Carnivorous Animals

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First Edition, 2012

ISBN 978-81-323-4099-7

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Published by:
White Word Publications
4735/22 Prakashdeep Bldg,
Ansari Road, Darya Ganj,
Delhi - 110002
Email: info@wtbooks.com

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Chapter 1

Carnivore

Lions are voracious carnivores; they require up to seven kilograms (15 lbs) of meat per day. A major component of their diet is the flesh of large mammals, like this African buffalo.

A **carnivore** is an organism that derives its energy and nutrient requirements from a diet consisting mainly or exclusively of animal tissue, whether through predation or scavenging. Animals that depend solely on animal flesh for their nutrient requirements are considered obligate carnivores while those that also consume non-animal food are considered facultative carnivores. Omnivores also consume both animal and non-animal food, and apart from the more general definition, there is no clearly defined ratio of plant to animal material that would distinguish a facultative carnivore from an omnivore, or an omnivore from a facultative herbivore, for that matter. A carnivore that sits at the top of the foodchain is an apex predator.

Plants that capture and digest insects are called carnivorous plants. Similarly, fungi that capture microscopic animals are often called carnivorous fungi.

Classification

The Venus flytrap, a well known carnivorous plant

Carnivores that eat insects and similar invertebrates primarily or exclusively are called insectivores, while those that eat fish primarily or exclusively are called piscivores. Large piscivore amphibians were the first vertebrates to conquer land, they evolved 400 million years ago. Insectivores evolved next and predators of other vertebrates after that.

The word "carnivore" sometimes refers to the mammalian Order Carnivora, but this is somewhat misleading. Although many Carnivora fit the definition of being exclusively meat eaters, not all do. For example, most species of bears are omnivorous, except for the giant panda, which is almost exclusively herbivorous, and the carnivorous polar bear. In addition, many carnivorous species are not members of Carnivora.

Outside the animal kingdom, there are several genera containing carnivorous plants and several phyla containing carnivorous fungi. The former are predominantly insectivores, while the latter prey mostly on microscopic invertebrates, such as nematodes, amoeba and springtails.

Obligate carnivores

This white Bengal tiger's sharp teeth and strong jaws are the classical physical traits expected from carnivorous mammalian predators

Obligate or true carnivores depend solely on the nutrients found in animal flesh for their survival. While they may consume small amounts of plant material, they lack the physiology required for the efficient digestion of vegetable matter and, in fact, some carnivorous mammals eat vegetation specifically as an emetic. The domestic cat is a prime example of an obligate carnivore, as are all of the other felids. The ability to produce synthetic forms of nutrients such as taurine in the lab has allowed feed manufacturers to formulate foods for carnivores (zoo animals and pets) with varying amounts of plant material.

The diet of a hypercarnivore consists of more than 70% meat, that of a mesocarnivore 50-70%, and that of a hypocarnivore less than 30%, with the balance consisting of nonvertebrate foods, which may include fungi, fruits, and other plant material.

Characteristics of carnivores

Characteristics commonly associated with carnivores include organs for capturing and disarticulating prey (teeth and claws serve these functions in many vertebrates) and status as a predator. In truth, these assumptions may be misleading, as some carnivores do not hunt and are scavengers (though most hunting carnivores will scavenge when the opportunity exists). Thus they do not have the characteristics associated with hunting carnivores. Carnivores have comparatively short digestive systems, as they are not required to break down tough cellulose found in plants. Carnivores will also generally possess eyes that face forward, affording binocular vision and depth perception necessary to pounce on prey, as contrasted to the usual herbivore arrangement of eyes set on opposite sides of the head, sacrificing binocular vision for a nearly 360 degree field of vision as a defense against predators.

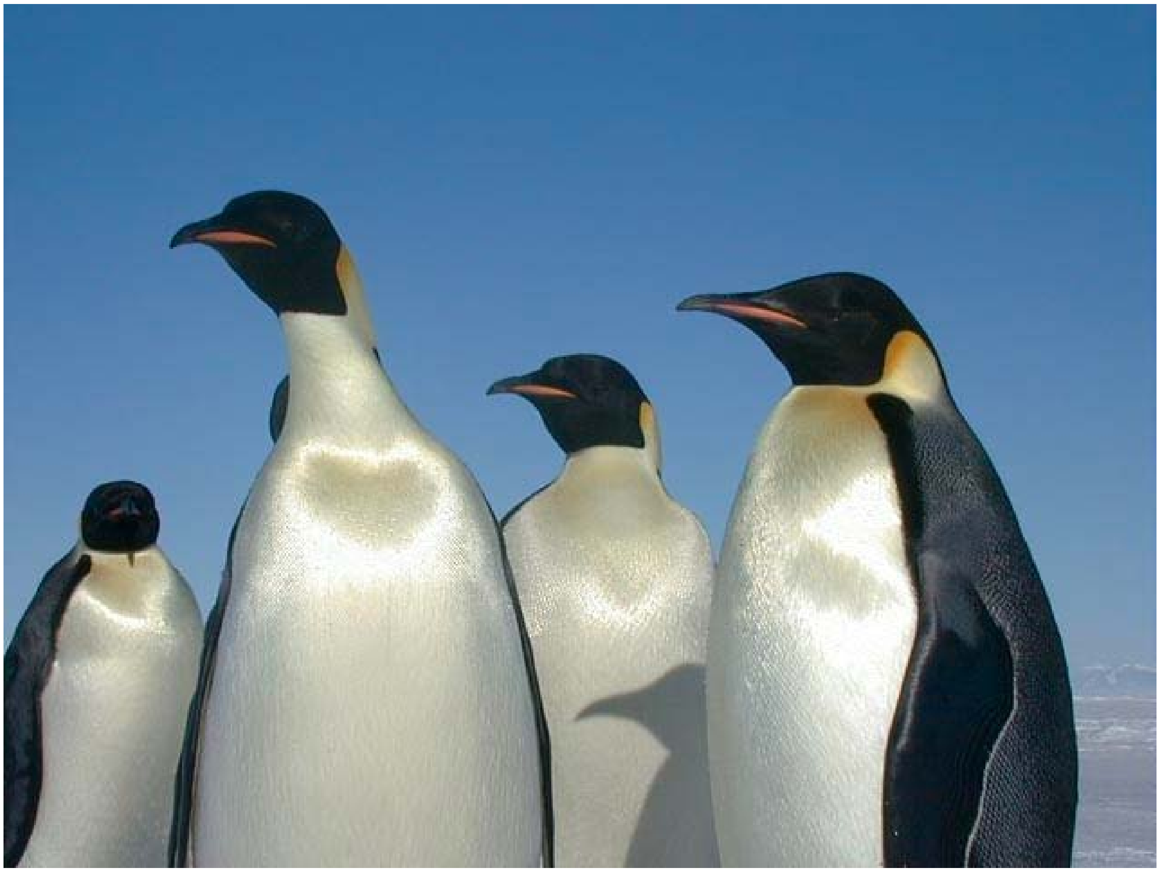
Prehistoric carnivores

The first vertebrate carnivores were fish, and then amphibians that lived moved on to land. Early tetrapods were large amphibious piscivores. While amphibians continued to feed on fish and later insects, reptiles began exploring two new food types, tetrapods (carnivory), and later, plants (herbivory). Carnivory was a natural transition from insectivory for medium and large tetrapods, requiring minimal adaptation (in contrast, a complex set of adaptations was necessary for feeding on highly fibrous plant materials).

Prehistoric mammals of the crown-clade Carnivoramorpha (Carnivora and Miacoidea without Creodonta), along with the early order Creodonta, and some mammals of the even earlier order Cimolesta, were true carnivores. The earliest carnivorous mammal is considered to be the *Cimolestes* that existed during the Late Cretaceous and Tertiary Periods in North America about 65 million years ago. Most species of *Cimolestes* were mouse to rat-sized, but the Late Cretaceous *Cimolestes magnus* reached the size of a marmot, making it one of the largest Mesozoic mammals known (20-60g). The cheek teeth combined the functions of piercing, shearing and grinding, and the molars of *Palaeoryctes* had extremely high and acute cusps that had little function other than piercing. The dentition of *Cimolestes* foreshadows the same cutting structures seen in all later carnivores. While the earlier smaller species were insectivores, the later marmot-sized *Cimolestes magnus* probably took larger prey and were definitely a carnivore to some degree. The cheek teeth of *Hyracolestes ermineus* (an ermine-like shrew - 40g) and *Sarcodon pygmaeus* ("pygmy flesh tooth" - 75g), were common in the latest Paleocene of Mongolia and China and occupied the small predator niche. The cheek teeth show the same characteristic notches that serve in today's carnivores to hold flesh in place to shear apart with cutting ridges.

The theropod dinosaurs such as *Tyrannosaurus rex* that existed during the Mesozoic Era were "obligate carnivores".

List of extant carnivores



In contrast to the tiger, these emperor penguins show that teeth and claws are not necessary to be a carnivore. They feed on crustaceans, fish, squid, and other small marine life.

Great Blue Heron with a snake

Some nematodes are also carnivorous, for instance this Mononchidae eating another Mononchidae.

Mammals

- All feliforms, such as domestic cats, big cats, hyenas, mongooses, civets
- Most caniforms, such as the dogs, wolves, foxes, ferrets, seals and walruses
- All cetaceans, such as dolphins, whales and porpoises
- All bats (except fruitbats)
- The carnivorous marsupials, such as the Tasmanian devil

Birds

- All birds of prey, such as hawks, eagles, falcons and all vultures (Old and New World)
- All owls
- Some waterfowl, such as gulls, penguins, pelicans, storks, and herons (Note, waterfowl is not being used in the taxonomic sense - e.g. Anseriformes - in this instance)

Reptiles

- All crocodilians, such as alligators, crocodiles, gharials and caimans
- All snakes, such as cobras, vipers, pythons and boas
- Some lizards, such as most skinks and all monitor lizards
- Some turtles, including the snapping turtle and most sea turtles

Fish and amphibians

- Most anurans, such as frogs and toads
- All sharks, such as tiger, great white, nurse and reef sharks
- Many bony fish, such as tuna, marlin, salmon, and bass

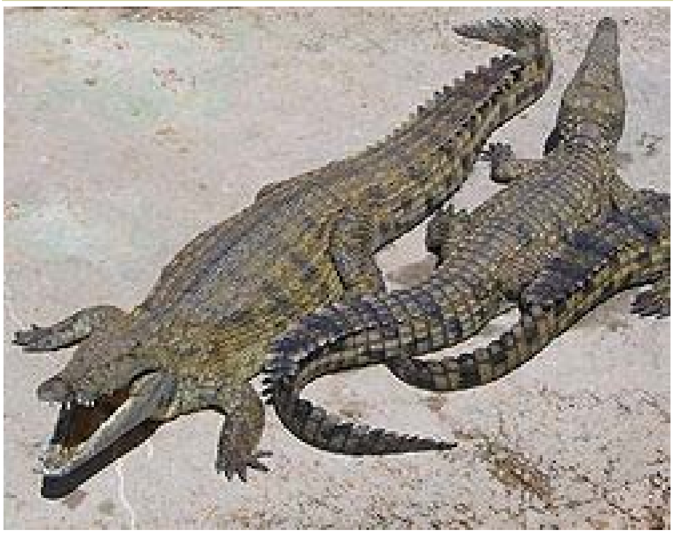
Invertebrates

- Some crustaceans, such as the coconut crab, though mainly omnivorous, will prey on turtle hatchlings, smaller crabs species, rats, and carrion
- Some molluscs, such as octopuses and squid, and some gastropods
- Most arachnids, such as spiders and scorpions
- Many insects, such as mantises, dragonflies and most wasps
- All jellyfish and sea stars
- All centipedes

Chapter 2

Crocodilia

Crocodilians
Temporal range: Cretaceous - Recent, 84–0 Ma



Nile crocodiles (*Crocodylus niloticus*)

Scientific classification [e]

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

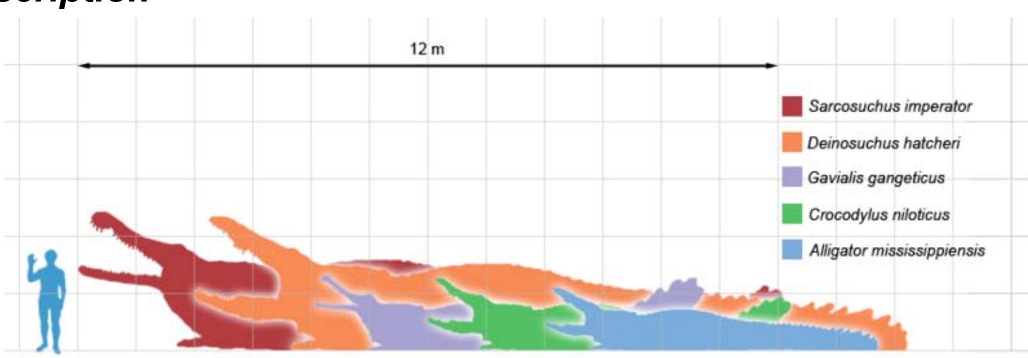
Crocodilia (or **Crocodylia**) is an order of large reptiles that appeared about 84 million years ago in the late Cretaceous Period (Campanian stage). They are the closest living relatives of birds, as the two groups are the only known survivors of the Archosauria. Members of the crocodilian total group, 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*).

Crocodilians 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.

Crocodilians 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

Crocodilians 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 crocodilia 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 CO_2 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.

Crocodilians 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 crocodiylian 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 Crocodilia, 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 3

Bat

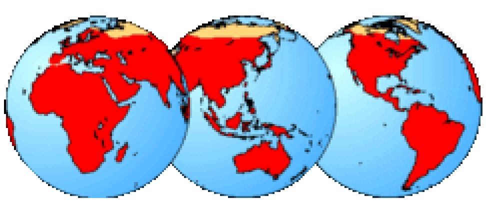
Bats
Temporal range: 52–0 Ma
Early Eocene – Recent

Townsend's big-eared bat, *Corynorhinus townsendii*

Scientific classification

Kingdom:	Animalia
Phylum:	Chordata
Class:	Mammalia
Infraclass:	Eutheria
Superorder:	Laurasiatheria
Order:	**Chiroptera** Blumenbach, 1779

Suborders



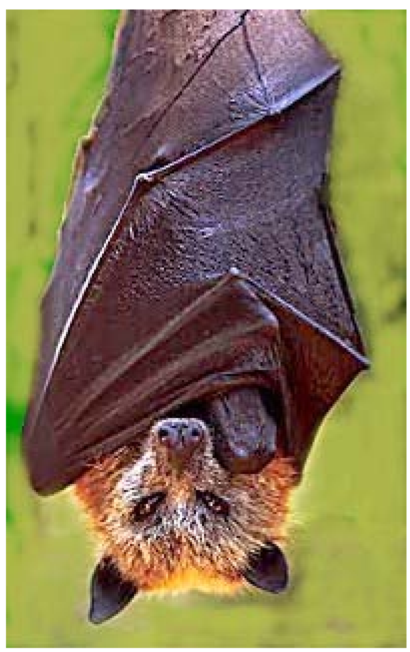
Worldwide distribution of bat species

Bats are flying mammals in the order **Chiroptera** . The forelimbs of bats are webbed and developed as wings, making them the only mammals naturally capable of true and sustained flight. By contrast, other mammals said to fly, such as flying squirrels, gliding possums and colugos, glide rather than fly, and can only glide for short distances. Bats do not flap their entire forelimbs, as birds do, but instead flap their spread out digits, which are very long and covered with a thin membrane or patagium. *Chiroptera* comes from two Greek words, *cheir* (χείρ) "hand" and *pteron* (πτερόν) "wing."

There are about 1,100 bat species worldwide, which represent about twenty percent of all classified mammal species. About seventy percent of bats are insectivores. Most of the rest are frugivores, or fruit eaters. A few species such as the Fish-eating Bat feed from animals other than insects, with the vampire bats being the only mammalian parasite species. Bats are present throughout most of the world and perform vital ecological roles such as pollinating flowers and dispersing fruit seeds. Many tropical plant species depend entirely on bats for the distribution of their seeds.

The smallest bat is the Kitti's Hog-nosed Bat, measuring 29–34 mm (1.14–1.34 in) in length, 15 cm (5.91 in) across the wings and 2–2.6 g (0.07–0.09 oz) in mass, The largest species of bat is the Giant Golden-crowned Flying-fox, which is 336–343 mm (13.23–13.50 in) long, has a wingspan of 1.5 m (4 ft 11 in) and weighs approximately 1.1–1.2 kg (2–3 lb).

Classification and evolution



Giant Golden-crowned Flying-fox, *Acerodon jubatus*.

Bats are mammals. Sometimes they are mistakenly called "flying rodents" or "flying rats", and they can also be mistaken for insects and birds. There are two traditionally recognized suborders of bats:

- Megachiroptera (megabats)
- Microchiroptera (microbats/echolocating bats)

Not all megabats are larger than microbats. The major distinctions between the two suborders are:

- Microbats use echolocation: megabats do not with the exception of *Rousettus* and relatives.
- Microbats lack the claw at the second toe of the forelimb.
- The ears of microbats do not close to form a ring: the edges are separated from each other at the base of the ear.
- Microbats lack underfur: they are either naked or have guard hairs.

Megabats eat fruit, nectar or pollen while most microbats eat insects; others may feed on the blood of animals, small mammals, fish, frogs, fruit, pollen or nectar. Megabats have a well-developed visual cortex and show good visual acuity, while microbats rely on echolocation for navigation and finding prey.

The phylogenetic relationships of the different groups of bats have been the subject of much debate. The traditional subdivision between Megachiroptera and Microchiroptera reflects the view that these groups of bats have evolved independently of each other for a long time, from a common ancestor that was already capable of flight. This hypothesis recognized differences between microbats and megabats and acknowledged that flight has only evolved once in mammals. Most molecular biological evidence supports the view that bats form a single or monophyletic group.

Researchers have proposed alternate views of chiropteran phylogeny and classification, but more research is needed.

Genetic evidence indicates that megabats originated during the early Eocene and should be placed within the four major lines of microbats.

Consequently, two new suborders based on molecular data have been proposed. The new suborder Yinpterochiroptera includes the Pteropodidae or megabat family as well as the Rhinolophidae, Hipposideridae, Craseonycteridae, Megadermatidae, and Rhinopomatidae families. The new suborder Yangochiroptera includes all the remaining families of bats (all of which use laryngeal echolocation). These two new suborders are strongly supported by statistical tests. Teeling (2005) found 100% bootstrap support in all maximum likelihood analyses for the division of Chiroptera into these two modified suborders. This conclusion is further supported by a fifteen-base pair deletion in BRCA1 and a seven-base pair deletion in PLCB4 present in all Yangochiroptera and absent in all Yinpterochiroptera. The Chiropteran phylogeny based on molecular evidence is controversial because microbat paraphyly implies that one of two seemingly unlikely hypotheses occurred. The first suggests that laryngeal echolocation evolved twice in Chiroptera, once in Yangochiroptera and once in the rhinolophoids. The second proposes that laryngeal echolocation had a single origin in Chiroptera, was subsequently lost in the family Pteropodidae (all megabats), and later evolved as a system of tongue-clicking in the genus *Rousettus*.

Common Pipistrelle, *Pipistrellus pipistrellus*.

Analyses of the sequence of the "vocalization" gene, *FoxP2* was inconclusive of whether laryngeal echolocation was secondarily lost in the pteropodids or independently gained in the echolocating lineages. However, analyses of the "hearing" gene, *Prestin* seemed to favor the independent gain in echolocating species rather than a secondary loss in the pteropodids.

