Ingestion in Reptiles and Amphibians

Introductory article

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Article Contents

The feeding stages of prey capture, ingestion, processing, intraoral transport and swallowing are accomplished in different ways in different species of amphibians (caecilians, salamanders and frogs) and reptiles (crocodilians, turtles, tuatara, lizards, amphisbaeneans and snakes – birds have diverged so much from other reptile groups that they can be considered separately). The structural and ecological diversity of amphibians and reptiles is reflected in the diversity of their feeding systems.

Introduction

Approximately 380 million years ago, the piscine ancestors of terrestrial vertebrates began a slow transition to life on land. Among the many challenges facing early tetrapods was how to capture and manipulate prey in the new environment. The ancestral mechanism of suction-feeding, effective within the viscous and supportive medium of water, was unworkable in air. A mobile, muscular tongue evolved in association with the hyoid and gill arch (hyobranchial) skeleton, and was used by tetrapods to capture and swallow food on land. The tongue remains an essential part of the feeding apparatus in most terrestrial vertebrates, including living amphibians and reptiles (**Figure 1**), although its specific role varies from group to group. In general, feeding involves a coordinated series of cyclical movements of the tongue, jaws and hyobranchial skeleton. Some amphibians and reptiles have returned to life in water, where they have evolved suction-feeding mechanisms secondarily.

In order to facilitate study and comparisons among species, scientists recognize several distinct feeding stages. Not all stages are present in every species, and one stage sometimes blends into the next, but each represents a potentially different mechanical 'task' performed by the feeding apparatus, involving different parts and movements: (1) Prey capture is the initial seizure and immobilization of a food item. In amphibians and reptiles, it is nearly always coincident with (2) ingestion, moving a food item from the environment into the mouth, usually after capture with the tongue or the jaws. (3) Processing is the mechanical reduction of a food item, usually by chewing. (4) Intraoral transport refers to the movement of the food into the pharynx and (5) swallowing is the passage of food from the pharynx into the oesophagus where peristalsis takes over the task of moving food through the gut.

Feeding in Amphibians

Amphibians include three living orders: frogs (Anura), salamanders (Urodela) and caecilians (Gymnophiona). With only a few exceptions, all species possess a tongue that is used to varying degrees during feeding. The morphology and function of the jaws and tongue vary widely, and each group has evolved unique adaptations for capturing, processing and swallowing prey.

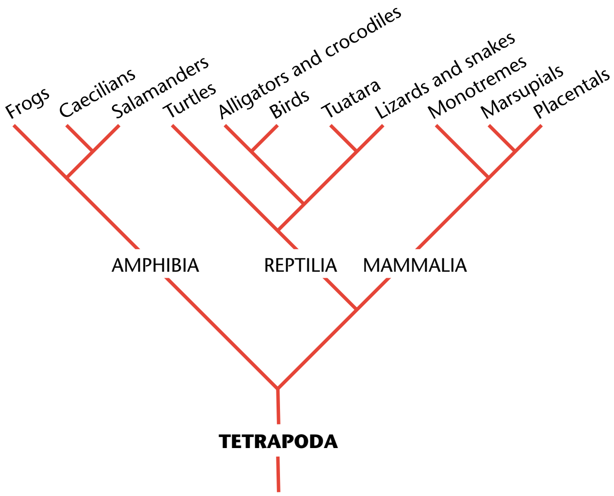

Figure 1 Evolutionary relationships among terrestrial vertebrates (tetrapods). The ancestors of tetrapods were a now-extinct group of fish that probably used suction to capture and manipulate prey. Feeding form and function of the various amphibian and reptile groups are discussed in the text. Scientific names for the amphibian and reptile groups shown in the figure are as follows: frogs (Anura); caecilians (Gymnophiona); salamanders (Urodela); turtles (Testudines); alligators and crocodiles (Crocodylia); birds (Aves); tuatara (Rhynchocephalia); lizards and snakes (Squamata).

Virtually all amphibians are carnivorous, typically eating small invertebrates such as insects, worms, snails or crustaceans. Amphibians occasionally eat other vertebrates. There are reports of caecilians eating lizards; of salamanders eating other salamanders, frogs, lizards, snakes and mice; and of frogs eating fish, mice and other frogs. Only a few species of frogs have been reported to include plant matter (fruits or leaves) in their diet.

