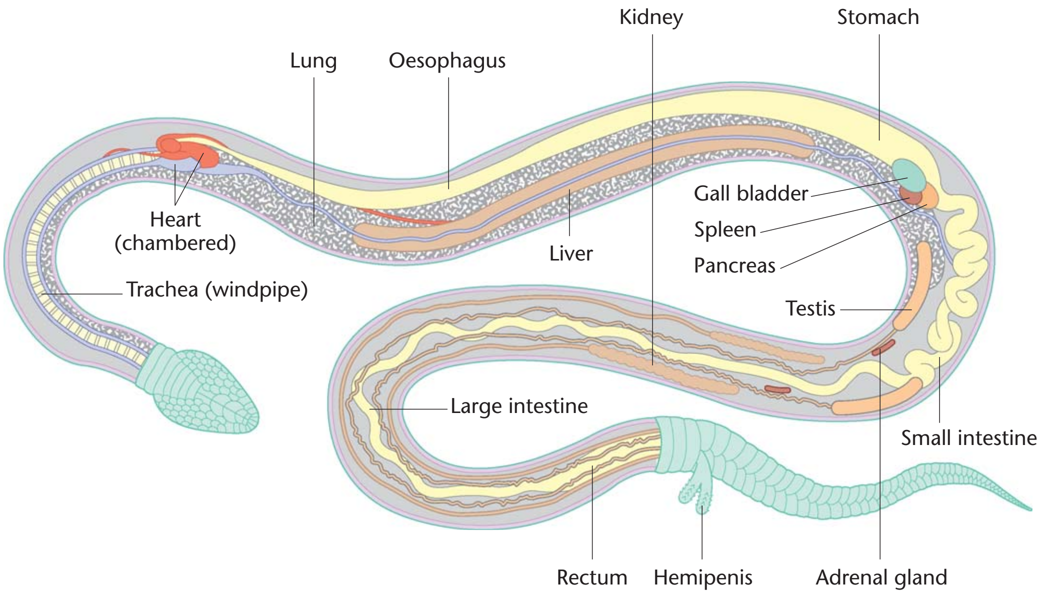

Figure 2 The internal anatomy of a typical snake in ventral (belly) view. This specimen is a male. After drawing by Kirshner D in Shine (2009).

between the major groups of snakes (e.g. Scanlon and Lee, 2011; Pyron *et al*., 2011), which are depicted in **Figure 3** (see section Phylogeny Reconstruction).

Among the living snakes, the most basal forms are the worm-like blindsnakes or Scolecophidians (Typhlopidae, Leptotyphlopidae and Anomalepididae). These small snakes are totally fossorial and accordingly have reduced eyes and cylindrical worm-like bodies. They have very small jaws and feed mainly on small invertebrates, especially ants or termites.

The remaining snakes, called alethinophidians, are characterised by evolutionary innovations such as slightly larger jaws and by the ability to constrict their prey (lost in some advanced venomous forms). They are usually larger and have more developed eyes.

The most primitive alethinophidians are the red pipe snakes (Aniliidae), Asian pipesnakes (Cylindrophidae) and shield-tail snakes (Uropeltidae). These are also largely fossorial, but some are also quite aquatic. The diet of most of these snakes includes vertebrates, such as frogs, rodents, eels, lizards and caecilians. Genetic data unite the dwarf-boas (family Tropidophiidae) with red pipesnakes, together forming an ancient New World snake lineage called Amerophidia (Vidal *et al*., 2007); this primitive position for dwarf-boas is surprising because they have many advanced traits otherwise restricted to macrostomatans (see below).

More advanced alethinophidians, called macrostomatans, have further evolutionary innovations such as lower jaws with distensible tips, and a single row of enlarged belly scales used in terrestrial locomotion (lost in most sea snakes). They are also active above ground for at least large parts of their lives. Macrostomatans include most 'familiar' snakes, such as boas and pythons, colubrids and all venomous forms.

Boas, sand boas and pythons (Boidae, Erycinae and Pythonidae) are mostly large, and include the biggest living snakes. Many are arboreal, and large warm-blooded (bird and mammal) prey is common. Accordingly, many boas and pythons have heat-sensitive lip organs that help detect prey, and constriction is very well developed. Round-island and dwarf 'boas' (families Bolyeriidae and Tropidophiidae) are small, boa-like snakes that are not particularly closely related to true boas; in fact, the latter might be closely related to the primitive pipesnakes. They feed principally on reptiles and amphibians. Round-island boas are remarkable in that each upper jaw element (maxilla) is divided into two movable halves, an adaptation for gripping slippery prey such as skinks.

File snakes (Acrochordidae) are highly aquatic snakes with granular skin and sluggish, limp bodies. They have huge jaws and can swallow extremely large fish prey; however, they feed very infrequently and have very slow metabolisms, perhaps reproducing only once every decade. They are closely related to colubroids.