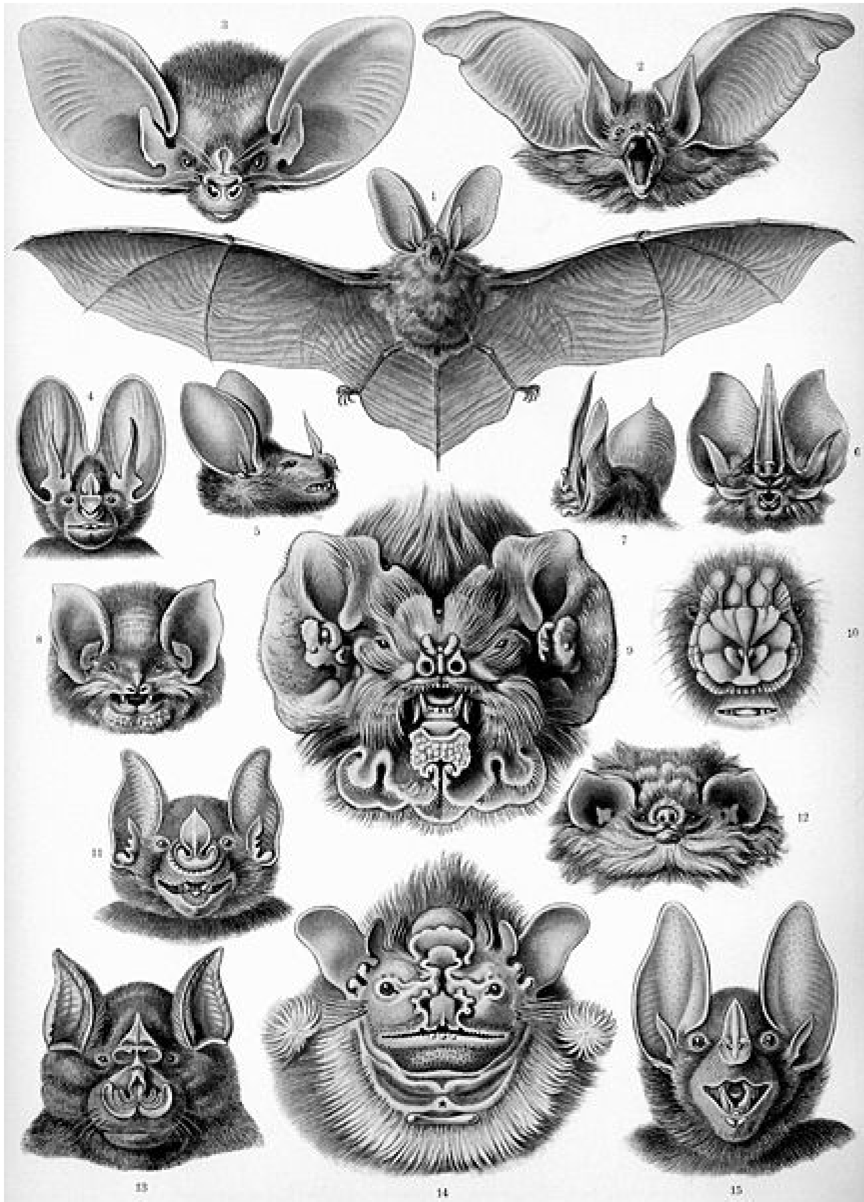
In addition to Yinpterochiroptera and Yangochiroptera, the names Pteropodiformes and Vespertilioniformes have also been proposed for these suborders. Under this new proposed nomenclature, the suborder Pteropodiformes includes all extant bat families more closely related to the genus *Pteropus* than the genus *Vespertilio*, while the suborder

Vespertilioniformes includes all extant bat families more closely related to the genus *Vespertilio* than to the genus *Pteropus*.

In the 1980s, a hypothesis based on morphological evidence was offered that stated that the Megachiroptera evolved flight separately from the Microchiroptera. The so-called flying primates theory proposed that when adaptations to flight are removed, the Megachiroptera are allied to primates by anatomical features that are not shared with Microchiroptera. One example is that the brains of megabats show a number of advanced characteristics that link them to primates. Although recent genetic studies support the monophyly of bats, debate continues as to the meaning of available genetic and morphological evidence.

Little fossil evidence is available to help map the evolution of bats, since their small, delicate skeletons do not fossilize very well. However a Late Cretaceous tooth from South America resembles that of an early Microchiropteran bat. The oldest known definitely identified bat fossils, such as *Icaronycteris*, *Archaeonycteris*, *Palaeochiropteryx* and *Hassianycteris*, are from the early Eocene period, 52.5 million years ago. These fossil bats were already very similar to modern microbats. *Archaeopteropus*, formerly classified as the earliest known megachiropteran, is now classified as a microchiropteran.

Bats were formerly grouped in the superorder Archonta along with the treeshrews (Scandentia), colugos (Dermoptera), and the primates, because of the apparent similarities between Megachiroptera and such mammals. Genetic studies have now placed bats in the superorder Laurasiatheria along with carnivorans, pangolins, odd-toed ungulates, even-toed ungulates, and cetaceans.



"Chiroptera" from Ernst Haeckel's *Kunstformen der Natur*, 1904

The traditional classification of bats is:

- Order Chiroptera
    - Suborder Megachiroptera (megabats)
        - Pteropodidae
    - Suborder Microchiroptera (microbats)
        - Superfamily Emballonuroidea
            - Emballonuridae (Sac-winged or Sheath-tailed bats)
        - Superfamily Molossoidea
            - Antrozoidae (Pallid Bat and Van Gelder's Bat)
            - Molossidae (Free-tailed bats)

    - Superfamily Nataloidea
        - Furipteridae (Smoky bats)
        - Myzopodidae (Sucker-footed bats)
        - Natalidae (Funnel-eared bats)
        - Thyropteridae (Disk-winged bats)
    - Superfamily Noctilionoidea
        - Mormoopidae (Ghost-faced or Moustached bats)
        - Mystacinidae (New Zealand short-tailed bats)
        - Noctilionidae (Bulldog bats or Fisherman bats)
        - Phyllostomidae (Leaf-nosed bats)
    - Superfamily Rhinolophoidea
        - Megadermatidae (False vampires)
        - Nycteridae (Hollow-faced or Slit-faced bats)
        - Rhinolophidae (Horseshoe bats)
    - Superfamily Rhinopomatoidea
        - Craseonycteridae (Bumblebee Bat or Kitti's Hog-nosed Bat)
        - Rhinopomatidae (Mouse-tailed bats)
    - Superfamily Vespertilionoidea
        - Vespertilionidae (Vesper bats or Evening bats)

Megabats primarily eat fruit or nectar. In New Guinea, they are likely to have evolved for some time in the absence of microbats. This has resulted in some smaller megabats of the genus *Nyctimene* becoming (partly) insectivorous to fill the vacant microbat ecological niche. Furthermore, there is some evidence that the fruit bat genus *Pteralopex* from the Solomon Islands, and its close relative *Mirimiri* from Fiji, have evolved to fill some niches that were open because there are no nonvolant or non-flying mammals in those islands.

Fossil bats

There are few fossilized remains of bats, as they are terrestrial and light-boned. An Eocene bat, *Onychonycteris finneyi*, was found in the fifty-two-million-year-old Green River Formation in South Dakota, United States, in 2004. It had characteristics indicating that it could fly, yet the well-preserved skeleton showed that the cochlea of the inner ear lacked development needed to support the greater hearing abilities of modern bats. This provided evidence that flight in bats developed well before echolocation. The team that found the remains of this species, named *Onychonycteris finneyi*, recognized that it lacked ear and throat features present not only in echolocating bats today, but also in other known prehistoric species. Fossil remains of another Eocene bat, *Icaronycteris*, were found in 1960.

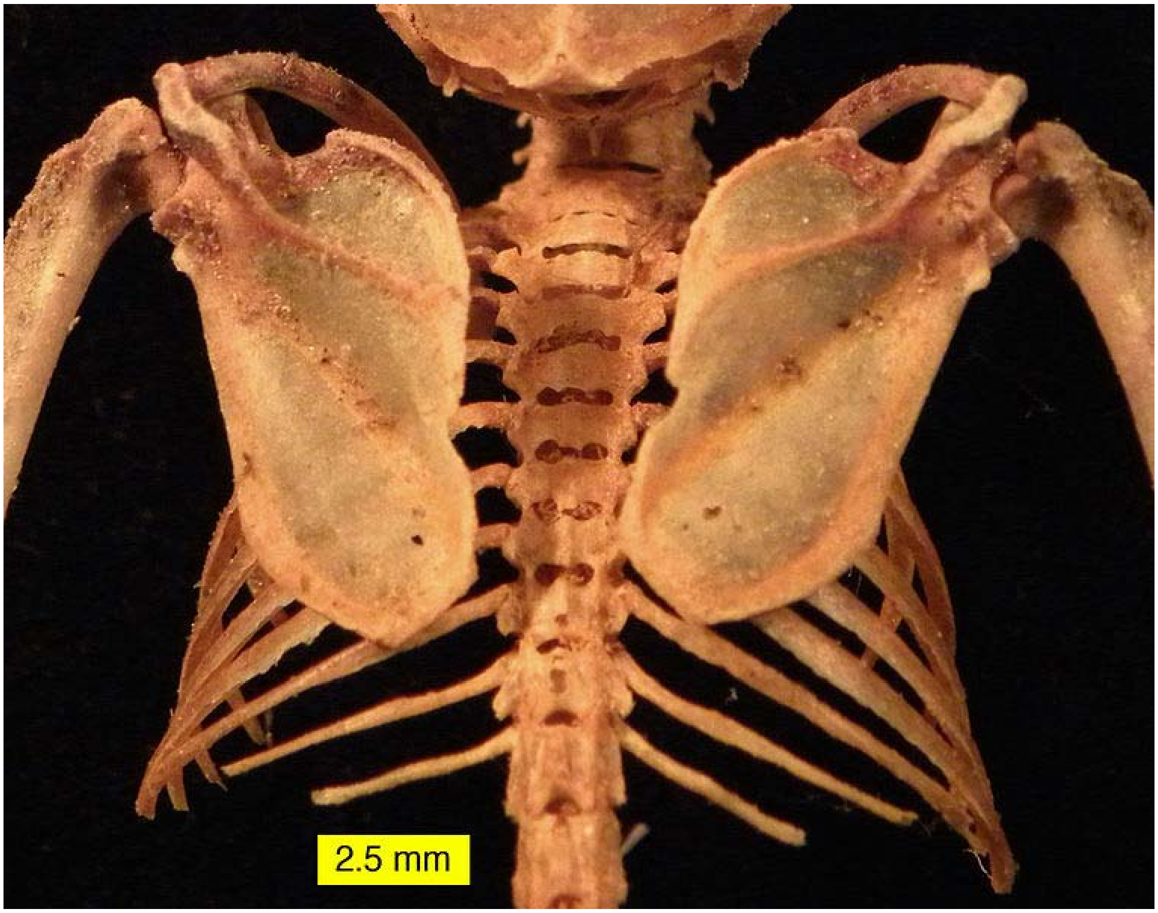
The appearance and flight movement of bats 52.5 million years ago were different from those of bats today. *Onychonycteris* had claws on all five of its fingers, whereas modern bats have at most two claws appearing on two digits of each hand. It also had longer hind legs and shorter forearms, similar to climbing mammals that hang under branches such as sloths and gibbons. This palm-sized bat had broad, short wings suggesting that it could not fly as fast or as far as later bat species. Instead of flapping its wings continuously while flying, *Onychonycteris* likely alternated between flaps and glides while in the air. Such physical characteristics suggest that this bat did not fly as much as modern bats do, rather flying from tree to tree and spending most of its waking day climbing or hanging on the branches of trees.

Habitats

Flight has enabled bats to become one of the most widely distributed groups of mammals. Apart from the Arctic, the Antarctic and a few isolated oceanic islands, bats exists all over the world. Bats are found in almost every habitat available on Earth. Different species select different habitat during different seasons — ranging from seasides to mountains and even deserts — but bat habitats have two basic requirements: roosts, where they spend the day or hibernate, and places for foraging. Bat roosts can be found in hollows, crevices, foliage, and even human-made structures; and include "tents" that bats construct by biting leaves.

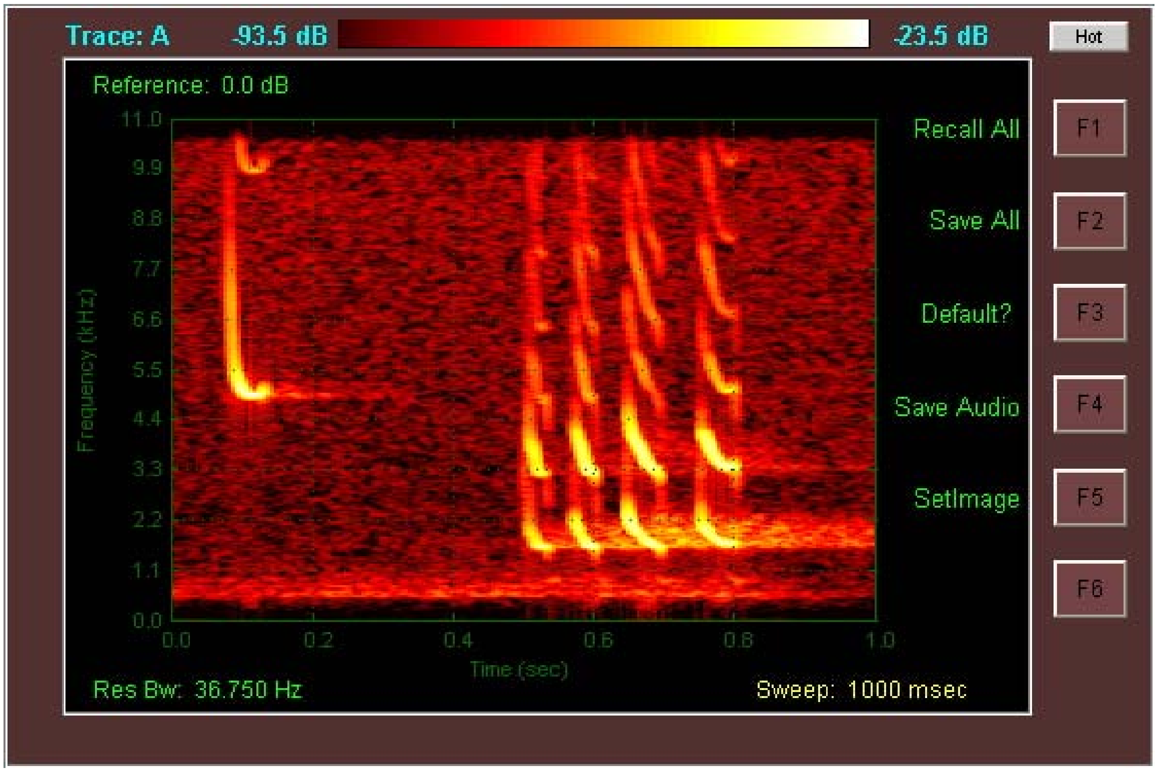
Anatomy

Skeleton of a Greater Mouse-eared Bat (*Myotis myotis*).



Scapulae, spine and ribs of *Myotis lucifugus* (Little Brown Bat).

Echolocation



Spectrogram of Pipistrellus Bat vocalizations. Detail is shown as the pulse duty cycle increases during a close approach to prey. The bat appears to use a hybrid pulse which combines a sharp falling frequency chirp with an extended constant frequency tail. Such a waveform may offer combined benefits of range estimation as well as Doppler shift detection. Spectrogram generated with Fatpigdog's PC based Real Time FFT Spectrum Analyzer.

Bat echolocation is a perceptual system where ultrasonic sounds are emitted specifically to produce echoes. By comparing the outgoing pulse with the returning echoes the brain and auditory nervous system can produce detailed images of the bat's surroundings. This allows bats to detect, localize and even classify their prey in complete darkness. At 130 decibels in intensity, bat calls are some of the most intense airborne animal sounds.

To clearly distinguish returning information, bats must be able to separate their calls from the echoes they receive. Microbats use two distinct approaches.

1. Low Duty Cycle Echolocation: Bats can separate their calls and returning echos by time. Bats that use this approach time their short calls to finish before echoes return. This is important because these bats contract their middle ear muscles when emitting a call so that they can avoid deafening themselves. The time interval between call and echo allows them to relax these muscles so they can clearly hear the returning echo. The delay of the returning echos provide the bat with the ability to estimate range to their prey.

2. High Duty Cycle Echolocation: Bats emit a continuous call and separate pulse and echo in frequency. The ears of these bats are sharply tuned to a specific frequency range. They emit calls outside of this range to avoid self-deafening. They then receive echoes back at the finely tuned frequency range by taking advantage of the Doppler shift of their motion in flight. The Doppler shift of the returning echos yield information relating to the motion and location of the bat's prey. These bats must deal with changes in the Doppler shift due to changes in their flight speed. They have adapted to change their pulse emission frequency in relation to their flight speed so echoes still return in the optimal hearing range.

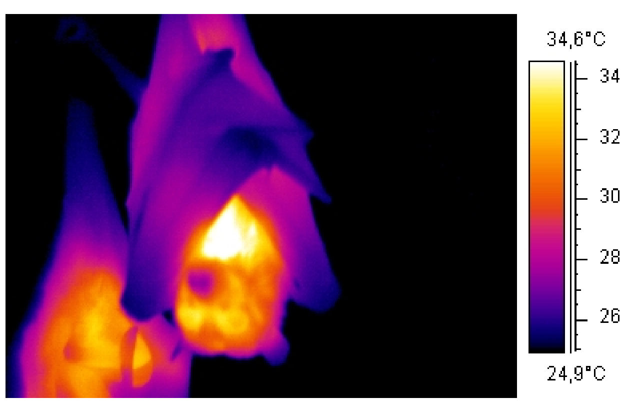
The new Yinpterochiroptera and Yangochiroptera classification of bats that are supported by molecular evidence, suggest two possibilities for the evolution of echolocation. It may have been gained once in a common ancestor of all bats and was then subsequently lost in the Old World fruit bats, only to be regained in the Horse-Shoe bats; or echolocation was evolved independent in both the Yinpterochiroptera and Yangochirpotera lineages.

Two groups of moths exploit a bat sense to echolocate: tiger moths produce ultrasonic signals to warn the bats that they (the moths) are chemically protected or aposematic. This was once thought to be the biological equivalent of "radar jamming", but this theory has yet to be confirmed. The moths Noctuidae have a hearing organ called a tympanum, which responds to an incoming bat signal by causing the moth's flight muscles to twitch erratically, sending the moth into random evasive manoeuvres.

Other senses

Although the eyes of most microbat species are small and poorly developed, leading to poor visual acuity, none of them are blind. Vision is used to navigate microbats especially for long distances when beyond the range of echolocation. It has even been discovered that some species are able to detect ultraviolet light. They also have a high quality sense of smell and hearing. Bats hunt at night to avoid competition with birds, and travel large distances at most 800 km, in their search for food.

Wings



Thermographic image of a bat using trapped air as insulation.

The finger bones of bats are much more flexible than those of other mammals. One reason is that the cartilage in their fingers lacks calcium and other minerals nearer the tips, increasing their ability to bend without splintering. The cross-section of the finger bone is also flattened compared to the circular cross section that human finger bones have, and is very flexible. The skin on their wing membranes has more elasticity and so can stretch much more than other mammals.

The wings of bats are much thinner than those of birds, so bats can maneuver more quickly and more accurately than birds. It is also delicate, ripping easily. However the tissue of the bat's membrane is able to regrow, such that small tears can heal quickly. The surface of their wings is equipped with touch-sensitive receptors on small bumps called Merkel cells, found in most mammals including humans, similarly found on our finger tips. These sensitive areas are different in bats as each bump has a tiny hair in the center, making it even more sensitive and allowing the bat to detect and collect information about the air flowing over its wings, thereby providing feedback to the bat to change its shape of its wing to fly more efficiently. An additional kind of receptor cell is found in the wing membrane of species that use their wings to catch prey. This receptor cell is sensitive to the stretching of the membrane. The cells are concentrated in areas of the membrane where insects hit the wings when the bats capture them.

Other

The teeth of microbats resemble insectivorans. They are very sharp to bite through the hardened armor of insects or the skin of fruit.

Mammals have one-way valves in veins to prevent the blood from flowing backwards, but bats also have one-way valves in arteries.

One species of bat has the longest tongue of any mammal relative to its body size. This is beneficial to them in terms of pollination and feeding. Their long narrow tongues can reach deep into the long cup shape of some flowers. When their tongue retracts, it coils up inside their rib cage.

Behaviour

Most microbats are nocturnal and are active at twilight. A large portion of bats migrate hundreds of kilometres to winter hibernation dens, some pass into torpor in cold weather, rousing and feeding when warm weather allows for insects to be active. Others retreat to caves for winter and hibernate for six months. Bats rarely fly in rain as the rain interferes with their echo location, and they are unable to locate their food.

The social structure of bats varies, with some bats leading a solitary life and others living in caves colonized by more than a million bats. The fission-fusion social structure is seen among several species of bats. The term "fusion" refers to a large numbers of bats that congregate together in one roosting area and "fission" refers to breaking up and the mixing of subgroups, with individual bats switching roosts with others and often ending up in different trees and with different roostmates.

Studies also show that bats make all kinds of sounds to communicate with others. Scientists in the field have listened to bats and have been able to identify some sounds with some behaviour bats will make after the sounds are made.

70% of bat species are insectivorous, locating their prey by means of echolocation. Of the remainder, most feed on fruits. Only three species sustain themselves with blood. Some species even prey on vertebrates: these are the leaf-nosed bats (*Phyllostomidae*) of Central America and South America, and the two bulldog bat (*Noctilionidae*) species, which feed on fish. At least two species of bat are known to feed on bats: the Spectral Bat, also known as the American False Vampire bat, and the Ghost Bat of Australia. One species, the Greater Noctule bat, catches and eats small birds in the air.

Predators of bats include bat hawks and bat falcons.

Reproduction

Newborn Common Pipistrelle, *Pipistrellus pipistrellus*.

Colony of Mouse-eared bats, *Myotis myotis*.

Most bats have a breeding season, which is in the spring for species living in a temperate climate. Bats may have one to three litters in a season, depending on the species and on environmental conditions such as the availability of food and roost sites. Females generally have one offspring at a time, which could be a result of the mother's need to fly to feed while pregnant. Female bats nurse their youngsters until they are nearly adult size; this is because a young bat cannot forage on its own until its wings are fully developed.