Terrestrial frogs and salamanders depend heavily on vision to locate prey, whereas terrestrial caecilians appear to rely primarily on olfaction. Many aquatic amphibians use lateral line electrosensory and/or mechanosensory organs to locate prey in water.

Morphology of the feeding apparatus

The feeding apparatus of living amphibians is morphologically diverse. It consists of the cranium, mandible, tongue, hyobranchium and associated muscles. Caecilians possess a heavily ossified cranium, powerful jaws, an articulated, partly bony hyobranchium and a simple, non-protrusible tongue. Most salamanders and frogs possess a weakly ossified cranium; relatively weak jaws; and complex, protrusible or projectile tongues. Like caecilians, salamanders possess a bony, articulated hyobranchium, whereas in frogs it is a fused, cartilaginous plate. Caecilian jaws are relatively powerful, but slow, whereas most salamanders and frogs exhibit rapid jaw movements with relatively low bite forces. Some plethodontid salamanders show special adaptations for generating powerful bites.

Some caecilians possess a highly specialized jaw-closing mechanism in which enlarged interhyoideus posterior muscles run from the throat to elongated retroarticular processes of the mandible. By pulling down on the processes behind the jaw joint, these muscles elevate the mandible with great force. The adductor mandibulae muscles, typically the most important jaw-closers, are reduced.

Most terrestrial salamanders and all frogs have attached, protrusible tongues and depend heavily upon lingual adhesion for capturing prey. In salamanders, the articulated hyobranchial skeleton forms an internal support for the tongue and intrinsic lingual muscles are present. In basal salamanders, the tongue is protracted using a combination of the genioglossus, geniohyoideus and subarcualis rectus muscles; rectus cervicis profundus and superficialis muscles retract the tongue. In derived species, the subarcualis rectus squeezes lubricated elements of the hyobranchium, ejecting the hyobranchium and its attached tongue pad out of the mouth toward the prey item. Tongue protrusion or projection is always caused by hyobranchial movement.

The anuran tongue consists of only two pairs of extrinsic muscles and associated connective tissues, with no intrinsic cartilaginous or bony skeleton. The hyobranchium is an unarticulated plate formed from the ontogenetic fusion of cartilaginous larval elements. It cannot be folded and does not leave the mouth with the tongue during feeding. In all frogs studied to date, the genioglossus muscles protract the tongue and the hyoglossus muscles retract it.

Function of the feeding apparatus

Aquatic amphibians use ram or suction feeding to capture prey. In ram feeding, the jaws are accelerated over the prey and buccal expansion is used to absorb the bow wave created by forward head movement (compensatory suction). In suction feeding (**Figure 2**), the prey is accelerated into the mouth by negative pressure generated from rapid expansion of the buccal cavity (inertial suction).

Terrestrial prey capture differs among the three orders. Caecilians lack a protrusible tongue and therefore use jaw prehension to capture prey. Frogs and salamanders use tongue prehension to capture small prey, but switch to jaw