Colubroids are by far the most species-rich group of snakes with more than 2800 species and are the dominant group of snakes on all continents; as such they have sometimes been called 'typical snakes'. They include racers (*Elaphe*), whipsnakes (*Coluber*), grass snakes (*Natrix*) and boomslangs (*Dispholidus*). They generally move more rapidly, and have a greater range of movements than the previous families, which is correlated with a tendency to use more open habitats. Colubroids also have more specialised dentition, and more extreme adaptations on the roof of the mouth for ratcheting prey down the throat. The two clades of colubroids that have independently evolved front fangs have long been recognised: the Viperidae and Elapidae. However, most colubroids either lack fangs (aglyphy), or have rear fangs (opisthoglyphy); until recently they were all lumped into a single family Colubridae *sensu lato*. There is

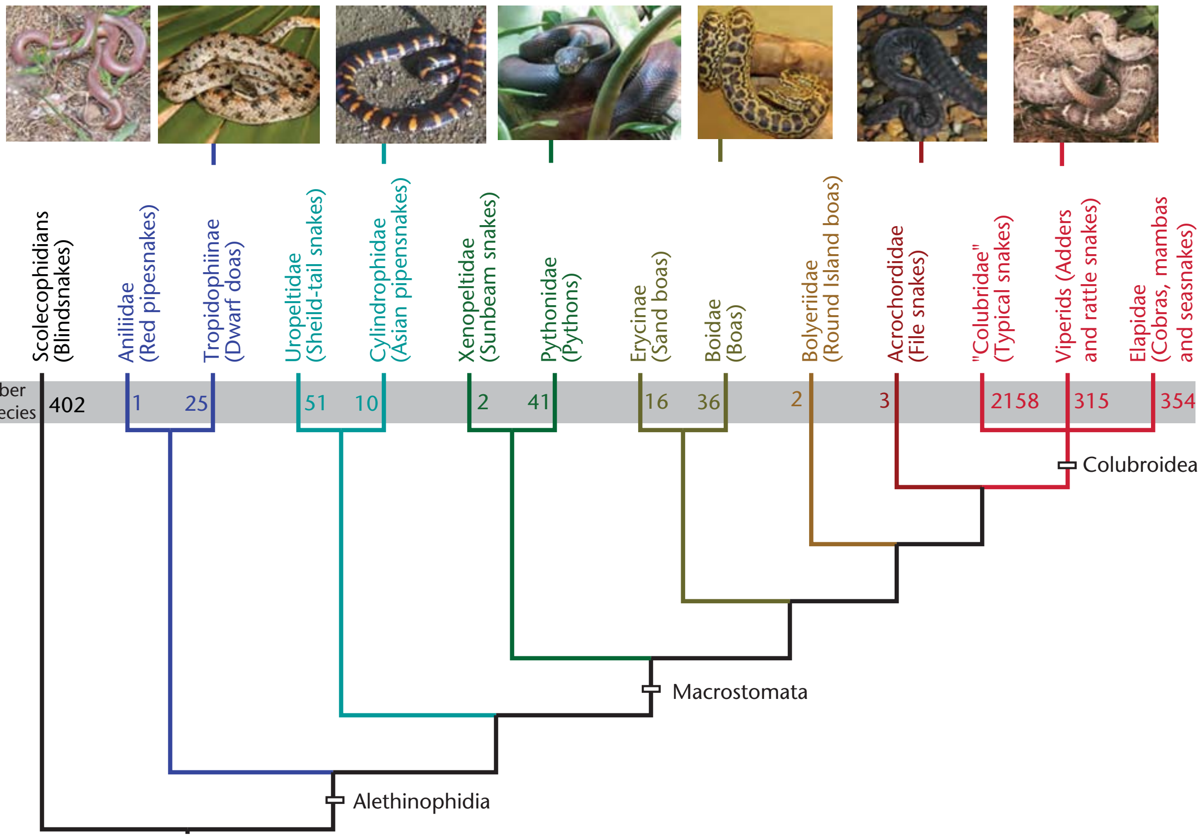

Figure 3 The evolutionary relationships of the major groups of living snakes; some minor groups are not shown. 'Colubridae' is in quotes because the taxonomy of this hugely diverse lineage is currently in flux (e.g. Pyron *et al.*, 2011). The numbers on the branches refer to species diversity of each lineage (from http://www.reptile-database.org, accessed on 2 February 2013); Photo credits (left to right) as follows: (1) Kapustin K, (2) Niemiller M, (3) Djatmiko WA, (4) Vickers T, (5) Jean P, (6) Macdonald S, (7) NBII public domain photograph. Photo 2 © Matthew Niemiller and used with permission, all other photos used are public domain images, courtesy of Wikimedia under their conditions.

widespread agreement that this heterogenous assemblage needs to be split, and one recent proposal divides it into Colubridae *sensu stricto*, Lamprophiidae, Homalopsidae, Pareatidae and Xenodermatidae (Pyron *et al.*, 2011).

Vipers (Viperidae) are characterised by front fangs that can be folded backwards when not in use (solenoglyphy), and which thus can be very long. They are generally stout-bodied, sit-and-wait predators, but some arboreal forms are more slender. The venom is usually haemotoxic (damaging the blood circulatory system, muscles and other tissues). Typical forms include rattlesnakes (*Crotalus*), adders (*Vipera*) and copperheads (*Agkistrodon*).