Female bats use a variety of strategies to control the timing of pregnancy and the birth of young, to make delivery coincide with maximum food ability and other ecological factors. Females of some species have delayed fertilization, in which sperm are stored in the reproductive tract for several months after mating. In many such cases, mating occurs in the fall, and fertilization does not occur until the following spring. Other species exhibit delayed implantation, in which the egg is fertilized after mating, but remains free in the reproductive tract until external conditions become favorable for giving birth and caring for the offspring. In yet another strategy, fertilization and implantation both occur but development of the fetus is delayed until favorable conditions prevail. All of these adaptations result in the pup being born during a time of high local production of fruit or insects.

At birth the wings are too small to be used for flight. Young microbats become independent at the age of 6 to 8 weeks, while megabats do not until they are four months old.

A single bat can live over 20 years, but the bat population growth is limited by the slow birth rate.

Hunting, feeding, and drinking

A very young bat in Tamil Nadu.

Newborn bats rely on the milk from their mother's nipples for sustenance. When they are a few weeks old, bats are expected to fly and hunt on their own. It is up to them to find and catch their prey, along with satisfying their thirst.

Hunting

Most bats are nocturnal creatures. Their daylight hours are spent grooming, sleeping, and resting; it is during the nighttime hours that they hunt. The means by which bats navigate while finding and catching their prey in the dark was unknown until the 1790s, when Lazzaro Spallanzani conducted a series of experiments on a group of blind bats. These bats were placed in a room submerged in total darkness, with silk threads strung across the room. Even then, the bats were able to navigate their way through the room. Spallanzani concluded that the bats were not using their eyes to fly through complete darkness, but something else.

Spallanzani decided that bats were able to catch and find their prey through the use of their ears. To prove this theory, Spallanzani plugged the ears of the bats in his experiment. To his pleasure, he found that the bats with plugged ears were not able to fly with the same amount of skill and precision that they were able to without their ears plugged.

Bats seem to use their ears to locate and catch their prey, but how they accomplish this wasn't discovered until the 1930s, by one Donald R. Griffin. Griffin, who was a biology student at Harvard College at the time, discovered that bats use echolocation to locate and catch their prey. When bats fly, they produce a constant stream of high-pitched sounds that only bats are able to hear. When the sound waves produced by these sounds hit an insect or other animal, the echoes bounce back to the bat, and guide them to the source.

Feeding and diet

The majority of food consumed by bats includes insects, fruits and flower nectar, vertebrates and blood. Almost three-fourths of the world's bats are insect eaters. Insects consumed by bats include both aerial insects, and ground-dwelling insects. Each bat is typically able to consume one third of its body weight in insects each night, and several hundred insects in a few hours. This means that a group of one thousand bats could eat four tons of insects each year. If bats were to become extinct, the insect population is calculated to reach an alarmingly high number.

Vitamin C

In a test of 34 bat species from six major families of bats, including major insect and fruit-eating bat families, found that bats in all tested families have lost the ability to make vitamin C, and this loss may derive from a common bat ancestor, as a single mutation.

Aerial insectivores

Watching a bat catch and eat an insect is difficult. The action is so fast that all one sees is a bat rapidly change directions, and continue on its way. Scientist Frederick A. Webster discovered how bats catch their prey. In 1960, Webster developed a high-speed camera that was able to take one thousand pictures per second. These photos revealed the fast and precise way in which bats catch insects. Occasionally, a bat will catch an insect in mid-air with its mouth, and eat it in the air. However, more often than not, a bat will use its tail membrane or wings to scoop up the insect and trap it in a sort of "bug net". Then, the bat will take the insect back to its roost. There, the bat will proceed to eat said insect, often using its tail membrane as a kind of napkin, to prevent its meal from falling to the ground.

Forage gleaners (diet of non-flying insects)

These bats typically fly down and grasp their prey off the ground with their teeth, and take it to a nearby perch to eat it. Generally, these bats don't use echolocation to locate their prey. Instead, they rely on the sounds produced by the insects. Some make unique sounds, and almost all make some noise while moving through the environment.

Fruits and flower nectar

A colony of Great Fruit-eating Bats

Fruit-eating, or frugivory, is a specific habit found in two families of bats. Megachiropterans and microchiropterans both include species of bat that feed on fruits. These bats feed on the juices of sweet fruits, and fulfill the needs of some seeds to be dispersed. The fruits preferred by most fruit-eating bats are fleshy and sweet, but not particularly strong smelling or colorful. To get the juice of these fruits, bats pull the fruit off the trees with their teeth, and fly back to their roost with the fruit in their mouth.

There, the bat will consume the fruit in a specific way. To do this, the bats crush open the fruit and eat the parts that satisfy their hunger. The remainder of the fruit; the seeds and pulp, are spat onto the ground. These seeds take root and begin to grow into new fruit trees. “Over one hundred and fifty types of plants depend on bats in order to reproduce”.

Some bats prefer the nectar of flowers to insects or other animals. These bats have evolved specifically for this purpose. For example, these bats possess long muzzles and long extrusible tongues covered in fine bristles that aid them in feeding on particular flowers and plants. When they sip the nectar from these flowers, pollen gets stuck to their fur, and is dusted off when the bat takes flight, thus pollinating the plants below them. The rainforest is said to be the most benefitted out off all the biomes that bats live in, because of the large variety of appealing plants. Because of their specific eating habits, nectar-feeding bats are more prone to extinction than any other type of bat. However, according to a study, bats benefit from eating fruits and nectar just as much from eating insects.

Vertebrates

Although most bats are not included in this group, there is a small group of carnivorous bats which feed on other vertebrates and are considered the top carnivores of the bat world. These bats typically eat a variety of animals, but normally consume frogs, lizards, birds, and sometimes other bats. For example, one vertebrate predator, *Trachops cirrhosus*, is particularly skilled at catching frogs. These bats locate large groups of frogs by distinguishing their mating calls from other sounds around them. They follow the sounds to the source and pluck them from the surface of the water with their sharp canine teeth. Another example is the Greater Noctule bat which is believed to catch birds on the wing.

There are also several species of bat that feed on fish. These types of bats are found on almost all continents. They use echolocation to detect tiny ripples in the water’s surface to locate fish. From there, the bats swoop down low, inches from the water, and use specially enlarged claws on their hind feet to grab the fish out of the water. The bats then take the fish to a feeding roost and consume the animal.

Blood

There are a few species of bat that consume blood exclusively as their diet. This type of diet is referred to as hematophagy, and three species of bat exhibit this behavior. These species include the Common Vampire Bat, the White-winged Vampire Bat, and the Hairy-legged Vampire Bat. The Common Vampire Bat typically consumes the blood of mammals, while the Hairy-legged and White-winged feed on the blood of birds.

Results of eating

Bats’ dung, or guano, is so rich in nutrients, that it is mined from caves, bagged, and used by farmers to fertilize their crops. Also, guano was used in the U.S. Civil War to make gunpowder.

There comes a time in the year that some bats will not eat to supply themselves with food for the night, but for the coming months. These bats are beginning to hibernate. To do this, the bat will eat as much food as its body can contain, being as fat as possible. The bat's body then takes from the supply of fat for energy, but very slowly, because all body activities have slowed down. This supply of fat will last until the spring season arrives.

Drinking

Generally, bats drink water. In 1960, Frederic A. Webster discovered how bats are able to acquire this water. To do this, Webster developed a high-speed camera and flashgun that could take one thousand photos per second. Webster's camera captured the bat's method of skimming the surface of a body of water, and lowering its jaw to get just one drop of water. It then skims again to get a second drop of water, and then again to get a third, and so on, until it has had its fill of water. Its precision and control is very fine, and it almost never misses. Other bats such as the flying fox or fruit bat gently skim the water's surface, then land nearby to lick water from their chest fur.

Conservation efforts

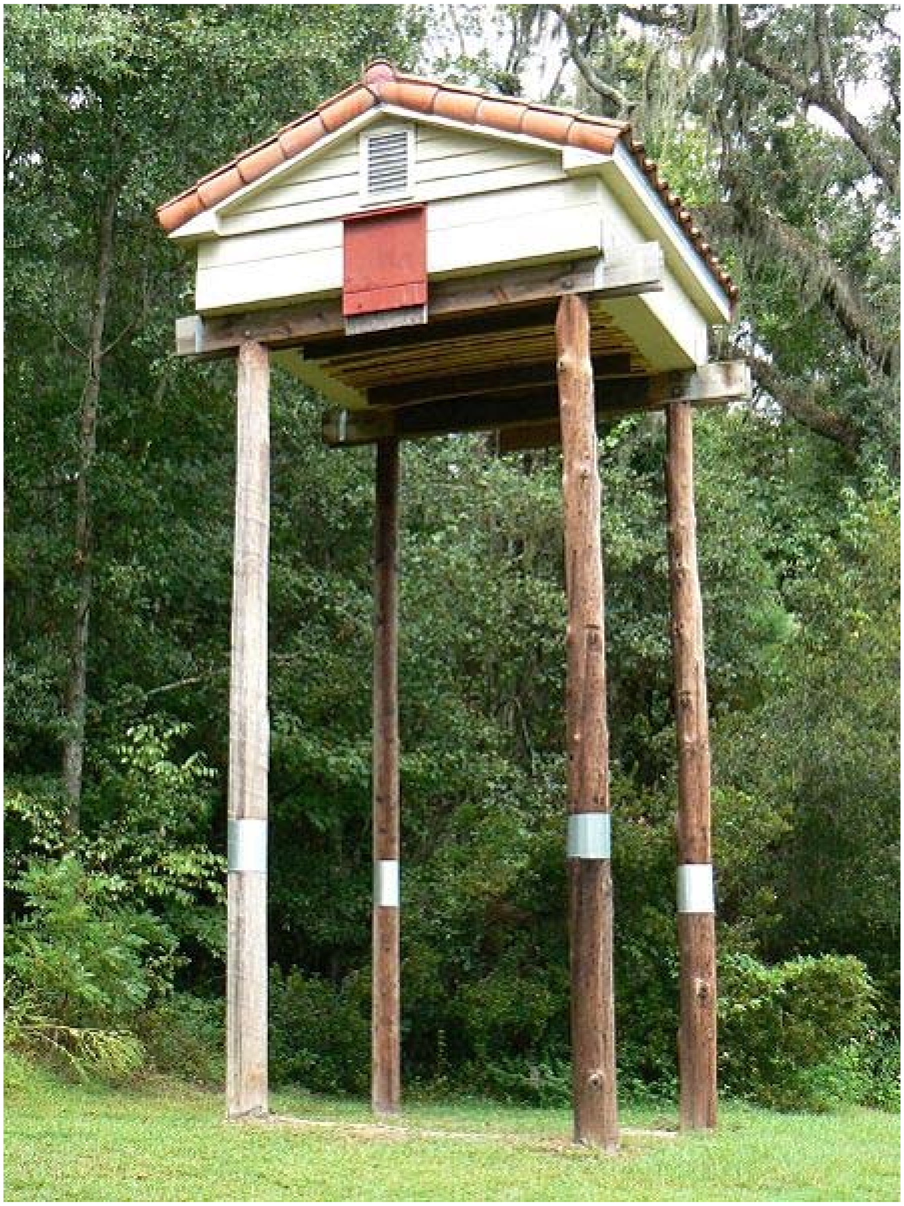
Through conservancy efforts, such as the Organization for Bat Conservation, bats are becoming better understood and people beginning to understand the crucial role bats play in insect control and pollination.

In the United Kingdom all bats are protected under the Wildlife and Countryside Acts, and even disturbing a bat or its roost can be punished with a heavy fine.

In Sarawak, Malaysia bats are protected species under the Wildlife Protection Ordinance 1998. The large Naked bat and Greater Nectar bat are consumed by the local communities.

Bats can be a tourist attraction. The Congress Avenue Bridge in Austin, Texas is the summer home to North America's largest urban bat colony, an estimated 1,500,000 Mexican free-tailed bats, which eat an estimated 10,000 to 30,000 pounds of insects each night. An estimated 100,000 tourists per year visit the bridge at twilight to watch the bats leave the roost.

Artificial roosts



Very large bat house, Tallahassee, Florida, United States.

Many people put up bat houses to attract bats just like many people put up birdhouses to attract birds. Reasons for this vary, but mostly center around the fact that bats are the primary nocturnal insectivores in most if not all ecologies. Bat houses can be made from scratch, made from kits, or bought ready made. Plans for bat houses exist on many web sites, as well as guidelines for designing a bat house. Some conservation societies are giving away free bat houses to bat enthusiasts worldwide.

A bat house constructed in 1991 at the University of Florida campus next to Lake Alice in Gainesville, Florida has a population of over 100,000 free-tailed bats.

In Britain, British hardened field defences of World War II have been converted to make roosts for bats. Pillboxes that are well dug-in and thick walled are naturally damp and provide a stable thermal environment that is required by bats that would otherwise hibernate in caves. With a few minor modifications, suitable pillboxes can be converted to artificial caves for bats.

Again in the UK, purpose-built bat houses are occasionally built when existing roosts are destroyed by developments such as new roads; one such has been built associated with bat bridges on the new (2008) A38 Dobwalls bypass.

Threats

A little brown bat with white nose syndrome.

While conservation efforts are in place to protect bats, many threats still remain.

White nose syndrome

White nose syndrome is a condition associated with the deaths of more than a million bats in the Northeastern United States. The disease is named after a white fungus found growing on the muzzles, ears, and wings of some afflicted bats, but it is not known if the fungus is the primary cause of the disease or is merely an opportunistic infection. Mortality rates of 90–100% have been observed in some caves. At least six species of hibernating bats are affected, including the endangered Indiana bat. Because the affected species have a long lifespan and a low birth rate of only about one offspring per year, it is not expected that populations will recover quickly.

Barotrauma and wind turbines

Evidence suggests Barotrauma is causing bat fatalities around wind farms. The lungs of bats are typical mammalian lungs, and unlike the lungs of birds it has been hypothesized they are more sensitive to sudden air pressure changes in their immediate vicinity such as wind turbines, and are more liable to rupture them to explain their apparent higher rate of mortality rate with such devices. Bats suffer a higher death rate than birds in the neighborhood of wind turbines since there are no signs of external trauma, the cause has been hypothesized to be a greater sensitivity to sudden pressure fluctuations in the mammalian lung than in that of birds. In addition, it has been suggested that bats are attracted to these structures, perhaps seeking roosts, and thereby increasing the death rate.

Pathogens and role in the transmission of zoonoses

Among ectoparasites, bats occasionally carry fleas, but are one of the few mammalian orders that cannot host lice (most of the others are water animals).

Bats are natural reservoir for a large number of zoonotic pathogens including rabies, severe acute respiratory syndrome (SARS), Henipavirus (i.e. Nipah virus and Hendra virus) and possibly ebola virus. Their high mobility, broad distribution, and social behaviour (communal roosting, fission-fusion social structure) make bats favourable hosts and vectors of disease. Many species also appear to have a high tolerance for harbouring pathogens and often do not develop disease while infected. However, contrary to folklore, this is not true of rabies, which is as fatal to bats as it is to all other species. However, a bat may be ill with rabies for a longer time than other mammals.

In regions where rabies is endemic, only 0.5% of bats carry the disease. However, of the few cases of rabies reported in the United States every year not caused by dogs, most are caused by bat bites. Those that are rabid may be clumsy, disoriented, and unable to fly, which makes it more likely that they will come into contact with humans. Although one should not have an unreasonable fear of bats, one should avoid handling them or having them in one's living space, as with any wild animal. If a bat is found in living quarters near a child, mentally handicapped person, intoxicated person, sleeping person, or pet, the person or pet should receive immediate medical attention for rabies. Bats have very small teeth and can bite a sleeping person without being felt. There is evidence that it is possible for the bat rabies virus to infect victims purely through airborne transmission, without direct physical contact of the victim with the bat itself.

If a bat is found in a house and the possibility of exposure cannot be ruled out, the bat should be sequestered and an animal control officer called immediately, so that the bat can be analysed. This also applies if the bat is found dead. If it is certain that nobody has been exposed to the bat, it should be removed from the house. The best way to do this is to close all the doors and windows to the room except one that opens to the outside. The bat should soon leave.

Due to the risk of rabies and also due to health problems related to their faecal droppings (guano), bats should be excluded from inhabited parts of houses. The Center for Disease Control and Prevention provides full detailed information on all aspects of bat management, including how to capture a bat, what to do in case of exposure, and how to bat-proof a house humanely. In certain countries, such as the United Kingdom, it is illegal to handle bats without a license.

Where rabies is not endemic, as throughout most of Western Europe, small bats can be considered harmless. Larger bats can give a nasty bite. They should be treated with the respect due to any wild animal.

Mythology

"Nightwing," a work of art by Dale Whistler in Austin, Texas.

The bat is sacred in Tonga and is often considered the physical manifestation of a separable soul. Bats are closely associated with vampires, who are said to be able to shapeshift into bats, fog, or wolves. Bats are also a symbol of ghosts, death, and disease. Among some Native Americans, such as the Creek, Cherokee and Apache, the bat is a trickster spirit.

Chinese lore claims the bat is a symbol of longevity and happiness, and is similarly lucky in Poland and geographical Macedonia and among the Kwakiutl and Arabs. The bat is also a heraldic animal of the Spanish autonomous community of Valencia.

Pre-Columbian cultures associated animals with gods and often displayed them in art. The Moche people depicted bats in their ceramics.

In Western Culture, the bat is often a symbol of the night and its foreboding nature. The bat is a primary animal associated with fictional characters of the night, both villains like Dracula and heroes like Batman. The association of the fear of the night with the animal was treated as a literary challenge by Kenneth Oppel, who created a best selling series of novels, beginning with *Silverwing*, which feature bats as the central heroic figures much as anthropomorphized rabbits were the central figures to the classic novel *Watership Down*.

An old wives' tale has it that bats will entangle themselves in people's hair. One likely source of this belief is that insect-eating bats seeking prey may dive erratically toward people, who attract mosquitoes and gnats, leading the squeamish to believe that the bats are trying to get in their hair.

Mesoamerica

Bat, Moche Culture 100 A.D. Larco Museum Lima, Peru.

In Mesoamerican mythology during the Classic-Contemporary period, bats symbolized the land of the dead, which was considered to be the underworld. They also symbolized destruction and decay. Bats may have symbolized in this way because they fly only at night and dwell in caves during the daytime and are associated with human skulls and bones by classic Maya ceramists. Central Mexicans sometimes depicted bats having snouts that looked like *sacrificial knives and carrying human head* in the Postclassic era. Bat images were engraved onto funerary urns and were emphasized with large claws and round ears by Zapotecs. They were commonly associated with death. The depiction of bats on funeral urns and goods took on some the characteristics of the jaguar which was and still is another entity of the night and the underworld. There have also been instances where bats are portrayed next to other unseemly animals including scorpions and other nocturnal animals such as owls.

A gigantic, life-size ceramic bat-man has been discovered and dug up from the Templo Mayor. The Templo Mayor is located in the center of the Mexica capital of Tenochtitlan. Known as a god of death, this statue has the clawed feet and hands of a bat, but the body of a man. The statue's human-like eyes bulged out from the bat-like head, making the Zapotec images very realistic and living. It was said that in the 1930s the Kaqchikel Maya proclaimed that the bat was the Devil’s provider. Kaqchikel would leave the Devil’s underworld home and collect blood from the animals to be used for scrumptious meals to feed the Devil. “In the myths, the beast of prey and the animal that is preyed upon play two significant roles. They represent two aspects of life—the aggressive, killing, conquering, creating aspect of life, and the one that is the matter or, you might say, the subject matter”. In the Devil’s underworld, dead sinners would work off their sins in order to get to heaven, indicating that the bat was too a sinner and worked under the authority of the Devil.

Oaxaca

Oaxacans believe that the jealousy of the bat in wanting birds' feathers that gently fit their bodies led him to become nocturnal. The bat feeling isolated and undesirable spoke to God after that he complained he was extremely cold. God, fair and just turned to birds in the animal kingdom and asked if they would show compassion and donate a feather to the bat so the feathers would keep him warm. The birds all agreed, and began to pluck one feather from their bodies to give to the bat. With all of the feathers, the bat became much magnificent looking than all birds, even able to spread color to the night sky. During daylight, the bat created rainbows that reflected vibrant colors from the sun. The bat soon became overly arrogant and conceited, due having this new and improved look. The birds grew tired of the bat’s self conceitedness and glorification, and so decided to fly up to heaven and speak to God to do something. The birds informed to God of the bat's behaviour, God was surprised and so decided to take a look himself. When on Earth, God called on the bat to show him what he was doing. The bat began to fly across the light blue sky, where one by one each feather began to fall out, uncovering the bat’s natural ugly looking body. The bat became ashamed and distressed of his appearance after all feathers came off, missing the beautiful, plentiful feathers that he had, that he decided to hide in caves during the day. He would only come out during the night, searching high and low for the feathers to avoid embarrassment that he will not be seen during his search.

East Nigeria

According to a particular East Nigerian tale, the bat developed its nocturnal habits after causing the death of his partner the bush-rat. The bat and the bush-rat would share activities such as rummaging through the grass and trees, hunting, talking and bonding during the day. When at night, the bat and the bush-rat would alternate in cooking duties cooking what was caught, and eat together. It appeared to a dedicated partnership, however the bat hated the bush-rat immensely. The bush rat always found the bat’s soup more appetising so when eating dinner one night asked the bat why the soup tasted better than his own and also asked how it was made. The bat agreed to show him how to make it the next day but instead was forming a malicious plan.