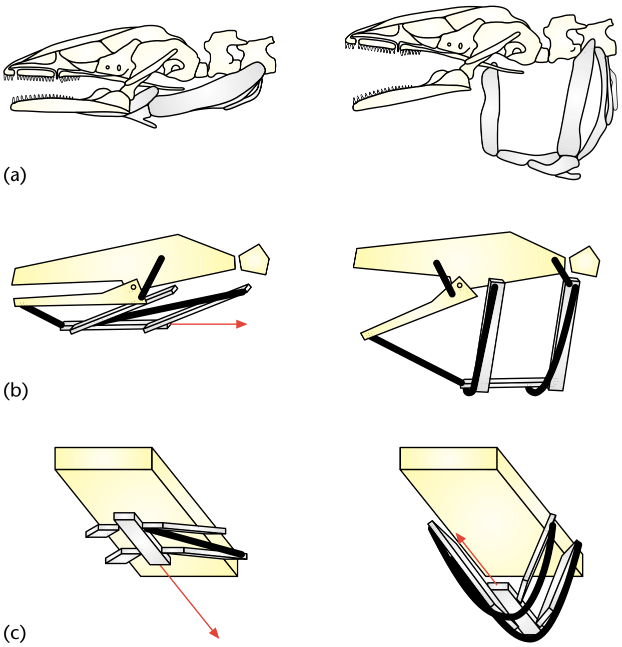

Figure 2 The mechanics of suction feeding in an aquatic larval salamander. The generation of suction requires very rapid expansion of the mouth and throat (pharynx) cavities by retraction and depression of the hyobranchial skeleton (shaded). This creates a negative pressure within the mouth. When water rushes in to equilibrate inside and outside pressures, small prey items are drawn in along with it. After capture, the mouth is closed and the pharynx compressed so that water is expelled either posteriorly through open gill slits, or anteriorly through the teeth. A very similar system is used by all suction feeding tetrapods. (a) The skull and hyobranchial apparatus in lateral view, at rest on the left and retracted on the right; (b) the skull and hyobranchial apparatus shown as mechanical units connected and moved by muscles (black lines); (c) oblique view from below showing the movements of the hyobranchial apparatus in three dimensions. Reproduced with permission from Deban and Wake (2000), copyright Academic Press/Harcourt, Inc.

prehension when the weight of the prey exceeds the adhesive force that can be applied to the prey by the tongue pad. Many frogs and salamanders are able to project their tongues ballistically from the oral cavity. Some bolitoglossine salamanders (family Plethodontidae), such as Hydromantes, can project the tongue to a distance nearly equal to snout-vent length (**Figure 3**). Several distantly related species of anurans, such as toads (family Bufonidae), true frogs (family Ranidae), and some tree frogs (family Hylidae) project their tongues ballistically, but typically to distances not exceeding twice the jaw length. In most frogs, the tongue is attached to the mandible anteriorly and projection causes the tongue to flip out of the mouth so its posterior end at rest comes to lie anteriorly. Salamanders vary in the extent to which the tongue is attached to the mandible, but in all cases the tongue is protruded tip first.

Although there have been reports that some salamanders and frogs can aim their tongues relative to the head, tongue aiming has been demonstrated convincingly only in species of the anuran families Microhylidae and Hemisotidae. Microhylids aim their tongues in distance and azimuth, whereas hemisotids aim the tongue in all three dimensions (distance, azimuth and elevation).

Relatively little is known about feeding stages other than prey capture (ingestion) in amphibians. Amphibians rarely process food, usually swallowing it whole, but some caecilians and salamanders crush prey between the teeth with powerful bites. Aquatic amphibians, like fish, modulate water flow within the mouth and pharynx, using inertial suction to transport prey to the throat for swallowing, whereas terrestrial amphibians display combinations of inertial and hyolingual transport. In inertial transport, the prey item is released by the jaws and accelerated toward the throat. In hyolingual transport, the food is moved posteriorly by cyclic actions of the tongue and hyobranchium. Inertial transport is less widespread in amphibians than in reptiles, owing to their small size. An unusual feature of some frogs and salamanders is use of the retractor bulbi muscles to draw the eyes into the orbits, pushing food from the buccal cavity into the oesophagus. Only caecilians exhibit cranial kinesis, in which the quadrate moves relative to the cranium during ingestion and transport. The functional significance of this movement remains unknown.

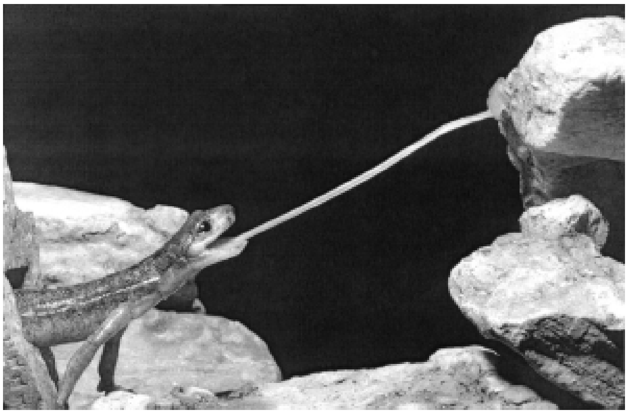

Figure 3 Hyolingual projection in a salamander, *Hydromantes supramontis* (Plethodontidae). The projectile includes the tongue pad (enveloping a fly on the rock) as well as the hyobranchial apparatus and retractor musculature. Tongue projection has evolved several times independently in salamanders and in frogs and also in chamaeleonid lizards. In chameleons, the tongue is projected off an extended hyobranchial skeleton and in frogs the tongue is attached at the front and flipped over the lower jaw; the hyobranchial apparatus does not participate directly in projection. Photograph by Stephen M. Deban. Reproduced with permission from Wake and Deban (2000), copyright Academic Press/ Harcourt, Inc.