Elapids (Elapidae) are characterised by fixed front fangs (proteroglyphy), which are usually shorter than those of vipers. Most are more slender and active than vipers, but again many exceptions exist. The venom is usually neurotoxic (interfering with the nervous system). Elapids include the most deadly snakes, and are the dominant snakes in Australia. Typical forms include cobras (*Naja*), coral snakes (*Micrurus*), mambas (*Dendroaspis*) and taipans (*Oxyuranus*).

Living sea snakes (Laticaudidae and Hydrophiidae) are descended from terrestrial elapids, and accordingly have fixed front fangs and potent neurotoxins. They have laterally compressed bodies and paddle-like tails to facilitate swimming, and valves in the nostrils to exclude water. Laticaudids periodically return to shore to deposit eggs, whereas hydrophiids are totally marine, bearing live young underwater. The two main groups of sea snakes (the oviparous sea kraits and viviparous true sea snakes) are probably not closely related, but represent two separate marine invasions (Sanders *et al.*, 2008). **See also**: Toxin Action: Molecular Mechanisms

General Ecology

Despite all being long and limbless, snakes are one of the most ecologically diverse groups of vertebrates. They occupy environments ranging from deserts to rainforests, and from mountains to the open ocean. There are burrowing, arboreal, terrestrial, aquatic and even gliding forms. Like most reptiles, snakes are ectotherms ('cold-blooded') and rely on external rather than metabolic heat for body warmth. Some pythons are a notable exception, being able to generate body heat via shivering while brooding their eggs (Hutchison *et al.*, 1966). Ectothermy means snakes are most diverse and abundant in tropical areas, scarcer in temperate zones and absent from polar regions. Temperate forms must hibernate during winter. **See also**: Hot Deserts; Tropical Forests

Snakes use four main modes of locomotion (Gans, 1986). Lateral undulation is the primitive and most common mode (and is also typical of other limb-reduced lizards): sinusoidal bends are propagated anteroposteriorly along the body and push against the substrate to propel the animal forwards. Marine snakes employ similar motions in swimming. Rectilinear locomotion is present in many large or stocky snakes; such snakes 'glide' over the substrate, propelled by flickering movements of the enlarged belly scales. Concertina locomotion is found in many fossorial or arboreal forms. As its name suggests, it involves repeated cycles of stretching the anterior region forwards, anchoring it and then contracting the entire body to drag the posterior region forwards. Sidewinding occurs in many vipers, and a few boas and colubrids, and appears to be an adaptation for rapid locomotion over loose sand. Such snakes move by alternately throwing the front of the body laterally, followed by the rear and then repeating this action.

Even the earliest snakes had extensive adaptations for predation, and this constraint appears to have prevented snakes from evolving into omnivores or herbivores. All snakes are carnivorous, and the diversity of prey is very great (Cundall and Greene, 2000). Tongue-flicking is used to pick up airborne molecules ('scents') of prey and other objects, and these are transmitted by the tongue to the vomeronasal organ in the roof of the mouth. Differences in the intensity of the scent between the two prongs of the forked tongue allow the direction of the source to be determined (Schwenk, 1994). Small reptiles and amphibians form the diet of many snakes; however, other items range from insects to large mammals, and buried fish eggs to bats caught in flight. Most primitive snakes that take larger prey kill by constriction and continuous bites. However, many advanced forms have evolved venom-delivery systems to subdue prey; many of these snakes do not constrict and often release their bite immediately after injecting venom, presumably to avoid injury caused by large struggling prey. **See also**: Predation (Including Parasites and Disease) and Herbivory

Most snakes are egg layers, but many are live bearers, especially in cooler climates, that is, high latitudes or altitudes (Shine, 2003). Reproduction is always seasonal in temperate zones, synchronised with warm weather, but might be aseasonal in tropical areas. Parental care is rare but occurs in pythons and some boids, vipers and elapids. The flower-pot blindsnake (*Ramphotyphlops braminus*) consists only of females, which reproduce via parthenogenesis (Nussbaum, 1980).

Fossil History

The fossil record of snakes consists mainly of isolated vertebrae, and relatively complete skeletons are rare. However, some exceptionally complete forms are known. *Najash*, from the middle Cretaceous of Argentina (Apesteguía and Zaher, 2006), was a moderate-sized terrestrial snake with a well developed pelvis and hindlimb. *Pachyrhachis*, a small-headed marine snake from the middle Cretaceous of the Middle East, also retains prominent legs (Caldwell and Lee, 1997): it is superficially similar to some modern front-fanged sea snakes that probe eel burrows with their tiny heads, though not closely related to these forms. *Najash* and *Pachyrhachis* are transitional forms, possessing some advanced snake-like features – such as a long body, some degree of skull flexibility, and loss of forelimbs and shoulder girdle – yet retaining some archaic lizard-like features such as most bones of the pelvis and hindlimbs. Their exact phylogenetic relationships remain debated, though there is increasing evidence that they lie somewhere near the base of snakes (Palci *et al*., 2013). **See also**: Fossils in Phylogenetic Reconstruction

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