Next day as bat prepared his soup, the bush-rat came, greeting him and asked if he could be shown what was agreed yesterday. Earlier, the bat has found a pot looking exactly like the one he used usually, but it held warm water and so decided to use this instead. The bat explained to the bush-rat that to make his soup, he had to boil himself prior to serving the soup where sweetness and flavor of the soup came from the flesh. The bat jumped in the pot seemingly excited, with the bush-rat mesmerised. After a few minutes the bat climbed out and while the bush-rat was distracted, switched pots. The bat then served his soup out of the soup pot, both tasted it. Over anxious and eager, the bush-rat, jumped into the pot of warm water. He stayed much longer in the pot dying in the process.

When the bush-rat’s wife returned that night to find her husband dead, she wept and ran to the chief of the land's house telling him about what happened and what she was sure what the bat had done. In hearing this, the chief became angry, ordering for the immediate arrest of the bat. It just so happened that the bat was flying over the house and overheard what was just said. He quickly went into hiding high up in a tree. When the chief's men went looking for the bat, he could not be found. The search to arrest the bat carried on over several days, but still could not be found. The bat needed to eat, so flew out of hiding every night to hunt for food to escape of being arrested. This, according to Eastern Nigeria mythology, is why bats only fly at night.

Chapter 4

Snake

Snakes **Temporal range: 145–0 Ma** **Cretaceous – Recent**	

Coast garter snake,
Thamnophis elegans terrestris

Scientific classification [e]	
Kingdom:	Animalia
Phylum:	Chordata
Class:	Reptilia
Order:	Squamata
Superfamily:	Varanoidea
(unranked):	Pythonomorpha
Suborder:	**Serpentes** Linnaeus, 1758

Infraorders

- Alethinophidia – Nopcsa, 1923
- Scolecophidia – Cope, 1864

World range of snakes
(rough range of sea snakes in blue)

Snakes are elongate, legless, carnivorous reptiles of the suborder **Serpentes** that can be distinguished from legless lizards by their lack of eyelids and external ears. Like all squamates, snakes are ectothermic, amniote vertebrates covered in overlapping scales. Many species of snakes have skulls with many more joints than their lizard ancestors, enabling them to swallow prey much larger than their heads with their highly mobile jaws. To accommodate their narrow bodies, snakes' paired organs (such as kidneys) appear one in front of the other instead of side by side, and most have only one functional lung. Some species retain a pelvic girdle with a pair of vestigial claws on either side of the cloaca.

Living snakes are found on every continent except Antarctica and on most islands. Fifteen families are currently recognized, comprising 456 genera and over 2,900 species. They range in size from the tiny, 10 cm-long thread snake to pythons and anacondas of up to 7.6 metres (25 ft) in length. The recently discovered fossil *Titanoboa* was 15 metres (49 ft) long. Snakes are thought to have evolved from either burrowing or aquatic lizards during the Cretaceous period (*c* 150 Ma). The diversity of modern snakes appeared during the Paleocene period (*c* 66 to 56 Ma).

Most species are nonvenomous and those that have venom use it primarily to kill and subdue prey rather than for self-defense. Some possess venom potent enough to cause painful injury or death to humans. Nonvenomous snakes either swallow prey alive or kill by constriction.

Etymology

The English word *snake* comes from Old English *snaca*, itself from Proto-Germanic **snak-an-* (cf. German *Schnake* "ring snake," Swedish *snok* "grass snake"), from Proto-Indo-European root **(s)nēg-o-* "to crawl, creep," which also gave *sneak* as well as Sanskrit *nāgá* "snake." The word ousted *adder*, as *adder* went on to narrow in meaning, though in Old English *nædre* was the general word for snake. The other term, *serpent*, is from French, ultimately from Indo-European **serp-* (to creep), which also gave Greek *érpo* (ερπω) "I crawl."

Evolution

The fossil record of snakes is relatively poor because snake skeletons are typically small and fragile, making fossilization uncommon. However, 150 million-year-old specimens, readily identifiable as snakes, yet with lizard-like skeletal structures, have been uncovered in South America and Africa. Based on comparative anatomy, there is consensus that snakes descended from lizards.

Pythons and boas—primitive groups among modern snakes—have vestigial hind limbs: tiny, clawed digits known as anal spurs, which are used to grasp during mating. The Leptotyphlopidae and Typhlopidae groups also possess remnants of the pelvic girdle, sometimes appearing as horny projections when visible.

Frontal limbs are nonexistent in all snakes. This is caused by the evolution of Hox genes, controlling limb morphogenesis. The axial skeleton of the snakes' common ancestor, like most other tetrapods, had regional specializations consisting of cervical (neck), thoracic (chest), lumbar (lower back), sacral (pelvic), and caudal (tail) vertebrae. Early in snake evolution, the Hox gene expression in the axial skeleton responsible for the development of the thorax became dominant. As a result, the vertebrae anterior to the hindlimb buds (when present) all have the same thoracic-like identity (except from the atlas, axis, and 1–3 neck vertebrae). In other words, most of a snake's skeleton is an extremely extended thorax. Ribs are found exclusively on the thoracic vertebrae. Neck, lumbar and pelvic vertebrae are very reduced in number (only 2–10 lumbar and pelvic vertebrae are present), while only a short tail remains of the caudal vertebrae. However, the tail is still long enough to be of important use in many species, and is modified in some aquatic and tree-dwelling species.

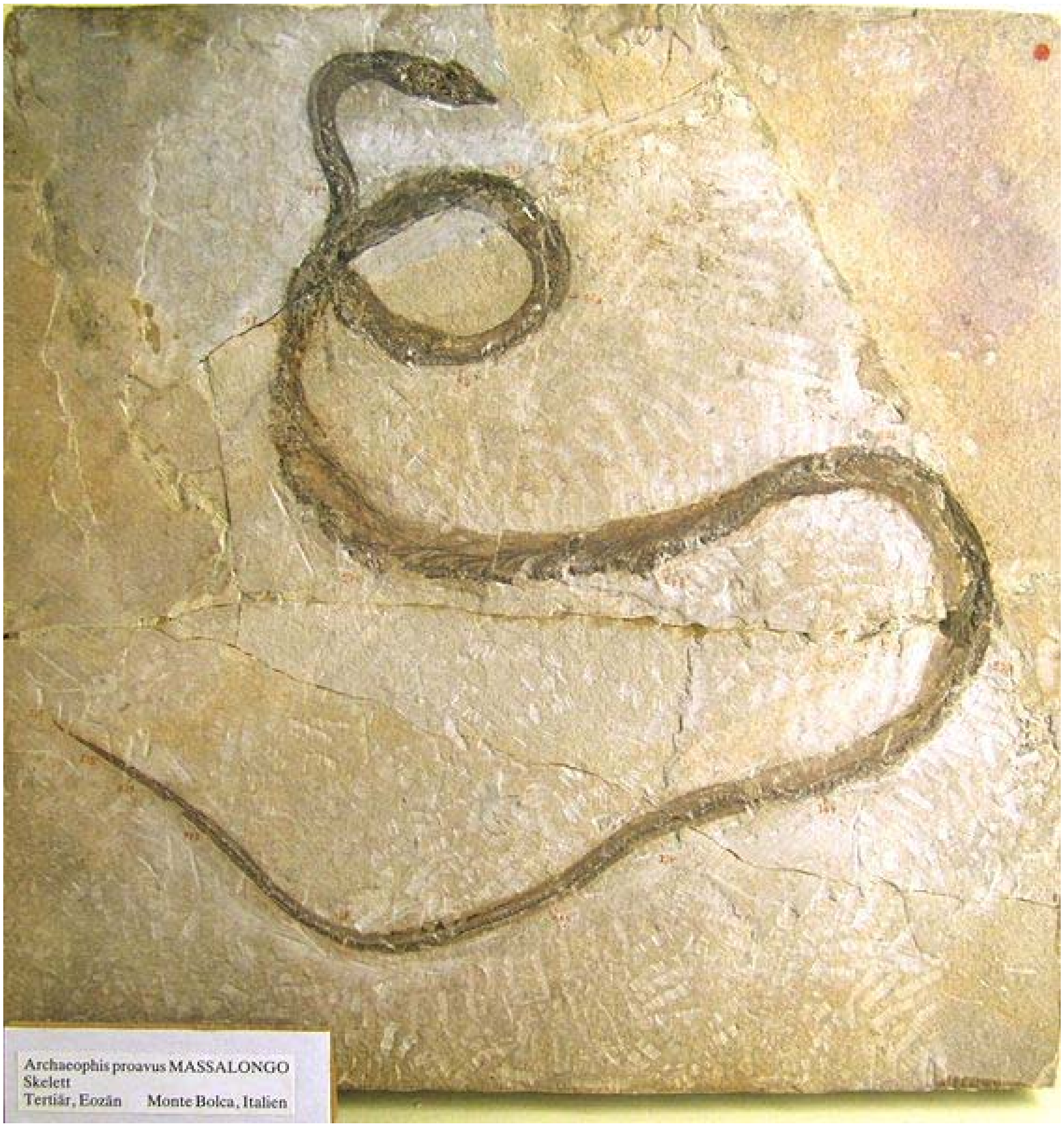
Modern snakes greatly diversified during the Paleocene. This occurred alongside the adaptive radiation of mammals, following the extinction of (non-avian) dinosaurs. The colubrids, one of the more common snake groups, became particularly diverse due to preying on rodents, an especially successful mammal group. There are over 2,900 species of snakes ranging as far northward as the Arctic Circle in Scandinavia and southward through Australia and Tasmania. Snakes can be found on every continent (with the exception of Antarctica), in the sea, and as high as 16,000 feet (4,900 m) in the Himalayan Mountains of Asia. There are numerous islands from which snakes are absent, such as Ireland, Iceland, and New Zealand.

Origins

The origin of snakes remains an unresolved issue. There are two main hypotheses competing for acceptance.

Burrowing Lizard Hypothesis

There is fossil evidence to suggest that snakes may have evolved from burrowing lizards, such as the varanids (or a similar group) during the Cretaceous Period. An early fossil snake, *Najash rionegrina*, was a two-legged burrowing animal with a sacrum, and was fully terrestrial. One extant analog of these putative ancestors is the earless monitor *Lanthanotus* of Borneo (though it also is semiaquatic). Subterranean species evolved bodies streamlined for burrowing, and eventually lost their limbs. According to this hypothesis, features such as the transparent, fused eyelids (brille) and loss of external ears evolved to cope with fossorial difficulties, such as scratched corneas and dirt in the ears. Some primitive snakes are known to have possessed hindlimbs, but their pelvic bones lacked a direct connection to the vertebrae. These include fossil species like *Haasiophis*, *Pachyrhachis* and *Eupodophis*, which are slightly older than *Najash*.



Fossil of *Archaeophis proavus*. Aquatic Mosasaur Hypothesis

An alternative hypothesis, based on morphology, suggests the ancestors of snakes were related to mosasaurs—extinct aquatic reptiles from the Cretaceous—which in turn are thought to have derived from varanid lizards. According to this hypothesis, the fused, transparent eyelids of snakes are thought to have evolved to combat marine conditions (corneal water loss through osmosis), and the external ears were lost through disuse in an aquatic environment. This ultimately lead to an animal similar to today's sea snakes. In the Late Cretaceous, snakes recolonized land, and continued to diversify into today's snakes. Fossilized snake remains are known from early Late Cretaceous marine sediments, which is consistent with this hypothesis; particularly so, as they are older than the terrestrial *Najash rionegrina*. Similar skull structure, reduced or absent limbs, and other anatomical features found in both mosasaurs and snakes lead to a positive cladistical correlation, although some of these features are shared with varanids.

Genetic studies in recent years have indicated snakes are not as closely related to monitor lizards as was once believed—and therefore not to mosasaurs, the proposed ancestor in the aquatic scenario of their evolution. However, more evidence links mosasaurs to snakes than to varanids. Fragmented remains found from the Jurassic and Early Cretaceous indicate deeper fossil records for these groups, which may potentially refute either hypothesis.

Taxonomy

All modern snakes are grouped within the suborder *Serpentes* in Linnean taxonomy, part of the order Squamata, though their precise placement within squamates is controversial.

There are two infraorders of *Serpentes*: Alethinophidia and Scolecophidia. This separation is based on morphological characteristics and mitochondrial DNA sequence similarity. Alethinophidia is sometimes split into Henophidia and Caenophidia, with the latter consisting of "colubroid" snakes (colubrids, vipers, elapids, hydrophiids, and attractaspids) and acrochordids, while the other alethinophidian families comprise Henophidia. While not extant today, the Madtsoiidae, a family of giant, primitive, python-like snakes, was around until 50,000 years ago in Australia, represented by genera such as Wonambi.

There are numerous debates in the systematics within the group. For instance, many sources classify Boidae and Pythonidae as one family, while some keep the Elapidae and Hydrophiidae (sea snakes) separate for practical reasons despite their extremely close relation.

Recent molecular studies support the monophyly of the clades of modern snakes, scolecophidians, typhlopids + anomalepidids, alethinophidians, core alethinophidians, uropeltids (*Cylindrophis*, *Anomochilus*, uropeltines), macrostomatans, booids, boids, pythonids and caenophidians.

Families

Infraorder **Alethinophidia** 15 families					
Family	**Taxon author**	**Genera**	**Species**	**Common name**	**Geographic range**
Acrochordidae	Bonaparte, 1831	1	3	Wart snakes	Western India and Sri Lanka through tropical Southeast Asia to the Philippines, south through the Indonesian/Malaysian island group to Timor, east through New Guinea to the northern coast of Australia to Mussau Island, the Bismark Archipelago and Guadalcanal Island in the Solomon Islands.
Aniliidae	Stejneger, 1907	1	1	False coral snake	Tropical South America.
Anomochilidae	Cundall, Wallach, 1993	1	2	Dwarf pipe snakes	West Malaysia and on the Indonesian island of Sumatra.
Atractaspididae	Günther, 1858	12	64	Burrowing asps	Africa and the Middle East.
Boidae	Gray, 1825	8	43	Boas	Northern, Central and South America, the Caribbean, southeastern Europe and Asia Minor, Northern, Central and East Africa, Madagascar and Reunion Island, the Arabian Peninsula, Central and southwestern Asia, India and Sri Lanka, the Moluccas and New Guinea through to Melanesia and Samoa.
Bolyeriidae	Hoffstetter, 1946	2	2	Splitjaw snakes	Mauritius.

Colubridae	Oppel, 1811	304	1938	Typical snakes	Widespread on all continents, except Antarctica.
Cylindrophiidae	Fitzinger, 1843	1	8	Asian pipe snakes	Sri Lanka east through Myanmar, Thailand, Cambodia, Vietnam and the Malay Archipelago to as far east as Aru Islands off the southwestern coast of New Guinea. Also found in southern China (Fujian, Hong Kong and on Hainan Island) and in Laos.
Elapidae	Boie, 1827	61	235	Elapids	On land, worldwide in tropical and subtropical regions, except in Europe. Sea snakes occur in the Indian Ocean and the Pacific.
Loxocemidae	Cope, 1861	1	1	Mexican burrowing snake	Along the Pacific versant from Mexico south to Costa Rica.
Pythonidae	Fitzinger, 1826	8	26	Pythons	Subsaharan Africa, India, Myanmar, southern China, Southeast Asia and from the Philippines southeast through Indonesia to New Guinea and Australia.
Tropidophiidae	Brongersma, 1951	4	22	Dwarf boas	From southern Mexico and Central America, south to northwestern South America in Colombia, (Amazonian) Ecuador and Peru, as well as in northwestern and southeastern Brazil. Also found in the West Indies.
Uropeltidae	Müller, 1832	8	47	Shield-tailed snakes	Southern India and Sri Lanka.

Viperidae	Oppel, 1811	32	224	Vipers	The Americas, Africa and Eurasia.
Xenopeltidae	Bonaparte, 1845	1	2	Sunbeam snakes	Southeast Asia from the Andaman and Nicobar Islands, east through Myanmar to southern China, Thailand, Laos, Cambodia, Vietnam, the Malay Peninsula and the East Indies to Sulawesi, as well as the Philippines.

Infraorder **Scolecophidia** 3 families					
Family	**Taxon author**	**Genera**	**Species**	**Common name**	**Geographic range**
Anomalepidae	Taylor, 1939	4	15	Primitive blind snakes	From southern Central America to northwestern South America. Disjunct populations in northeastern and southeastern South America.
Leptotyphlopidae	Stejneger, 1892	2	87	Slender blind snakes	Africa, western Asia from Turkey to northwestern India, on Socotra Island, from the southwestern United States south through Mexico and Central to South America, though not in the high Andes. In Pacific South America they occur as far south as southern coastal Peru, and on the Atlantic side as far as Uruguay and Argentina. In the Caribbean they are found on the Bahamas, Hispaniola and the Lesser Antilles.
Typhlopidae	Merrem, 1820	6	203	Typical blind snakes	Most tropical and many subtropical regions around the world, particularly in Africa, Madagascar, Asia, islands in the Pacific, tropical America and in

					southeastern Europe.

Biology

When compared, the skeletons of snakes are radically different from those of most other reptiles (such as the turtle, right), being made up almost entirely of an extended ribcage.

Skeleton

The skeleton of most snakes consists solely of the skull, hyoid, vertebral column, and ribs, though henophidian snakes retain vestiges of the pelvis and rear limbs. The skull of the snake consists of a solid and complete braincase, to which many of the other bones are only loosely attached, particularly the highly mobile jaw bones, which facilitate manipulation and ingestion of large prey items. The left and right sides of the lower jaw are joined only by a flexible ligament at the anterior tips, allowing them to separate widely, while the posterior end of the lower jaw bones articulate with a quadrate bone, allowing further mobility. The bones of the mandible and quadrate bones can also pick up ground borne vibrations. The hyoid is a small bone located posterior and ventral to the skull, in the 'neck' region, which serves as an attachment for muscles of the snake's tongue, as it does in all other tetrapods.

The vertebral column consists of anywhere between 200 to 400 (or more) vertebrae. Tail vertebrae are comparatively few in number (often less than 20% of the total) and lack ribs, while body vertebrae each have two ribs articulating with them. The vertebrae have projections that allow for strong muscle attachment enabling locomotion without limbs. Autotomy of the tail, a feature found in some lizards is absent in most snakes. Caudal autotomy in snakes is rare and is intervertebral, unlike that in lizards, which is intravertebral—that is, the break happens along a predefined fracture plane present on a vertebra.

In some snakes, most notably boas and pythons, there are vestiges of the hindlimbs in the form of a pair of pelvic spurs. These small, claw-like protrusions on each side of the cloaca are the external portion of the vestigial hindlimb skeleton, which includes the remains of an ilium and femur.

Internal organs

The snake's heart is encased in a sac, called the *pericardium*, located at the bifurcation of the bronchi. The heart is able to move around, however, owing to the lack of a diaphragm. This adjustment protects the heart from potential damage when large ingested prey is passed through the esophagus. The spleen is attached to the gall bladder and pancreas and filters the blood. The thymus gland is located in fatty tissue above the heart and is responsible for the generation of immune cells in the blood. The cardiovascular system of snakes is also unique for the presence of a renal portal system in which the blood from the snake's tail passes through the kidneys before returning to the heart.

The vestigial left lung is often small or sometimes even absent, as snakes' tubular bodies require all of their organs to be long and thin. In the majority of species, only one lung is functional. This lung contains a vascularized anterior portion and a posterior portion that does not function in gas exchange. This 'saccular lung' is used for hydrostatic purposes to adjust buoyancy in some aquatic snakes and its function remains unknown in terrestrial species. Many organs that are paired, such as kidneys or reproductive organs, are staggered within the body, with one located ahead of the other.

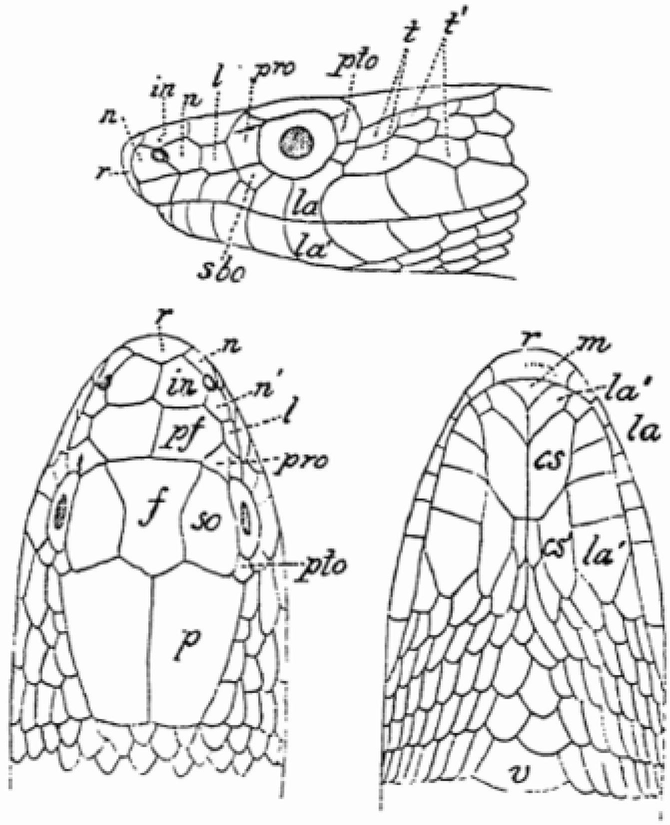
Snakes have no lymph nodes.