Evolution of the feeding apparatus

Within caecilians, many unique features of the feeding apparatus appear to be adaptations that promote a powerful bite while minimizing head diameter in association with head-first burrowing. The primitive condition, associated with a semiaquatic life style, is the presence of a terminal mouth, a tear duct modified into a chemosensory tentacle used to locate prey, a fenestrated skull with relatively large adductor mandibulae muscles, a relatively small retroarticular process and a relatively small interhyoideus posterior muscle. As caecilians became more fossorial, the mouth became subterminal and the tentacle became protrusible. The quadrate expanded to cover the temporal fenestra and the jaw adductors were reduced, while the retroarticular process and the interhyoideus posterior were enlarged. The transition from use of the adductors to the intermandibularis muscles for jaw closing permitted a large increase in bite force without a concomitant increase in head diameter, which would increase the energetic cost of head-first burrowing exponentially.

In salamanders, evolutionary trends are associated with the independent evolution of ballistic tongue projection in the newts (family Salamandridae), lungless salamanders (family Plethodontidae), and the family Hynobiidae. Extremes of projection distance occur in the bolitoglossine plethodontids. These derived lineages share several features, including loss of the genioglossus muscle (which originates near the mandibular symphysis and inserts in the tongue pad, and therefore acts to restrict tongue projection distance) and an increase in the length of the ceratobranchials (the hyobranchial elements squeezed by the subarcualis rectus muscles to effect projection).

Frog tongues are relatively homogeneous morphologically, yet at least three different mechanisms are used to protract the tongue during prey capture. Primitively, frog tongues shorten upon protrusion as the genioglossus muscles contract to move the tongue pad upward and forward from the floor of the mouth. Two different mechanisms have evolved by which frogs can elongate their tongues during protraction. In hydrostatic elongation, known only in members of the families Microhylidae and Hemisotidae, a new dorsoventral compartment of the genioglossus contracts to elongate the tongue hydrostatically during protrusion. Several anuran lineages have evolved an inertial elongation mechanism independently. In inertial elongation, the tongue elongates under the angular momentum produced by mouth opening, rather than by muscular action. Both inertial and hydrostatic elongation are associated with a reduced amount of connective tissue in the tongue and a reorientation of collagen fibres towards transverse, facilitating elongation.

Feeding in Reptiles

Living reptiles are a diverse group including turtles (Testudines), tuatara (Rhynchocephalia), lizards, snakes and amphisbaenians (Squamata), crocodiles and alligators (Crocodylia), and birds (Aves). Although related to crocodilians, birds have diverged sufficiently from other reptile groups that they are not considered here.

Reptile diets are diverse. Crocodilians are fully carnivorous, feeding on other vertebrates, including prey as large as zebras. Snakes are also carnivorous and many regularly consume prey in excess of their own weight. Some species specialize on invertebrates, such as slugs, or immobile food items, such as eggs. Most marine turtles are carnivorous, but one species (the green turtle) is herbivorous, as are most fully terrestrial turtles (tortoises). Freshwater turtles are usually omnivorous, eating a variety of plant and animal food. Tuataras mostly consume invertebrates, but often feed on the eggs and young of ground-nesting birds. Most lizards eat insects and other invertebrates, though many are omnivorous and a few are fully herbivorous, eating leaves, fruits, nectar, pollen and/or seeds.

Most reptiles are visual predators, but squamates rely heavily on the nasal chemical senses, especially the vomeronasal system (stimulated by tongue-flicking), to locate and identify food. Some snakes have thermal sensors on the snout or jaws to help locate warm-bodied prey.

Morphology of the feeding apparatus

The principal elements of the feeding apparatus are the skull, mandible, teeth, jaw muscles, tongue and hyobranchial apparatus. Although there is a great deal of variation in these parts, most of it reflects taxonomic affiliation and mode of feeding, not diet or other ecological variables.

Turtle skulls are massive and solid. The jaw muscles run from the braincase over a bony shelf to insert on the lower jaw. This pulley-like mechanism creates a powerful bite. In some species, the jaw muscles (adductor mandibulae) are covered by a solid, bony roof, but in most the bone is emarginated from the back to expose the underlying muscles. Teeth are absent and the jaws are covered by a horny beak with sharp edges. In terrestrial species, the tongue is large and muscular, but in aquatic species it is reduced. The hyobranchial skeleton is especially robust in aquatic species that generate suction by pharyngeal expansion.

Crocodilians likewise have massive, bony skulls. The back of the skull and the mandible are penetrated by openings, called fenestrae, which lighten it somewhat. In most species, the snout is broad and flat, but in gavials it is long and narrow for fish-eating. Teeth are conical and socketed, like mammals. The tongue lacks intrinsic musculature and cannot be protruded. The bite is rapid and forceful by virtue of the jaws' inertia. The hyobranchium contains a large, flat plate that supports the tongue and floor of the mouth.

In the tuatara, the temporal part of the skull has two large fenestrae that expose the underlying jaw muscles. Jaw adductors are complex and subdivided. There are two rows of teeth in each upper jaw between which the lower tooth row slides when the jaws close. The tongue is large, muscular, mobile and covered with long, glandular papillae that enhance the tongue's prehensile function. The hyobranchium contains several articulated elements that support and move the tongue and pharynx.

Most lizards are similar to the tuatara except that the skull is even lighter and more open. The quadrate (upper jaw joint) bone is attached only at the top so that it potentially swings back and forth with the mandible (streptostyly). In many scleroglossan lizards, an intracranial joint allows the snout and upper jaws to flex up and down (cranial kinesis). Tongue form varies extensively: lingual-feeding iguanians have papillose tongues similar to the tuatara, whereas jaw-feeding scleroglossans have variable, smoother, narrower tongues that are often forked in association with chemosensory function. Tooth form is variable. Most are conical and sharp, but in some herbivores, they are spatulate with multiple cusps and in a few species they are rounded and molariform. In some species, upper and lower teeth occlude and are sharpened by wear.

Snakes have highly modified skulls that in most cases are even more mobile than in lizards. 'Advanced' (macrostomatan) snakes have an extreme form of cranial kinesis in which the tip of the snout can be flexed, the snout and upper jaws are movably articulated on a solid braincase, upper jaw and palatal bones can move independently left and right, the quadrates can swing in any direction and the lower jaw is unconnected at the front. The flexibility of the skull permits a large gape, the capacity to ingest very large prey and the ability to alternate skull movements left and right to pull the snake's head over the prey. Skull mobility is attended by a high degree of complexity in the jaw musculature. The teeth are usually slender, pointed and recurved. Venomous species have enlarged grooved or hollow fangs. The hyobranchium is reduced to a splint that anchors a long, slender, highly protrusible and deeply forked tongue. Neither hyobranchium nor tongue participates in feeding.

Function of the feeding apparatus

Crocodilians capture prey with a rapid, sideways snap of the jaws, facilitated in fish-eaters (e.g. gavials) by a long, narrow snout. Small prey are transported inertially ('bolted') with thrusts of the head. Large prey are killed with crushing bites or dismembered by axial rotation. Prey are sometimes stored underwater until softened by decomposition. During swallowing, hyobranchial elevation and retraction compresses the pharynx, forcing food into the oesophagus. The tongue is elevated to close the throat and protect the airway during underwater prey capture, but otherwise does not participate in feeding (**Figure 4**).