An adult Barbados threadsnake, Leptotyphlops carlae, on an American quarter dollar.

Size

The now extinct *Titanoboa cerrejonensis* snakes found were 12–15 meters (39–49 ft) in length. By comparison, the largest extant snakes are the reticulated python, which measures about 9 meters (30 ft) long, and the anaconda, which measures about 7.5 meters (25 ft) long and is considered the heaviest snake on Earth.

At the other end of the scale, the smallest extant snake is *Leptotyphlops carlae*, with a length of about 10 centimeters (4 in). Most snakes are fairly small animals, approximately 3 feet in length.



Three views of head of *Zamenis ventrimaculatus*, to explain the terminology of the head-shields.

cs. Chin-shields (anterior).
cs'. Chin-shields (posterior).
f. Frontal.
in. Internasal.
l. Loreal.
la. Upper labial.
la'. Lower labial.
m. Mental.
n. Nasal.
p. Parietal.
pf. Præfrontal.
pro. Præocular.
pto. Postocular.
r. Rostral.
sbo. Subocular.
so. Supraocular.
t. Temporals (first row).
t'. Temporals (second row).
v. First ventral.

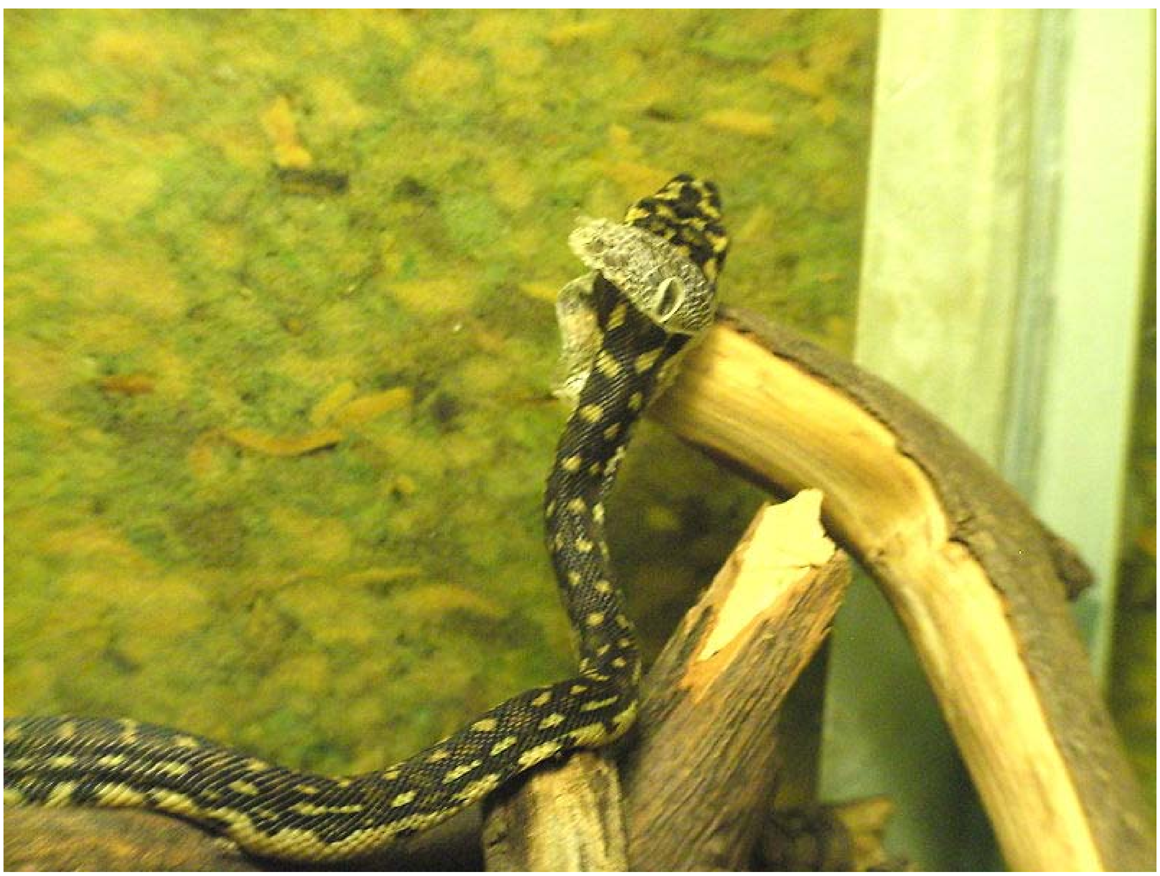
A line diagram from G.A. Boulenger's Fauna of British India (1890) illustrating the terminology of shields on the head of a snake.

Skin

The skin of a snake is covered in scales. Contrary to the popular notion of snakes being slimy because of possible confusion of snakes with worms, snakeskin has a smooth, dry texture. Most snakes use specialized belly scales to travel, gripping surfaces. The body scales may be smooth, keeled, or granular. The eyelids of a snake are transparent "spectacle" scales, which remain permanently closed, also known as brille.

The shedding of scales is called *ecdysis* (or in normal usage, *moulting* or *sloughing*). In the case of snakes, the complete outer layer of skin is shed in one layer. Snake scales are not discrete, but extensions of the epidermis—hence they are not shed separately but as a complete outer layer during each moult, akin to a sock being turned inside out.

The shape and number of scales on the head, back, and belly are often characteristic and used for taxonomic purposes. Scales are named mainly according to their positions on the body. In "advanced" (Caenophidian) snakes, the broad belly scales and rows of dorsal scales correspond to the vertebrae, allowing scientists to count the vertebrae without dissection.



Eye scales visible during the moult of a Diamond Python.

Snakes' eyes are covered by their clear scales (the brille) rather than movable eyelids. Their eyes are always open, and for sleeping, the retina can be closed or the face buried among the folds of the body.

Moulting

Moulting serves a number of functions. Firstly, the old and worn skin is replaced; secondly, it helps get rid of parasites such as mites and ticks. Renewal of the skin by moulting is supposed to allow growth in some animals such as insects; however, this has been disputed in the case of snakes.

A snake shedding its skin.

Moulting occurs periodically throughout a snake's life. Before a moult, the snake stops eating and often hides or moves to a safe place. Just before shedding, the skin becomes dull and dry looking and the eyes become cloudy or blue-colored. The inner surface of the old skin liquefies. This causes the old skin to separate from the new skin beneath it. After a few days, the eyes clear and the snake "crawls" out of its old skin. The old skin breaks near the mouth and the snake wriggles out, aided by rubbing against rough surfaces. In many cases, the cast skin peels backward over the body from head to tail in one piece, like pulling a sock off inside-out. A new, larger, brighter layer of skin has formed underneath.

An older snake may shed its skin only once or twice a year. But a younger snake, still growing, may shed up to four times a year. The discarded skin gives a perfect imprint of the scale pattern, and it is usually possible to identify the snake if the discarded skin is reasonably intact. This periodic renewal has led to the snake being a symbol of healing and medicine, as pictured in the Rod of Asclepius.

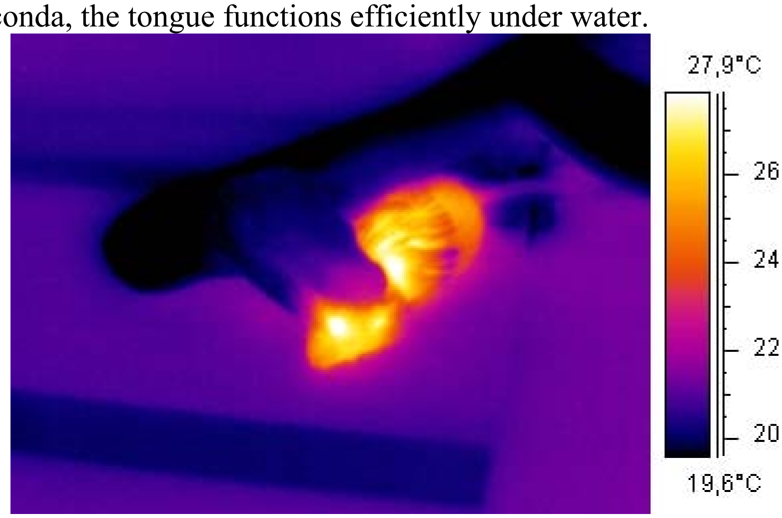
Perception

Eyesight

Snake vision varies greatly, from only being able to distinguish light from dark to keen eyesight, but the main trend is that their vision is adequate although not sharp, and allows them to track movements. Generally, vision is best in arboreal snakes and weakest in burrowing snakes. Some snakes, such as the Asian vine snake (genus *Ahaetulla*), have binocular vision, with both eyes capable of focusing on the same point. Most snakes focus by moving the lens back and forth in relation to the retina, while in the other amniote groups, the lens is stretched.

Smell

Snakes use smell to track their prey. They smell by using their forked tongues to collect airborne particles, then passing them to the vomeronasal organ or *Jacobson's organ* in the mouth for examination. The fork in the tongue gives snakes a sort of directional sense of smell and taste simultaneously. They keep their tongues constantly in motion, sampling particles from the air, ground, and water, analyzing the chemicals found, and determining the presence of prey or predators in the local environment. In water-dwelling snakes, such as the Anaconda, the tongue functions efficiently under water.



Thermographic image of a snake eating a mouse

Vibration sensitivity

The part of the body in direct contact with the ground is very sensitive to vibration; thus, a snake can sense other animals approaching by detecting faint vibrations in the air and on the ground.

Infrared sensitivity

Pit vipers, pythons, and some boas have infrared-sensitive receptors in deep grooves between the nostril and eye, although some have labial pits on their upper lip just below the nostrils (common in pythons), which allow them to "see" the radiated heat of warm-blooded prey mammals.

Venom

Milk snakes are often mistaken for coral snakes, whose venom is deadly to humans.

Cobras, vipers, and closely related species use venom to immobilize or kill their prey. The venom is modified saliva, delivered through fangs. The fangs of 'advanced' venomous snakes like viperids and elapids are hollow to inject venom more effectively, while the fangs of rear-fanged snakes such as the boomslang merely have a groove on the posterior edge to channel venom into the wound. Snake venoms are often prey specific, their role in self-defense is secondary.

Venom, like all salivary secretions, is a predigestant that initiates the breakdown of food into soluble compounds, facilitating proper digestion. Even nonvenomous snake bites (like any animal bite) will cause tissue damage.

Certain birds, mammals, and other snakes (such as kingsnakes) that prey on venomous snakes have developed resistance and even immunity to certain venoms. Venomous snakes include three families of snakes, and do not constitute a formal classification group used in taxonomy.

The term **poisonous snake** is mostly incorrect. Poison is inhaled or ingested, whereas venom is injected. There are, however, two exceptions: *Rhabdophis* sequesters toxins from the toads it eats, then secretes them from nuchal glands to ward off predators, and a small population of garter snakes in Oregon retains enough toxin in their liver from the newts they eat to be effectively poisonous to small local predators (such as crows and foxes).

Snake venoms are complex mixtures of proteins, and are stored in poison glands at the back of the head. In all venomous snakes, these glands open through ducts into grooved or hollow teeth in the upper jaw. These proteins can potentially be a mix of neurotoxins (which attack the nervous system), hemotoxins (which attack the circulatory system), cytotoxins, bungarotoxins and many other toxins that affect the body in different ways. Almost all snake venom contains *hyaluronidase*, an enzyme that ensures rapid diffusion of the venom.

Venomous snakes that use hemotoxins usually have fangs in the front of their mouths, making it easier for them to inject the venom into their victims. Some snakes that use neurotoxins (such as the mangrove snake) have fangs in the back of their mouths, with the fangs curled backwards. This makes it both difficult for the snake to use its venom and for scientists to milk them. *Elapids*, however, such as cobras and kraits are *proteroglyphous*—they possess hollow fangs that cannot be erected toward the front of their mouths, and cannot "stab" like a viper. They must actually bite the victim.

It has recently been suggested that all snakes may be venomous to a certain degree, with harmless snakes having weak venom and no fangs. Most snakes currently labelled “nonvenomous” would still be considered harmless according to this theory, as they either lack a venom delivery method or are incapable of delivering enough to endanger a human. This theory postulates that snakes may have evolved from a common lizard ancestor that was venomous—and that venomous lizards like the gila monster, beaded lizard, monitor lizards, and the now-extinct mosasaurs may also have derived. They share this venom clade with various other saurian species.

Venomous snakes are classified in two taxonomic families:

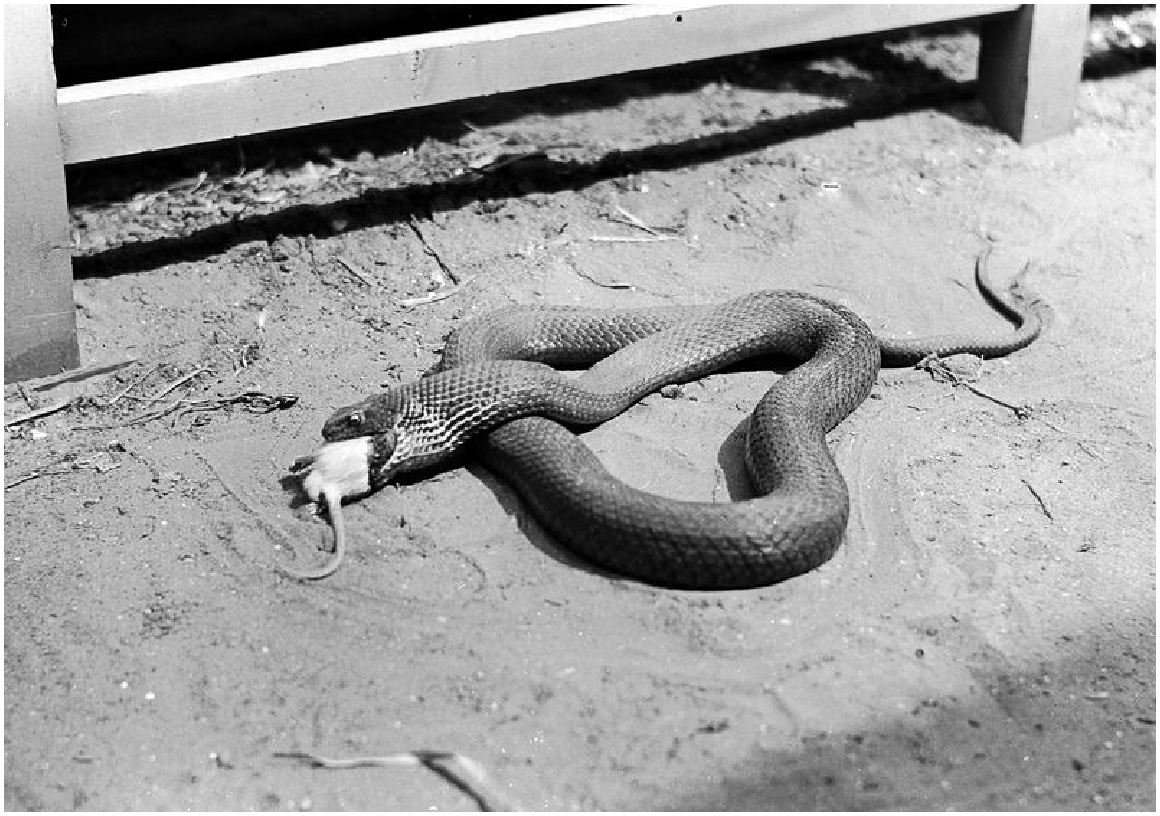
- Elapids – cobras including king cobras, kraits, mambas, Australian copperheads, sea snakes, and coral snakes.
- Viperids – vipers, rattlesnakes, copperheads/cottonmouths, adders and bushmasters.

There is a third family containing the *opistoglyphous* (rear-fanged) snakes (as well as the majority of other snake species):

- Colubrids – boomslangs, tree snakes, vine snakes, mangrove snakes, although not all colubrids are venomous.

Behavior

Feeding and diet



Snake eating a rodent.

Carpet python constricting and consuming a chicken.

All snakes are strictly carnivorous, eating small animals including lizards, other snakes, small mammals, birds, eggs, fish, snails or insects. Because snakes cannot bite or tear their food to pieces, they must swallow prey whole. The body size of a snake has a major influence on its eating habits. Smaller snakes eat smaller prey. Juvenile pythons might start out feeding on lizards or mice and graduate to small deer or antelope as an adult, for example.

African egg-eating snake.

The snake's jaw is a complex structure. Contrary to the popular belief that snakes can dislocate their jaws, snakes have a very flexible lower jaw, the two halves of which are not rigidly attached, and numerous other joints in their skull, allowing them to open their mouths wide enough to swallow their prey whole, even if it is larger in diameter than the snake itself, as snakes do not chew. For example, the African egg-eating snake has flexible jaws adapted for eating eggs much larger than the diameter of its head. This snake has no teeth, but does have bony protrusions on the inside edge of its spine, which it uses to break shells when it eats eggs.

While the majority of snakes eat a variety of prey animals, there is some specialization by some species. King cobras and the Australian bandy-bandy consume other snakes.

Pareas iwesakii and other snail-eating colubrids of subfamily Pareatinae have more teeth on the right side of their mouths than on the left, as the shells of their prey usually spiral clockwise

Some snakes have a venomous bite, which they use to kill their prey before eating it. Other snakes kill their prey by constriction. Still others swallow their prey whole and alive.

After eating, snakes become dormant while the process of digestion takes place. Digestion is an intense activity, especially after consumption of large prey. In species that feed only sporadically, the entire intestine enters a reduced state between meals to conserve energy. The digestive system is then 'up-regulated' to full capacity within 48 hours of prey consumption. Being ectothermic ("cold-blooded"), the surrounding temperature plays a large role in snake digestion. The ideal temperature for snakes to digest is 30 °C (86 °F). So much metabolic energy is involved in a snake's digestion that in the Mexican rattlesnake (*Crotalus durissus*), surface body temperature increases by as much as 1.2 °C (2.2 °F) during the digestive process. Because of this, a snake disturbed after having eaten recently will often regurgitate its prey to be able to escape the perceived threat. When undisturbed, the digestive process is highly efficient, with the snake's digestive enzymes dissolving and absorbing everything but the prey's hair (or feathers) and claws, which are excreted along with waste.

Locomotion

The lack of limbs does not impede the movement of snakes. They have developed several different modes of locomotion to deal with particular environments. Unlike the gaits of limbed animals, which form a continuum, each mode of snake locomotion is discrete and distinct from the others; transitions between modes are abrupt.

Lateral undulation

Lateral undulation is the sole mode of aquatic locomotion, and the most common mode of terrestrial locomotion. In this mode, the body of the snake alternately flexes to the left and right, resulting in a series of rearward-moving "waves." While this movement appears rapid, snakes have rarely been documented moving faster than two body-lengths per second, often much less. This mode of movement has the same net cost of transport (calories burned per meter moved) as running in lizards of the same mass.

Terrestrial

Terrestrial lateral undulation is the most common mode of terrestrial locomotion for most snake species. In this mode, the posteriorly moving waves push against contact points in the environment, such as rocks, twigs, irregularities in the soil, etc. Each of these environmental objects, in turn, generates a reaction force directed forward and towards the midline of the snake, resulting in forward thrust while the lateral components cancel out. The speed of this movement depends upon the density of push-points in the environment, with a medium density of about 8 along the snake's length being ideal. The wave speed is precisely the same as the snake speed, and as a result, every point on the snake's body follows the path of the point ahead of it, allowing snakes to move through very dense vegetation and small openings.

Aquatic

Banded sea krait, *Laticauda sp*.

When swimming, the waves become larger as they move down the snake's body, and the wave travels backwards faster than the snake moves forwards. Thrust is generated by pushing their body against the water, resulting in the observed slip. In spite of overall similarities, studies show that the pattern of muscle activation is different in aquatic versus terrestrial lateral undulation, which justifies calling them separate modes. All snakes can laterally undulate forward (with backward-moving waves), but only sea snakes have been observed reversing the motion (moving backwards with forward-moving waves).

Sidewinding

A Mojave rattlesnake (Crotalus scutulatus) sidewinding.

Most often employed by colubroid snakes (colubrids, elapids, and vipers) when the snake must move in an environment that lacks irregularities to push against (rendering lateral undulation impossible), such as a slick mud flat, or a sand dune. Sidewinding is a modified form of lateral undulation in which all of the body segments oriented in one direction remain in contact with the ground, while the other segments are lifted up, resulting in a peculiar "rolling" motion. This mode of locomotion overcomes the slippery nature of sand or mud by pushing off with only static portions on the body, thereby minimizing slipping. The static nature of the contact points can be shown from the tracks of a sidewinding snake, which show each belly scale imprint, without any smearing. This mode of locomotion has very low caloric cost, less than ⅓ of the cost for a lizard or snake to move the same distance. Contrary to popular belief, there is no evidence that sidewinding is associated with the sand being hot.