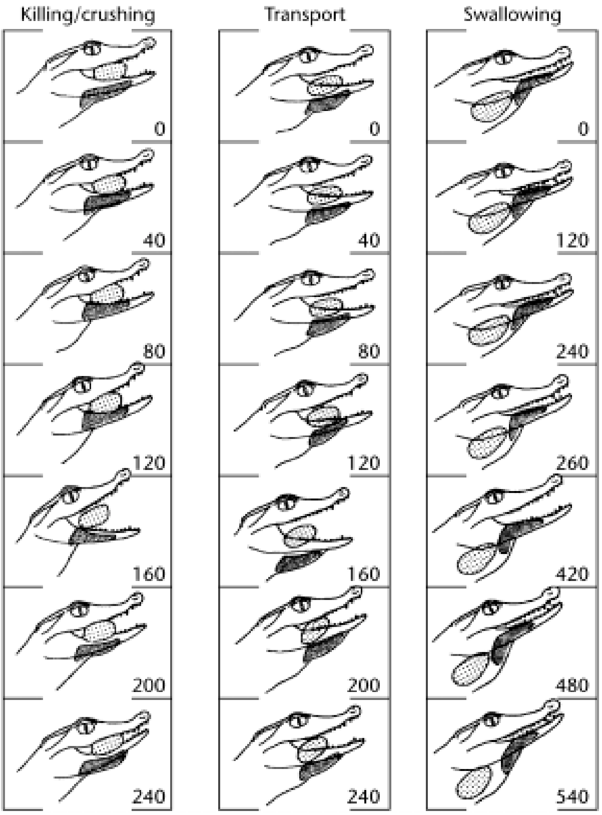

Figure 4 Three stages of feeding in a small crocodile, *Caiman crocodilus*, based on X-ray movies. The prey item is shown as a stippled oval and the hyolingual apparatus (tongue plus hyobranchial skeleton) is shaded. Frames 1 to 4 for each sequence show the slow-opening phase, frame 5 is maximum gape, and frame 6 is the following jaws closed position. Frame 7 shows the crushing phase in the killing/crushing sequence and the beginning of the next jaw-opening cycle in the other two sequences. The numbers represent elapsed time in milliseconds. Note that all stages of feeding require coordination of jaw and hyolingual movements, as is typical for most tetrapod feeding. Reproduced with permission from Cleuren and De Vree (2000), copyright Academic Press/Harcourt, Inc.

Most terrestrial turtles use the tongue to pick up food, but the jaws also participate during ingestion in some species. Food is cropped by the sharp edges of the beak and transported by hyolingual movements. During swallowing, food is 'packed' into the pharynx with the tongue. Aquatic turtles have reduced tongues and use suction-feeding driven by rapid hyobranchial retraction and pharyngeal expansion. In most, suction is only compensatory but at least one species (matamata) uses inertial suction. Another species (alligator snapper) uses a lingual lure to attract fish into the mouth. Hidden-necked turtles (Cryptodira) extend the head anteriorly during a strike, but side-necked turtles (Cryptodira) sweep the neck laterally. Transport is hydraulic, involving inertial suction; swallowing is by pharyngeal compression.

Tuatara capture small prey with the tongue and large prey with the jaws. Prey are reduced by biting and a unique shearing mechanism: the lower tooth row slides between two upper tooth rows to slice prey into manageable parts. Prey are transported by hyolingual movements and swallowed by pharyngeal packing.

Iguanian lizards also protrude the tongue to capture prey (**Figure 5**). Chameleons project the tongue off the hyobranchium ballistically for distances of one to two body lengths to snare insects and even birds; the tongue produces suction for an effective bond. Scleroglossan lizards use the jaws and teeth to capture prey, as do iguanians for large prey. Two species are venomous (Helodermatidae), but the venom is used defensively, not for feeding. Chewing is a simple up-down movement of the jaws that kills and softens prey for swallowing (puncture-crushing). Transport is usually hyolingual, but sometimes inertial thrusts are used, especially for large prey. Swallowing involves a combination of pharyngeal packing and compression. In monitor lizards (Varanidae), the tongue is reduced to a slender, forked chemoreceptor and hardly participates in feeding. Transport is inertial and hyobranchial movements compress the pharynx for swallowing.

Cranial kinesis is important during jaw-capture in some scleroglossan lizards. The snout bends up, then down at the moment of capture to facilitate prehension. In some lizards, the quadrate and lower jaw swing back-and-forth during feeding, a movement called 'streptostyly'. Its function is unknown, but it may make some jaw-closing muscles more effective; in other species (acrodonts), it may align upper and lower teeth for occlusion, so that they can shear or crop their food.

Snake feeding departs radically from that of other reptiles. An elongate body with a small head severely

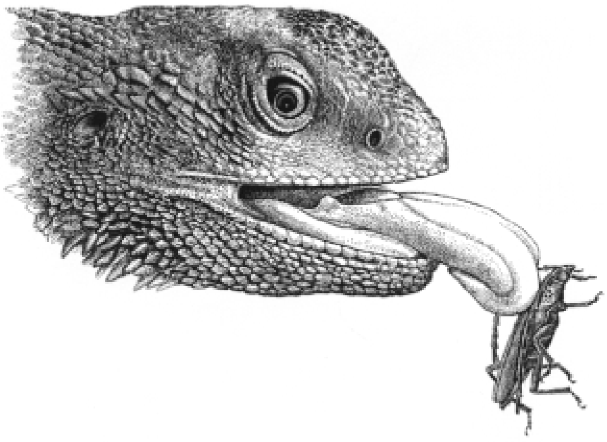

Figure 5 Tongue protrusion and lingual prey capture in an iguanian lizard (*Pogona barbata*, Agamidae). During prey capture (ingestion), the tongue is protruded beyond the lower jaw and curled downward so that its dorsal (top) surface is presented toward the prey item. Long, sticky papillae provide an adhesive surface to which the prey adheres for rapid retraction into the mouth. Reproduced with permission from Schwenk (2000b), copyright Academic Press/Harcourt, Inc.