Concertina

When push-points are absent, but there is not enough space to use sidewinding because of lateral constraints, such as in tunnels, snakes rely on concertina locomotion. In this mode, the snake braces the posterior portion of its body against the tunnel wall while the front of the snake extends and straightens. The front portion then flexes and forms an anchor point, and the posterior is straightened and pulled forwards. This mode of locomotion is slow and very demanding, up to seven times the cost of laterally undulating over the same distance. This high cost is due to the repeated stops and starts of portions of the body as well as the necessity of using active muscular effort to brace against the tunnel walls.

Rectilinear

The slowest mode of snake locomotion is rectilinear locomotion, which is also the only one where the snake does not need to bend its body laterally, though it may do so when turning. In this mode, the belly scales are lifted and pulled forward before being placed down and the body pulled over them. Waves of movement and stasis pass posteriorly, resulting in a series of ripples in the skin. The ribs of the snake do not move in this mode of locomotion and this method is most often used by large pythons, boas, and vipers when stalking prey across open ground as the snake's movements are subtle and harder to detect by their prey in this manner.

Other

The movement of snakes in arboreal habitats has only recently been studied. While on tree branches, snakes use several modes of locomotion depending on species and bark texture. In general, snakes will use a modified form of concertina locomotion on smooth branches, but will laterally undulate if contact points are available. Snakes move faster on small branches and when contact points are present, in contrast to limbed animals, which do better on large branches with little 'clutter'.

Gliding snakes (*Chrysopelea*) of Southeast Asia launch themselves from branch tips, spreading their ribs and laterally undulating as they glide between trees. These snakes can perform a controlled glide for hundreds of feet depending upon launch altitude and can even turn in midair.

Reproduction

Although a wide range of reproductive modes are used by snakes, all snakes employ internal fertilization. This is accomplished by means of paired, forked hemipenes, which are stored, inverted, in the male's tail. The hemipenes are often grooved, hooked, or spined in order to grip the walls of the female's cloaca.

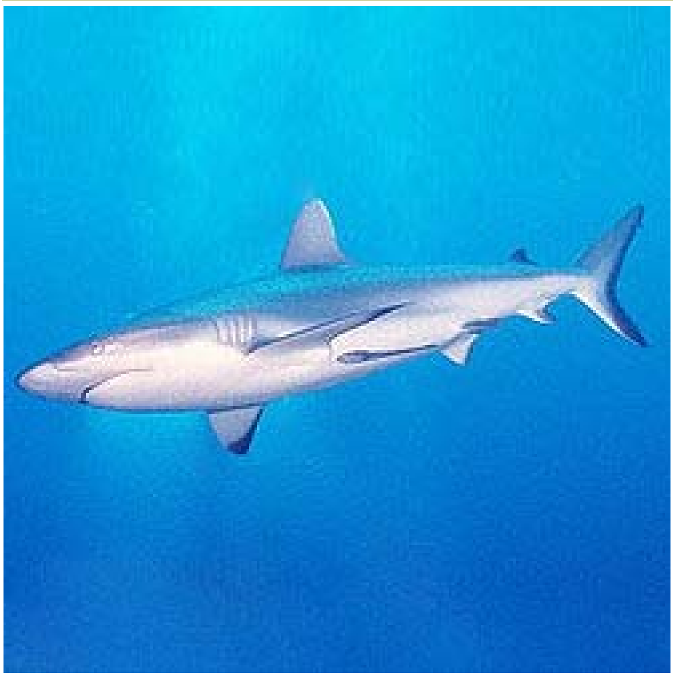
Most species of snakes lay eggs, but most snakes abandon the eggs shortly after laying. However, a few species (such as the King cobra) actually construct nests and stay in the vicinity of the hatchlings after incubation. Most pythons coil around their egg-clutches and remain with them until they hatch. A female python will not leave the eggs, except to occasionally bask in the sun or drink water. She will even “shiver” to generate heat to incubate the eggs.

Some species of snake are ovoviviparous and retain the eggs within their bodies until they are almost ready to hatch. Recently, it has been confirmed that several species of snake are fully viviparous, such as the boa constrictor and green anaconda, nourishing their young through a placenta as well as a yolk sac, which is highly unusual among reptiles, or anything else outside of placental mammals. Retention of eggs and live birth are most often associated with colder environments, as the retention of the young within the female.

Chapter 5

Shark

Sharks Temporal range: Silurian–Recent	



Grey reef shark *(Carcharhinus amblyrhynchos)*

Scientific classification	
Kingdom:	Animalia
Phylum:	Chordata
Class:	Chondrichthyes
Subclass:	Elasmobranchii
Superorder:	**Selachimorpha**

Orders

Carcharhiniformes
Heterodontiformes

Hexanchiformes
Lamniformes
Orectolobiformes
Pristiophoriformes
Squaliformes
Squatiniformes
† Symmoriida
† Cladoselachiformes
† Xenacanthida (Xenacantiformes)
† Eugeneodontida
† Hybodontiformes

Sharks (superorder **Selachimorpha**) are a type of fish with a full cartilaginous skeleton and a highly streamlined body. The earliest known sharks date from more than 420 million years ago.

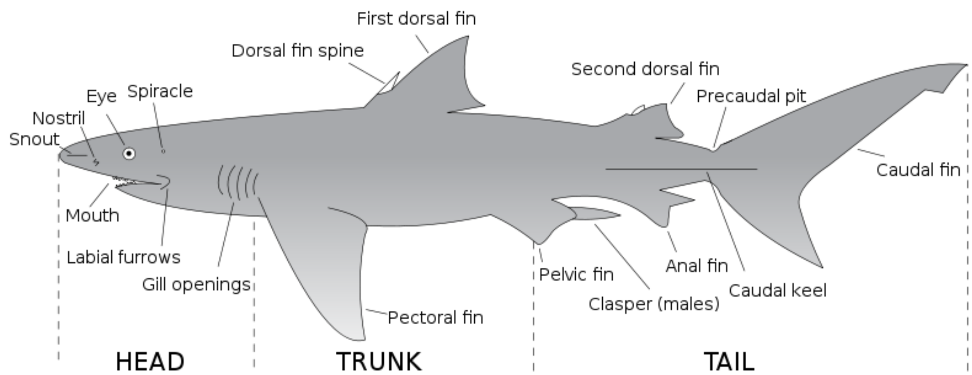
Since that time, sharks have diversified into 440 species, ranging in size from the small dwarf lanternshark, *Etmopterus perryi*, a deep sea species of only 17 centimetres (6.7 in) in length, to the whale shark, *Rhincodon typus*, the largest fish, which reaches approximately 12 metres (39 ft 4 in) and which feeds only on plankton, squid, and small fish by filter feeding. Sharks are found in all seas and are common down to depths of 2,000 metres (6,600 ft). They generally do not live in freshwater, with a few exceptions such as the bull shark and the river shark which can live both in seawater and freshwater. They breathe through five to seven gill slits. Sharks have a covering of dermal denticles that protects their skin from damage and parasites, and improves their fluid dynamics so the shark can move faster. They have several sets of replaceable teeth.

Well-known species such as the great white shark, tiger shark, blue shark, mako shark, and the hammerhead are apex predators, at the top of the underwater food chain. Their extraordinary skills as predators fascinate and frighten humans, even as their survival is under serious threat from fishing and other human activities.

Etymology

Until the 16th century, sharks were known to mariners as "sea dogs". According to the OED the name "shark" first came into use after Sir John Hawkins' sailors exhibited one in London in 1569 and used the word to refer to the large sharks of the Caribbean Sea, and later as a general term for all sharks. It has also been suggested to be derived from the Yucatec Maya word for shark, *xok*, pronounced 'shok'.

Anatomy



Teeth

The teeth of the tiger shark are oblique and serrated for sawing through flesh.

Shark teeth are embedded in the gums rather than directly affixed to the jaw, and are constantly replaced throughout life. Multiple rows of replacement teeth grow in a groove on the inside of the jaw and steadily move forward as in a "conveyor belt"; some sharks lose 30,000 or more teeth in their lifetime. The rate of tooth replacement varies from once every 8–10 days to several months. In most species teeth are replaced one at a time, except in cookiecutter sharks the entire row of teeth is replaced simultaneously.

Tooth shape depends on diet: sharks that feed on mollusks and crustaceans have dense flattened teeth for crushing, those that feed on fish have needle-like teeth for gripping, and those that feed on larger prey such as mammals have pointed lower teeth for gripping and triangular upper teeth with serrated edges for cutting. The teeth of plankton-feeders such as the basking shark are smaller and non-functional.

Skeleton

Shark skeletons are very different from those of bony fish and terrestrial vertebrates. Sharks and other cartilaginous fish (skates and rays) have skeletons made of cartilage and connective tissue. Cartilage is flexible and durable, yet has about half the density of bone. This reduces the skeleton’s weight, saving energy. Sharks have no rib cage and therefore on land a shark's own weight can crush it.

Jaw

Like its relatives, rays and skates, the shark's jaw is not attached to the cranium. The jaw's surface, like the shark's vertebrae and gill arches, needs extra support due to its heavy exposure to physical stress and its need for strength. It has a layer of tiny hexagonal plates called "tesserae", which are crystal blocks of calcium salts arranged as a mosaic. This gives these areas much of the same strength found in the bony tissue found in other animals.

Generally sharks have only one layer of tesserae, but the jaws of large specimens, such as the bull shark, tiger shark, and the great white shark, have two to three layers or more, depending on body size. The jaws of a large great white shark may have up to five layers. In the rostrum (snout), the cartilage can be spongy and flexible to absorb the power of impacts.

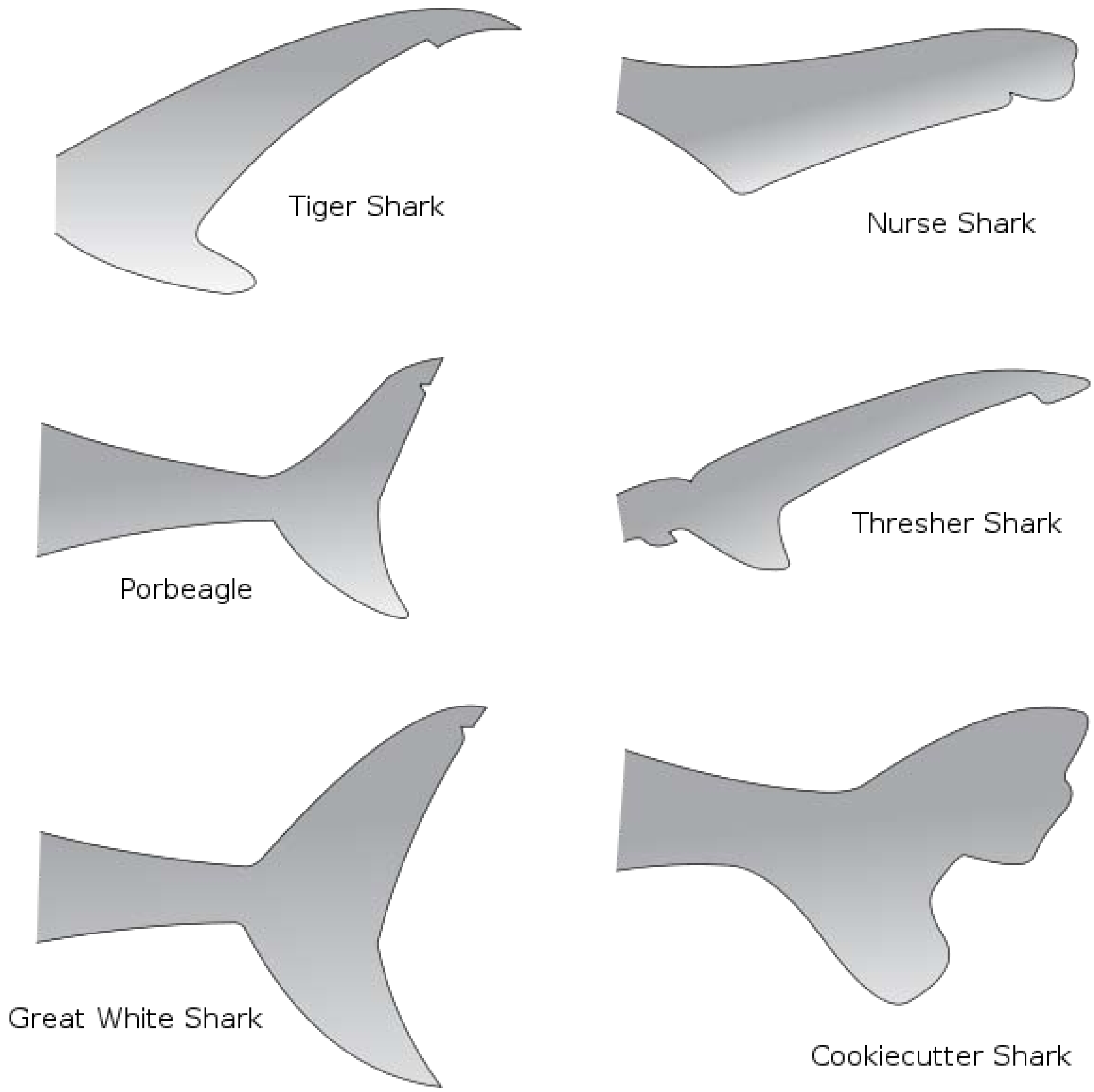
Fins

Fin skeletons are elongated and supported with soft and unsegmented rays named ceratotrichia, filaments of elastic protein resembling the horny keratin in hair and feathers. Sharks can only drift away from objects directly in front of them because their fins do not allow them to move in the tail-first direction.

Dermal denticles

Unlike bony fish, sharks have a complex dermal corset made of flexible collagenous fibers and arranged as a helical network surrounding their body. This works as an outer skeleton, providing attachment for their swimming muscles and thus saving energy. In the past, sharkskin has been used as sandpaper. Their dermal teeth give them hydrodynamic advantages as they reduce turbulence when swimming.

Tails



The range of shark tail shapes

Varying tail shapes have evolved in sharks adapted for different environments. Tail (caudal fins) vary considerably between species. The tail provides thrust, making speed and acceleration dependent on tail shape. Sharks possess a heterocercal caudal fin in which the dorsal portion is usually noticeably larger than the ventral portion. This is because the shark's vertebral column extends into that dorsal portion, providing a greater surface area for muscle attachment. This allows more efficient locomotion among these negatively buoyant cartilaginous fishes. By contrast, most bony fishes possess a homocercal caudal fin.

The tiger shark's tail has a large upper lobe which delivers maximum power for slow cruising or sudden bursts of speed. The tiger shark must be able to twist and turn in the water easily when hunting to support its varied diet, whereas the porbeagle, which hunts schooling fish such as mackerel and herring has a large lower lobe to help it keep pace with its fast-swimming prey. Some tail adaptations have other purposes. The thresher feeds on fish and squid, which it herds and stuns with its powerful and elongated upper lobe.

Physiology

Buoyancy

Unlike bony fish, sharks do not have gas-filled swim bladders for buoyancy. Instead, sharks rely on a large liver, filled with oil that contains squalene and the fact that cartilage is about half as dense as bone. The liver constitutes up to 30% of their body mass. The liver's effectiveness is limited, so sharks employ dynamic lift to maintain depth, sinking when they stop swimming. Sand tiger sharks store air in their stomachs, using it as a form of swim bladder. Most sharks need to constantly swim in order to breathe and cannot sleep very long, if at all, without sinking. However certain shark species, like the nurse shark, are capable of pumping water across their gills, allowing them to rest on the ocean bottom.

Some sharks, if inverted or stroked on the nose, enter a natural state of tonic immobility. Researchers use this condition to handle sharks safely.

Respiration

Like other fish, sharks extract oxygen from seawater as it passes over their gills. Unlike other fish, shark gill slits are not covered, but lie in a row behind the head. A modified slit called a spiracle lies just behind the eye; the spiracle assists water intake during respiration and plays a major role in bottom–dwelling sharks. Spiracles are reduced or missing in active pelagic sharks. While the shark is moving, water passes through the mouth and over the gills in a process known as "ram ventilation". While at rest, most sharks pump water over their gills to ensure a constant supply of oxygenated water. A small number of species have lost the ability to pump water through their gills and must swim without rest. These species are *obligate ram ventilators* and would presumably asphyxiate if unable to move. Obligate ram ventilation is also true of some pelagic bony fish species.

The respiration and circulation process begins when deoxygenated blood travels to the shark's two-chambered heart. Here the shark pumps blood to its gills via the ventral aorta artery where it branches into afferent brachial arteries. Reoxygenation takes place in the gills and the reoxygenated blood flows into the efferent brachial arteries, which come together to form the dorsal aorta. The blood flows from the dorsal aorta throughout the body. The deoxygenated blood from the body then flows through the posterior cardinal veins and enters the posterior cardinal sinuses. From there blood enters the heart ventricle and the cycle repeats.

Thermoregulation

Most sharks are "cold-blooded", or more precisely poikilothermic, meaning that their internal body temperature matches that of their ambient environment. Members of the family Lamnidae, such as the shortfin mako shark and the great white shark, are homeothermic and maintain a higher body temperature than the surrounding water. In these sharks, a strip of aerobic red muscle located near the center of the body generates the heat, which the body retains via a countercurrent exchange mechanism by a system of blood vessels called the rete mirabile ("miraculous net"). The common thresher shark has a similar mechanism for maintaining an elevated body temperature, which is thought to have evolved independently.

Osmoregulation

In contrast to bony fish, with the exception of the Coelacanth, the blood and other tissue of sharks and Chondrichthyes in general is isotonic to their marine environments because of the high concentration of urea and trimethylamine N-oxide (TMAO), allowing them to be in osmotic balance with the seawater. This adaptation prevents most sharks from surviving in fresh water, and they are therefore confined to marine environments. A few exceptions to this rule exist, such as the bull shark which has developed a way to change its kidney function to excrete large amounts of urea. When a shark dies the urea is broken down to ammonia by bacteria — because of this, the dead body will gradually start to smell strongly of ammonia.

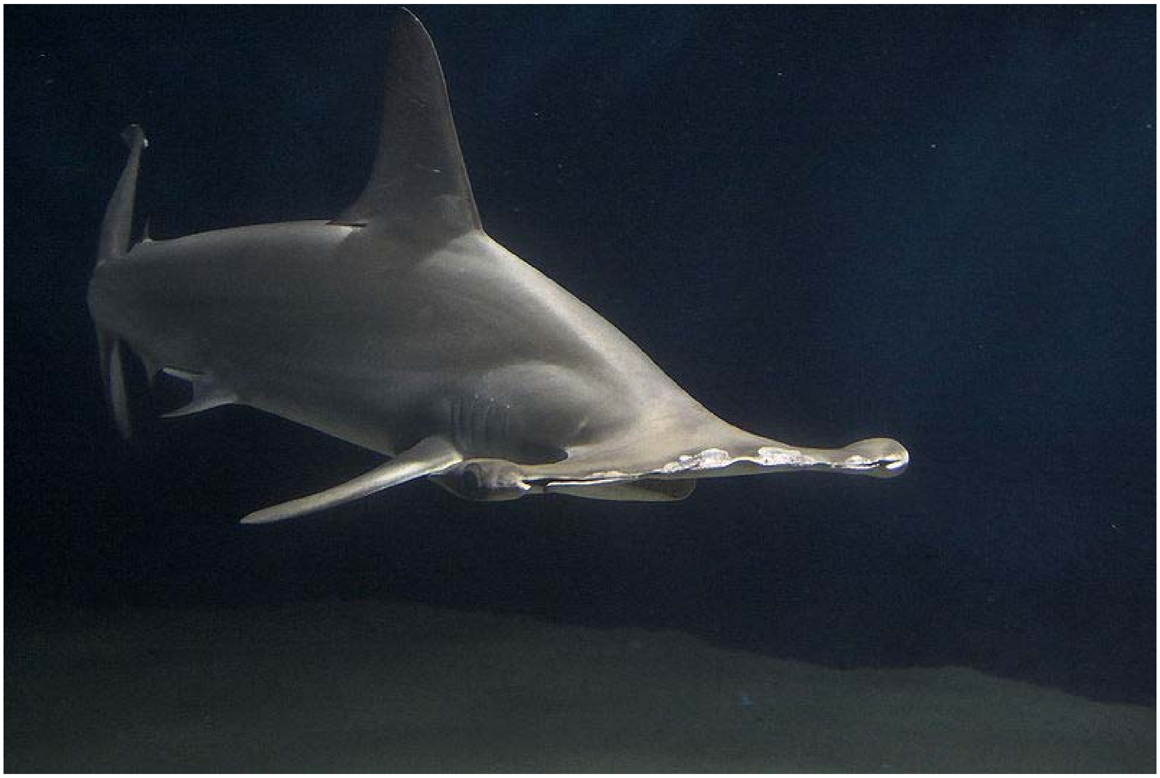
Digestion

Digestion can take a long time. The food moves from the mouth to a 'J' shaped stomach, where it is stored and initial digestion occurs. Unwanted items may never get past the stomach, and instead the shark either vomits or turns its stomachs inside out and ejects unwanted items from its mouth.