constrains prey size and type. Basal snakes (Scolecophidia) consume tiny prey, such as ant eggs and larvae, which they sweep into the mouth using specialized movements of the upper or lower jaws. Other primitive snakes must consume small or narrow, elongate prey, but macrostomatans have evolved a highly kinetic skull that permits an extremely wide gape and the ingestion of large prey (**Figure 6**). Prey are seized in the jaws and held or are constricted by coils of the body. Constriction causes rapid death by cardiac disruption and cessation of blood flow to the brain, not crushing as widely supposed. Several groups of snakes kill prey by injecting venom through hollow fangs. Transport and swallowing occur either by pushing the head over the pinned prey item, or by pulling the head over the prey using asymmetrical movements of the skull in which the upper tooth rows are alternately 'walked' over the prey. Once in the throat, sinuous waves of the body (and the oesophagus internally) force the prey item toward the stomach.

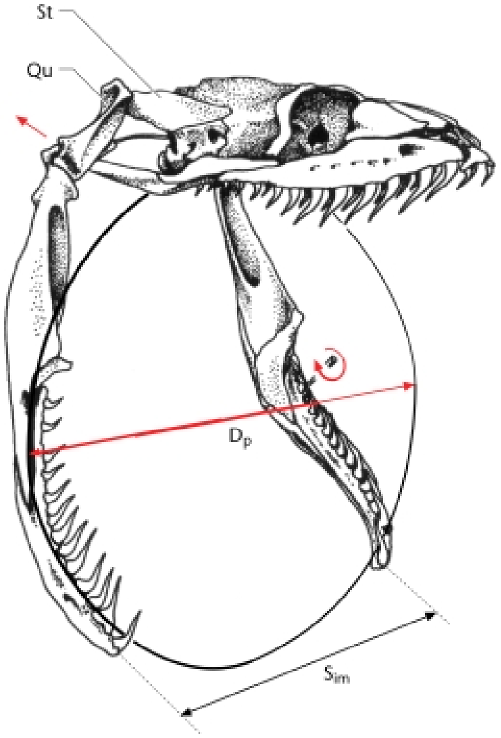

Figure 6 A python (snake) skull showing adaptations for swallowing large prey. Most important is the ability of the mandibles to separate at the front. Unlike most tetrapods in which each half of the mandible is fused to the other by a tight joint called a symphysis, in snakes the halves remain unfused and joined only by soft, elastic tissue (S_{im}). The effective length of the mandibles, and therefore the size of the gape, is also increased by adding to it mobile and elongate bones of the upper jaw, the quadrate (Qu) and supratemporal (St). These traits permit the jaws of 'advanced' snakes to spread very wide, enabling them to swallow large-diameter prey (D_p). In addition, left and right upper jaw bones are independently mobile, so that the snake can literally 'walk' its head over the prey item (a form of cranial kinesis). Reproduced with permission from Cundall and Greene (2000), copyright Academic Press/Harcourt, Inc.

Evolution of feeding apparatus

Ancestral reptiles probably captured prey with their tongues. Cyclic movements of the hyobranchium and its attached muscular tongue moved food through the mouth and pushed it into the throat for swallowing, as retained in most living reptiles. Crocodilians have secondarily simplified their tongues, probably in response to aquatic life, and use the jaws to capture prey. However, they continue to use cyclic hyobranchial movements for transport and swallowing. Although terrestrial turtles retain many aspects of the primitive tetrapod feeding pattern, ancestral turtles may have been aquatic, therefore terrestrial feeding may have re-evolved in the group. In tuatara and lizards, lingual prey capture is the ancestral feeding mode, as is hyolingual transport and swallowing. One group of squamates, however, became specialized jaw-feeders and the evolution of cranial kinesis is associated with this prey capture mode. Snakes evolved from a branch of these jaw-feeders in which the tongue and hyobranchium were progressively modified for chemosensory function at the cost of feeding function. Extreme cranial kinesis, ingestion of very large prey and total reliance on inertial (as opposed to hyolingual) food transport are characteristic of macrostomatan, but not basal snakes. Venom delivery systems evolved several times independently within macrostomatans (vipers, cobras, marine snakes and colubroids).

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