One of the biggest differences between shark and mammalian digestion is sharks' extremely short intestine. This short length is achieved by the spiral valve with multiple turns within a single short section instead of a long tube-like intestine. The valve provides a long surface area, requiring food to circulate inside the short gut until fully digested, when remaining waste products pass into the cloaca.

Senses

Smell



The shape of the hammerhead shark's head may enhance olfaction by spacing the nostrils further apart.

Sharks have keen olfactory senses, located in the short duct (which is not fused, unlike bony fish) between the anterior and posterior nasal openings, with some species able to detect as little as one part per million of blood in seawater. They are more attracted to the chemicals found in the guts of many species, and as a result often linger near or in sewage outfalls. Some species, such as nurse sharks, have external barbels that greatly increase their ability to sense prey.

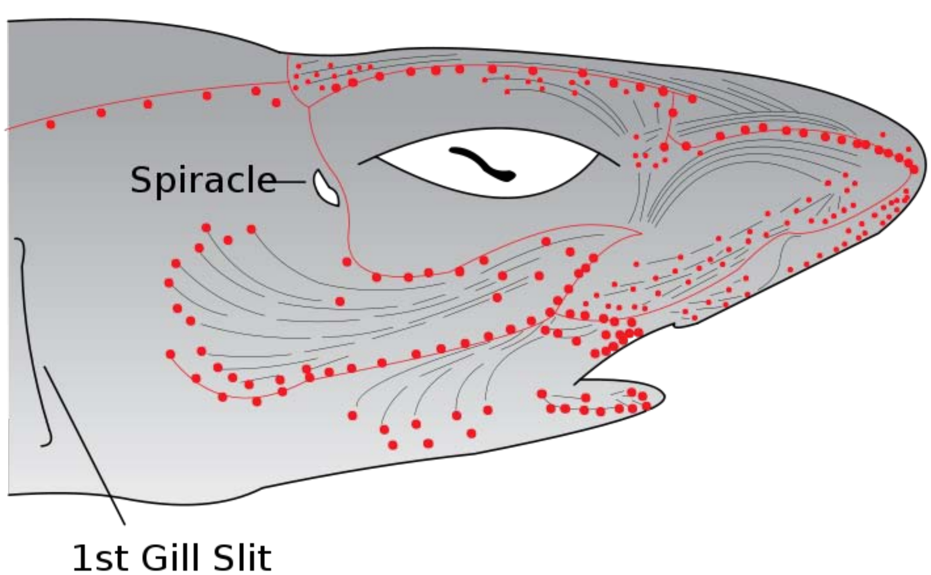
Sight

Shark eyes are similar to the eyes of other vertebrates, including similar lenses, corneas and retinas, though their eyesight is well adapted to the marine environment with the help of a tissue called tapetum lucidum. This means that sharks can contract and dilate their pupils, like humans, something no teleost fish can do. This tissue is behind the retina and reflects light back to it, thereby increasing visibility in the dark waters. The effectiveness of the tissue varies, with some sharks having stronger nocturnal adaptations. Sharks have eyelids, but they do not blink because the surrounding water cleans their eyes. To protect their eyes some species have nictitating membranes. This membrane covers the eyes while hunting and when the shark is being attacked. However, some species, including the great white shark (*Carcharodon carcharias*), do not have this membrane, but instead roll their eyes backwards to protect them when striking prey. The importance of sight in shark hunting behavior is debated. Some believe that electro- and chemoreception are more significant, while others point to the nictating membrane as evidence that sight is important. Presumably, the shark would not protect its eyes were they unimportant. The use of sight probably varies with species and water conditions. The shark's field of vision can swap between monocular and stereoscopic at any time. A micro-spectrophotometry study of 17 species of Shark found 10 had only rod photoreceptors and no cone cells in their retinas giving them good night vision while making them colorblind. The remaining seven species had in addition to rods a single type of cone photoreceptor sensitive to green and, seeing only in shades of grey and green, are believed to be effectively colorblind. The study indicates that an object's contrast against the background, rather than colour, may be more important for object detection.

Hearing

Although it is hard to test sharks' hearing, they may have a sharp sense of hearing and can possibly hear prey many miles away. A small opening on each side of their heads (not the spiracle) leads directly into the inner ear through a thin channel. The lateral line shows a similar arrangement, and is open to the environment via a series of openings called lateral line pores. This is a reminder of the common origin of these two vibration- and sound-detecting organs that are grouped together as the acoustico-lateralis system. In bony fish and tetrapods the external opening into the inner ear has been lost.

Electroreception



Electromagnetic field receptors (Ampullae of Lorenzini) and motion detecting canals in the head of a shark

The Ampullae of Lorenzini are the electroreceptor organs. They number in the hundreds to thousands. Sharks use the Ampullae of Lorenzini to detect the electromagnetic fields that all living things produce. This helps sharks (particularly the hammerhead shark) find prey. The shark has the greatest electrical sensitivity of any animal. Sharks find prey hidden in sand by detecting the electric fields they produce. Ocean currents moving in the magnetic field of the Earth also generate electric fields that sharks can use for orientation and possibly navigation.

Lateral line

This system is found in most fish, including sharks. It detects motion or vibrations in water. The shark can sense frequencies in the range of 25 to 50 Hz.

Life history

The claspers of male spotted wobbegong

Shark lifespans vary by species. Most live 20 to 30 years. The spiny dogfish has the longest lifespan at more than 100 years. Whale sharks (*Rhincodon typus*) may also live over 100 years.

Reproduction

Unlike most bony fishes, sharks are K-selected reproducers, meaning that they produce a small number of well-developed young as opposed to a large number of poorly developed young. Fecundity in sharks ranges from 2 to over 100 young per reproductive cycle. Sharks mature slowly relative to many other fish. For example, lemon sharks reach sexual maturity at around age 13–15.

Sexual

Sharks practice internal fertilization. The posterior part of a male shark's pelvic fins are modified into a pair of intromittent organs called claspers, analogous to a mammalian penis, of which one is used to deliver sperm into the female.

Mating has rarely been observed in sharks. The smaller catsharks often mate with the male curling around the female. In less flexible species the two sharks swim parallel to each other while the male inserts a clasper into the female's oviduct. Females in many of the larger species have bite marks that appear to be a result of a male grasping them to maintain position during mating. The bite marks may also come from courtship behavior: the male may bite the female to show his interest. In some species, females have evolved thicker skin to withstand these bites.

Asexual

There are two documented cases in which a female shark who has not been in contact with a male has conceived a pup on her own through parthenogenesis. The details of this process are not well understood, but genetic fingerprinting showed that the pups had no paternal genetic contribution, ruling out sperm storage. The extent of this behavior in the wild is unknown, as is whether other species have this capability. Mammals are now the only major vertebrate group in which asexual reproduction has not been observed.

Scientists assert that asexual reproduction in the wild is rare, and probably a last ditch effort to reproduce when a mate is not present. Asexual reproduction diminishes genetic diversity, which helps build defenses against threats to the species. Species that rely solely on it risk extinction. Asexual reproduction may have contributed to the blue shark's decline off the Irish coast.

Brooding

Sharks display three ways to bear their young, varying by species, oviparity, viviparity and ovoviviparity.

The spiral egg case of a Port Jackson shark

Ovoviviparity

Most sharks are ovoviviparous, meaning that the eggs hatch in the oviduct within the mother's body and that the egg's yolk and fluids secreted by glands in the walls of the oviduct nourishes the embryos. The young continue to be nourished by the remnants of the yolk and the oviduct's fluids. As in viviparity, the young are born alive and fully functional. Lamniforme sharks practice *oophagy*, where the first embryos to hatch eat the remaining eggs. Grey nurse shark pups intrauterine cannibalistically take this a step further and consume other developing embryos. The survival strategy for ovoviviparous species is to brood the young to a comparatively large size before birth. The whale shark is now classified as ovoviviparous rather than oviparous, because extrauterine eggs are now thought to have been aborted. Most ovoviviparous sharks give birth in sheltered areas, including bays, river mouths and shallow reefs. They choose such areas for protection from predators (mainly other sharks) and the abundance of food. Dogfish have the longest known gestation period of any shark, at 18 to 24 months. Basking sharks and frilled sharks appear to have even longer gestation periods, but accurate data are lacking.

Oviparity

Some species are oviparous like most other fish, laying their eggs in the water. In most oviparous shark species, an egg case with the consistency of leather protects the developing embryo(s). These cases may be corkscrewed into crevices for protection. Once empty, the egg case is known as the *mermaid's purse*, and can wash up on shore. Oviparous sharks include the horn shark, catshark, Port Jackson shark, and swellshark.

Viviparity

Finally some sharks maintain a *placental* link to the developing young, this method is called viviparity. This is more analogous to mammalian gestation than that of other fishes. The young are born alive and fully functional. Hammerheads, the requiem sharks (such as the bull and blue sharks), and smoothhounds are viviparous.

Behavior

The classic view describes a solitary hunter, ranging the oceans in search of food. However, this applies to only a few species. Most live far more sedentary, benthic lives. Even solitary sharks meet for breeding or at rich hunting grounds, which may lead them to cover thousands of miles in a year. Shark migration patterns may be even more complex than in birds, with many sharks covering entire ocean basins.

Sharks can be highly social, remaining in large schools. Sometimes more than 100 scalloped hammerheads congregate around seamounts and islands, e.g., in the Gulf of California. Cross-species social hierarchies exist. For example, oceanic whitetip sharks dominate silky sharks of comparable size during feeding.

When approached too closely some sharks perform a threat display. This usually consists of exaggerated swimming movements, and can vary in intensity according to the threat level.

Speed

In general, sharks swim ("cruise") at an average speed of 8 kilometres per hour (5.0 mph) but when feeding or attacking, the average shark can reach speeds upwards of 19 kilometres per hour (12 mph). The shortfin mako shark, the fastest shark and one of the fastest fish, can burst at speeds up to 50 kilometres per hour (31 mph). The great white shark is also capable of speed bursts. These exceptions may be due to the warm-blooded, or homeothermic, nature of these sharks' physiology.

Intelligence

Contrary to the common wisdom that sharks are instinct-driven "eating machines", recent studies have indicated that many species possess powerful problem-solving skills, social skills and curiosity. The brain- to body-mass ratios of sharks are similar to mammals and birds. In 1987, near Smitswinkle Bay, South Africa, a group of up to seven great white sharks worked together to move a partially beached dead whale to deeper waters to feed. Sharks can engage in playful activities. Porbeagle sharks have been seen repeatedly rolling in kelp and chasing an individual who trailed a piece of kelp behind it.

Sleep

Some sharks can lie on the bottom while actively pumping water over their gills, but their eyes remain open and actively follow divers. When a shark is resting, it does not use its nares, but rather its spiracles. If a shark tried to use its nares while resting on the ocean floor, it would "inhale" sand rather than water. Many scientists believe this is one of the reasons sharks have spiracles. The spiny dogfish's spinal cord, rather than its brain, coordinates swimming, so spiny dogfish can continue to swim while sleeping. It is also possible that sharks sleep in a manner similar to dolphins, one cerebral hemisphere at a time, thus maintaining some consciousness and cerebral activity at all times.

Ecology

Feeding

Like many sharks, the great white shark is an apex predator in its environment.

Most sharks are carnivorous. Some species, including tiger sharks, eat almost anything. The vast majority seek particular prey, and rarely vary their diet. Whale, basking and megamouth sharks filter feed. These three independently evolved plankton feeding using different strategies. Whale sharks use suction to take in plankton and small fishes. Basking sharks are ram-feeders, swimming through plankton blooms with their mouth wide open. Megamouth sharks make suction feeding more efficient, using luminescent tissue inside the mouth to attract prey in the deep ocean. This type of feeding requires gill rakers, long slender filaments that form a very efficient sieve, analogous to the baleen plates of the great whales. The shark traps the plankton in these filaments and swallows from time to time in huge mouthfuls. Teeth in these species are comparatively small because they are not needed for feeding.

Other highly specialized feeders include cookiecutter sharks, which feed on flesh sliced out of other larger fish and marine mammals. Cookiecutter teeth are enormous compared to the animal's size. The lower teeth are particularly sharp. Although they have never been observed feeding, they are believed to latch onto their prey and use their thick lips to make a seal, twisting their bodies to rip off flesh.

Some seabed–dwelling species are highly effective ambush predators. Angel sharks and wobbegongs use camouflage to lie in wait and suck prey into their mouths. Many benthic sharks feed solely on crustaceans which they crush with their flat molariform teeth.

Other sharks feed on squid or fish, which they swallow whole. The viper dogfish has teeth it can point outwards to strike and capture prey that it then swallows intact. The great white and other large predators either swallow small prey whole or take huge bites out of large animals. Thresher sharks use their long tails to stun shoaling fishes, and sawsharks either stir prey from the seabed or slash at swimming prey with their tooth-studded rostra.

Many sharks, including the whitetip reef shark are cooperative feeders and hunt in packs to herd and capture elusive prey. These social sharks are often migratory, traveling huge distances around ocean basins in large schools. These migrations may be partly necessary to find new food sources.

Range and habitat

Sharks are found in all seas. They generally do not live in freshwater, with a few exceptions such as the bull shark and the river shark which can swim both in seawater and freshwater. Sharks are common down to depths of 2,000 metres (7,000 ft), and some live even deeper, but they are almost entirely absent below 3,000 metres (10,000 ft). The deepest confirmed report of a shark is a Portuguese dogfish at 3,700 metres (12,100 ft).

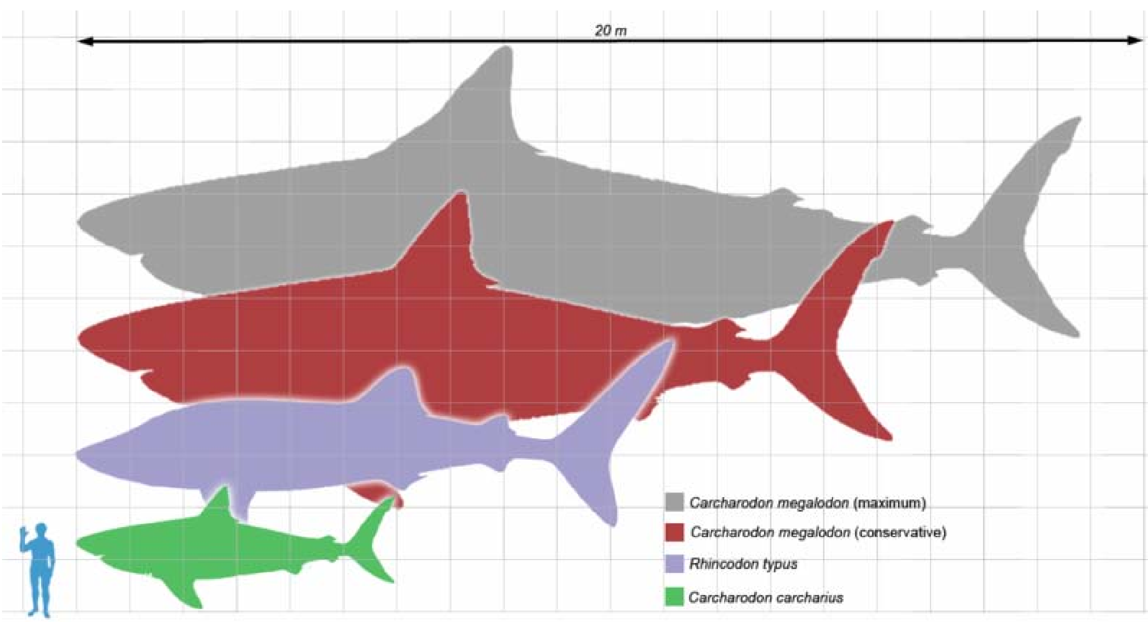
Evolution

A collection of fossilized shark teeth

Evidence for the existence of sharks dates from the Ordovician period, over 450–420 million years ago, before land vertebrates existed and before many plants had colonized the continents. Only scales have been recovered from the first sharks and not all paleontologists agree that these are from true sharks. The oldest generally accepted shark scales are from about 420 million years ago, in the Silurian period. The first sharks looked very different from modern sharks. The majority of modern sharks can be traced back to around 100 million years ago. Most fossils are of teeth, often in large numbers. Partial skeletons and even complete fossilized remains have been discovered. Estimates suggest that sharks grow tens of thousands of teeth over a lifetime, which explains the abundant fossils. The teeth consist of easily fossilized calcium phosphate, an apatite. When a shark dies, the decomposing skeleton breaks up, scattering the apatite prisms. Preservation requires rapid burial in bottom sediments.

Among the most ancient and primitive sharks is *Cladoselache*, from about 370 million years ago, which has been found within Paleozoic strata in Ohio, Kentucky and Tennessee. At that point in Earth's history these rocks made up the soft bottom sediments of a large, shallow ocean, which stretched across much of North America. *Cladoselache* was only about 1 metre (3.3 ft) long with stiff triangular fins and slender jaws. Its teeth had several pointed cusps, which wore down from use. From the small number of teeth found together, it is most likely that *Cladoselache* did not replace its teeth as regularly as modern sharks. Its caudal fins had a similar shape to the great white sharks and the pelagic shortfin and longfin makos. The presence of whole fish arranged tail-first in their stomachs suggest that they were fast swimmers with great agility.

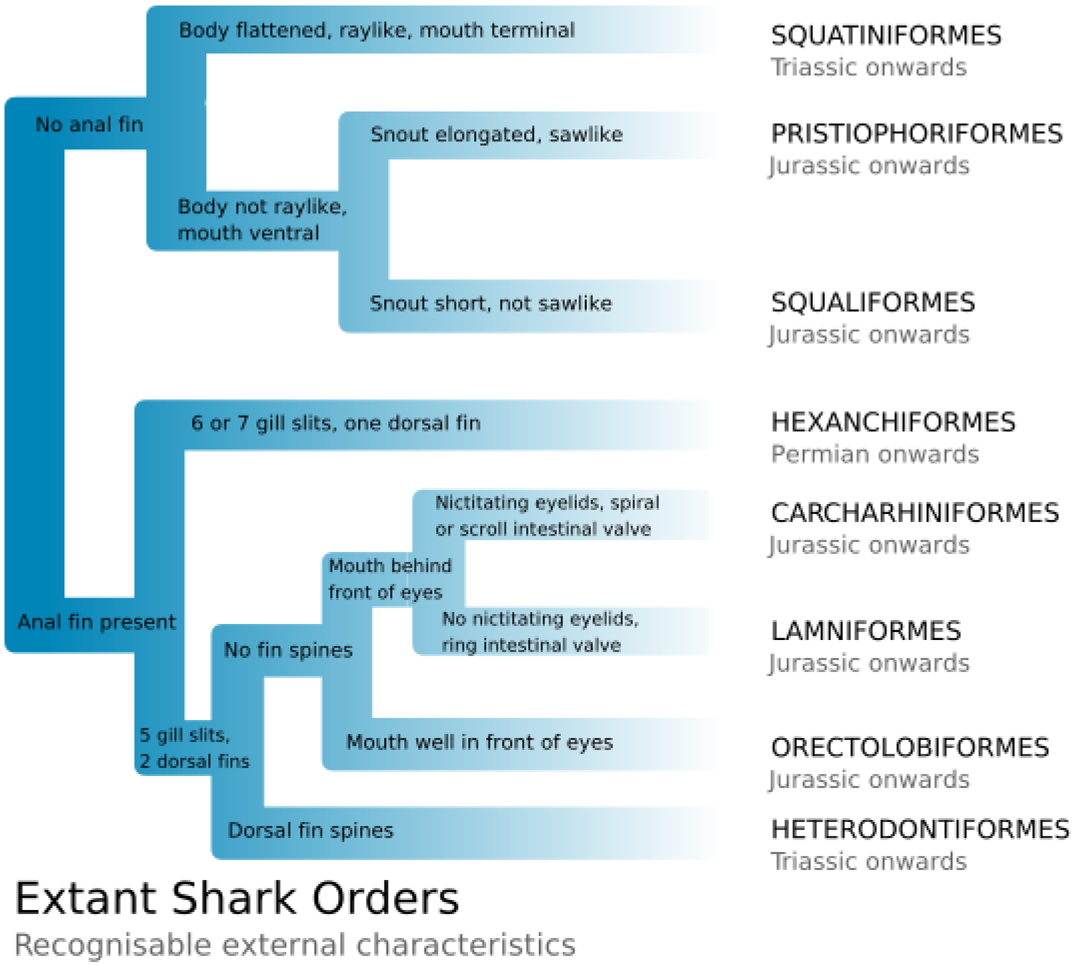
Most fossil sharks from about 300 to 150 million years ago can be assigned to one of two groups. The Xenacanthida was almost exclusive to freshwater environments. By the time this group became extinct about 220 million years ago, they had spread worldwide. The other group, the hybodonts, appeared about 320 million years ago and lived mostly in the oceans, but also in freshwater.



Megalodon with the whale shark, great white shark, and a human for scale

Modern sharks began to appear about 100 million years ago. Fossil mackerel shark teeth date to the Lower Cretaceous. One of the most recently evolved families is the hammerhead shark (family Sphyrnidae), which emerged in the Eocene. The oldest white shark teeth date from 60 to 65 million years ago, around the time of the extinction of the dinosaurs. In early white shark evolution there are at least two lineages: one lineage is of white sharks with coarsely serrated teeth and it probably gave rise to the modern great white shark, and another lineage is of white sharks with finely serrated teeth. These sharks attained gigantic proportions and include the extinct megatoothed shark, *C. megalodon*. Like most extinct sharks, *C. megalodon* is also primarily known from its fossil teeth and vertebrae. This giant shark reached a total length (TL) of more than 16 metres (52 ft). *C. megalodon* may have approached a maxima of 20.3 metres (67 ft) in total length and 103 metric tons (114 short tons) in mass. Paleontological evidence suggests that this shark was an active predator of large cetaceans.

Taxonomy



Sharks belong to the superorder Selachimorpha in the subclass Elasmobranchii in the class Chondrichthyes. The Elasmobranchii also include rays and skates; the Chondrichthyes also include Chimaeras. It is currently thought that the sharks form a polyphyletic group: some sharks are more closely related to rays than they are to some other sharks.

The superorder Selachimorpha is divided into Galea (or Galeomorphii), and Squalea. The Galeans are the Heterodontiformes, Orectolobiformes, Lamniformes, and Carcharhiniformes. Lamnoids and Carcharhinoids are usually placed in one clade, but recent studies show the Lamnoids and Orectoloboids are a clade. Some scientists now think that Heterodontoids may be Squalean. The Squalea is divided into Hexanchoidei and Squalomorpha. The Hexanchoidei includes the Hexanchiformes and Chlamydoselachiformes. The Squalomorpha contains the Squaliformes and the Hypnosqualea. The Hypnosqualea may be invalid. It includes the Squatiniformes, and the Pristorajea, which may also be invalid, but includes the Pristiophoriformes and the Batoidea.

More than 440 species of sharks split across eight orders, listed below in roughly their evolutionary relationship from ancient to modern:

- Hexanchiformes: Examples from this group include the cow sharks, frilled shark and even a shark that resembles a marine snake.
- Squaliformes: This group includes the bramble sharks, dogfish and roughsharks, and prickly shark.
- Pristiophoriformes: These are the sawsharks, with an elongated, toothed snout that they use for slashing their prey.
- Squatiniformes: Also known as angel sharks, they are flattened sharks with a strong resemblance to stingrays and skates.
- Heterodontiformes: They are generally referred to as the bullhead or horn sharks.
- Orectolobiformes: They are commonly referred to as the carpet sharks, including zebra sharks, nurse sharks, wobbegongs and the whale shark.
- Carcharhiniformes: Commonly known as groundsharks, the species include the blue, tiger, bull, grey reef, blacktip reef, Caribbean reef, blacktail reef, whitetip reef and oceanic whitetip sharks (collectively called the requiem sharks) along with the houndsharks, catsharks and hammerhead sharks. They are distinguished by an elongated snout and a nictitating membrane which protects the eyes during an attack.
- Lamniformes: They are commonly known as the mackerel sharks. They include the goblin shark, basking shark, megamouth shark, the thresher sharks, shortfin and longfin mako sharks, and great white shark. They are distinguished by their large jaws and ovoviviparous reproduction. The Lamniformes include the extinct megalodon, *Carcharodon megalodon*.

Chapter 6

Insect

Insects Temporal range: 396–0 Ma Early Devonian – Recent	

Clockwise from top left: dancefly (*Empis livida*), long-nosed weevil (*Rhinotia hemistictus*), mole cricket (*Gryllotalpa brachyptera*), German wasp (*Vespula germanica*), emperor gum moth (*Opodiphthera eucalypti*), assassin bug (Harpactorinae)

Scientific classification [e]	
Kingdom:	Animalia
Phylum:	Arthropoda
Subphylum:	Hexapoda
Class:	**Insecta** Linnaeus, 1758

Subclasses and classes

Monocondylia
Archaeognatha
Dicondylia
Pterygota

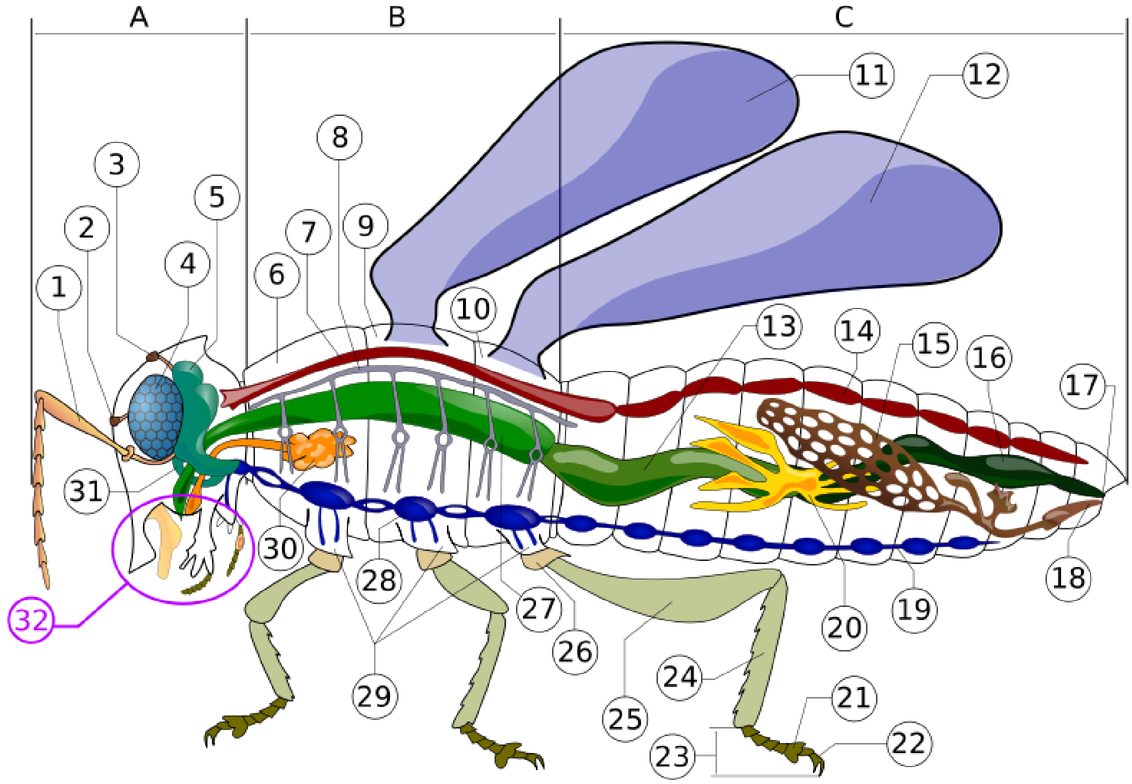
Insects (from Latin *insectum*, a calque of Greek ἔντομον [*éntomon*], "cut into sections") are a class within the arthropods that have a chitinous exoskeleton, a three-part body (head, thorax, and abdomen), three pairs of jointed legs, compound eyes, and two antennae. They are among the most diverse group of animals on the planet and include more than a million described species and represent more than half of all known living organisms. The number of extant species is estimated at between six and ten million, and potentially represent over 90% of the differing metazoan life forms on Earth. Insects may be found in nearly all environments, although only a small number of species occur in the oceans, a habitat dominated by another arthropod group, the crustaceans.

The life cycles of insects vary but most hatch from eggs. Insect growth is constrained by the inelastic exoskeleton and development involves a series of molts. The immature stages can differ from the adults in structure, habit and habitat and can include a passive pupal stage in those groups that undergo complete metamorphosis. Insects that undergo incomplete metamorphosis lack a pupal stage and adults develop through a series of nymphal stages. The higher level relationship of the hexapoda is unclear. Fossilized insects of enormous size have been found from the Paleozoic Era, including giant dragonflies with wingspans of 55 to 70 cm (22–28 in). The most diverse insect groups appear to have coevolved with flowering plants.

Insects typically move about by walking, flying or occasionally swimming. Because it allows for rapid yet stable movement, many insects adopt a tripedal gait in which they walk with their legs touching the ground in alternating triangles. Insects are the only invertebrates to have evolved flight. Many insects spend at least part of their life underwater, with larval adaptations that include gills and some adult insects are aquatic and have adaptations for swimming. Some species, like water striders, are capable of walking on the surface of water. Insects are mostly solitary, but some insects, such as certain bees, ants, and termites are social and live in large, well-organized colonies. Some insects, like earwigs, show maternal care, guarding their eggs and young. Insects can communicate with each other in a variety of ways. Male moths can sense the pheromones of female moths over distances of many kilometers. Other species communicate with sounds: crickets stridulate, or rub their wings together, to attract a mate and repel other males. Lampyridae in the beetle order Coleoptera communicate with light.

Humans regard certain insects as pests and attempt to control them using insecticides and a host of other techniques. Some insects damage crops by feeding on sap, leaves or fruits, a few bite humans and livestock, alive and dead, to feed on blood and some are capable of transmitting diseases to humans, pets and livestock. Many other insects are considered ecologically beneficial and a few provide direct economic benefit. Silkworms and bees have been domesticated by humans for the production of silk and honey, respectively.

External Morphology



Insect morphology

A- Head **B**- Thorax **C**- Abdomen

1. antenna
2. ocelli (lower)
3. ocelli (upper)
4. compound eye
5. brain (cerebral ganglia)
6. prothorax
7. dorsal blood vessel
8. tracheal tubes (trunk with spiracle)
9. mesothorax
10. metathorax
11. forewing
12. hindwing
13. mid-gut (stomach)
14. dorsal tube (Heart)
15. ovary
16. hind-gut (intestine, rectum & anus)
17. anus
18. oviduct
19. nerve chord (abdominal ganglia)
20. Malpighian tubes

21. tarsal pads
22. claws
23. tarsus
24. tibia
25. femur
26. trochanter
27. fore-gut (crop, gizzard)
28. thoracic ganglion
29. coxa
30. salivary gland
31. subesophageal ganglion
32. mouthparts

General body plan

Insects have segmented bodies supported by an exoskeleton, a hard outer covering made mostly of chitin. The segments of the body are organized into three distinctive but interconnected units, or tagmata: a head, a thorax, and an abdomen. The head supports a pair of sensory antennae, a pair of compound eyes, and, if present, one to three simple eyes (or ocelli) and three sets of variously modified appendages that form the mouthparts. The thorax has six segmented legs—one pair each for the prothorax, mesothorax and the metathorax segments making up the thorax—and, if present in the species, two or four wings. The abdomen consists of eleven segments, though in a few species of insects these segments may be fused together or reduced in size. The abdomen also contains most of the digestive, respiratory, excretory and reproductive internal structures. There is considerable variation and many adaptations in the body parts of insects especially wings, legs, antenna, mouth-parts etc.

Exoskeleton

Insect outer skeleton, the cuticle, is made up of two layers: the epicuticle, which is a thin and waxy water resistant outer layer and contains no chitin, and a lower layer called the procuticle. The procuticle is chitinous and much thicker than the epicuticle and has two layers: an outer layer known as the exocuticle and an inner layer known as the endocuticle. The tough and flexible endocuticle is built from numerous layers of fibrous chitin and proteins, criss-crossing each others in a sandwich pattern, while the exocuticle is rigid and hardened. The exocuticle is greatly reduced in many soft-bodied insects (e.g., caterpillars), especially during their larval stages.

Insects are the only invertebrates to have developed active flight capability, and this has played an important role in their success. These muscles are able to contract multiple times for each single nerve impulse, allowing the wings to beat faster than would ordinarily be possible. Having their muscles attached to their exoskeletons is more efficient and allows more muscle connections; crustaceans also use the same method, though all spiders use hydraulic pressure to extend their legs, a system inherited from their pre-arthropod ancestors. Unlike insects, though, most aquatic crustaceans are biomineralized with calcium carbonate extracted from the water.

Internal Morphology

Nervous system

The nervous system of an insect can be divided into a brain and a ventral nerve cord. The head capsule is made up of six fused segments, each with a pair of ganglia, or a cluster of nerve cells outside of the brain. The first three pairs of ganglia are fused into the brain, while the three following pairs are fused into a structure of three pairs of ganglia under the insect's esophagus, called the subesophageal ganglion.

The thoracic segments have one ganglion on each side, which are connected into a pair, one pair per segment. This arrangement is also seen in the abdomen but only in the first eight segments. Many species of insects have reduced numbers of ganglia due to fusion or reduction. Some cockroaches have just six ganglia in the abdomen, whereas the wasp *Vespa crabro* has only two in the thorax and three in the abdomen. Some insects, like the house fly *Musca domestica*, have all the body ganglia fused into a single large thoracic ganglion.

At least a few insects have nociceptors, cells that detect and transmit sensations of pain. This was discovered in 2003 by studying the variation in reactions of larvae of the common fruitfly Drosophila to the touch of a heated probe and an unheated one. The larvae reacted to the touch of the heated probe with a stereotypical rolling behavior that was not exhibited when the larvae were touched by the unheated probe. Although nociception has been demonstrated in insects, there is not a consensus that insects feel pain consciously.

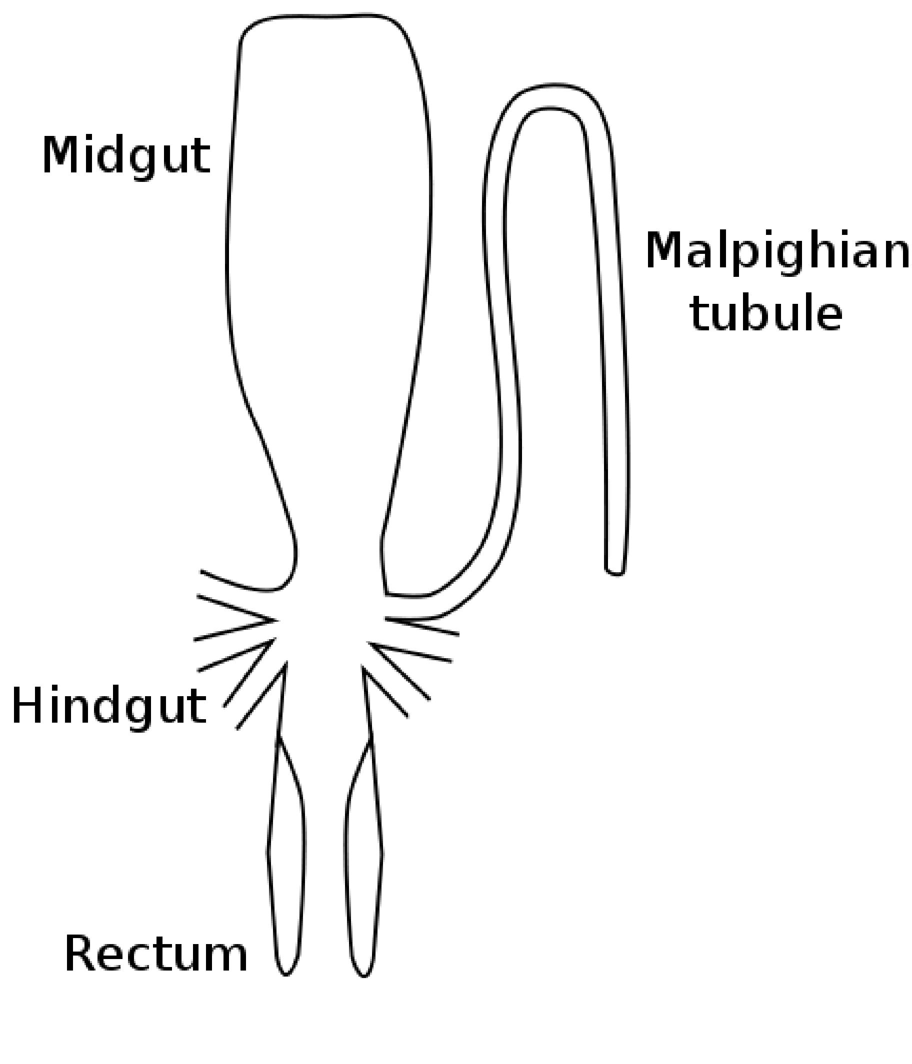
Digestive system

An insect uses its digestive system to extract nutrients and other substances from the food it consumes. Most of this food is ingested in the form of macromolecules and other complex substances like proteins, polysaccharides, fats, and nucleic acids. These macromolecules must be broken down by catabolic reactions into smaller molecules like amino acids and simple sugars before being used by cells of the body for energy, growth, or reproduction. This break-down process is known as digestion.

The main structure of an insect's digestive system is a long enclosed tube called the alimentary canal, which runs lengthwise through the body. The alimentary canal directs food unidirectionally from the mouth to the anus. It has three sections, each of which performs a different process of digestion. In addition to the alimentary canal, insects also have paired salivary glands and salivary reservoirs. These structures usually reside in the thorax, adjacent to the foregut.

The salivary glands (element 30 in numbered diagram) in an insect's mouth produce saliva. The salivary ducts lead from the glands to the reservoirs and then forward through the head to an opening called the salivarium, located behind the hypopharynx. By moving its mouthparts (element 32 in numbered diagram) the insect can mix its food with saliva. The mixture of saliva and food then travels through the salivary tubes into the mouth, where it begins to break down. Some insects, like flies, have extra-oral digestion. Insects using extra-oral digestion expel digestive enzymes onto their food to break it down. This strategy allows insects to extract a significant proportion of the available nutrients from the food source. The gut is where almost all of insects' digestion takes place. It can be divided into the foregut, midgut and hindgut.

Foregut



Stylized diagram of insect digestive tract showing malpighian tubule, from an insect of the order Orthoptera.

The first section of the alimentary canal is the foregut (element 27 in numbered diagram), or stomodaeum. The foregut is line with a cuticular lining made of chitin and proteins as protection from tough food. The foregut includes the buccal cavity (mouth), pharynx, esophagus, and Crop and proventriculus (any part may be highly modified) which both store food and signify when to continue passing onward to the midgut. Here, digestion starts as partially chewed food is broken down by saliva from the salivary glands. As the salivary glands produce fluid and carbohydrate-digesting enzymes (mostly amylases), strong muscles in the pharynx pump fluid into the buccal cavity, lubricating the food like the salivarium does, and helping blood feeders, and xylem and phloem feeders.

From there, the pharynx passes food to the esophagus, which could be just a simple tube passing it on to the crop and proventriculus, and then on ward to the midgut, as in most insects. Alternately, the foregut may expand into a very enlarged crop and proventriculus, or the crop could just be a diverticulum, or fluid filled structure, as in some Diptera species.

Bee defecating. Note the contraction of the anus which provides internal pressure.

Midgut

Once food leaves the crop, it passes to the midgut (element 13 in numbered diagram), also known as the mesenteron, where the majority of digestion takes place. Microscopic projections from the midgut wall, called microvilli, increase the surface area of the wall and allow more nutrients to be absorbed; they tend to be close to the origin of the midgut. In some insects, the role of the microvilli and where they are located may vary. For example, specialized microvilli producing digestive enzymes may more likely be near the end of the midgut, and absorption near the origin or beginning of the midgut.

Hindgut

In the hindgut (element 16 in numbered diagram), or proctodaeum, undigested food particles are joined by uric acid to form fecal pellets. The rectum absorbs 90% of the water in these fecal pellets, and the dry pellet is then eliminated through the anus (element 17), completing the process of digestion. The uric acid is formed using hemolymph waste products diffused from the Malpighian tubules (element 20). It is then emptied directly into the alimentary canal, at the junction between the midgut and hindgut. The number of Malpighian tubules possessed by a given insect varies between species, ranging from only two tubules in some insects to over 100 tubules in others.

Respiration and circulation

Insect respiration is accomplished without lungs. Instead, the insect respiratory system uses a system of internal tubes and sacs through which gases either diffuse or are actively pumped, delivering oxygen directly to tissues that need it via their trachea (element 8 in numbered diagram). Since oxygen is delivered directly, the circulatory system is not used to carry oxygen, and is therefore greatly reduced. The insect circulatory system has no veins or arteries, and instead consists of little more than a single, perforated dorsal tube which pulses peristaltically. Toward the thorax, the dorsal tube (element 14) divides into chambers and acts like the insect's heart. The opposite end of the dorsal tube is like the aorta of the insect circulating the hemolymph, arthropods' fluid analog of blood, inside the body cavity. Air is taken in through openings on the sides of the abdomen called spiracles.

There are many different patterns of gas exchange demonstrated by different groups of insects. Gas exchange patterns in insects can range from continuous and diffusive ventilation, to discontinuous gas exchange. During continuous gas exchange, oxygen is taken in and carbon dioxide is released in a continuous cycle. In discontinuous gas exchange, however, the insect takes in oxygen while it is active and small amounts of carbon dioxide are released when the insect is at rest. Diffusive ventilation is simply a form of continuous gas exchange that occurs by diffusion rather than physically taking in the oxygen. Some species of insect that are submerged also have adaptations to aid in respiration. As larvae, many insects have gills that can extract oxygen dissolved in water, while others need to rise to the water surface to replenish air supplies which may be held or trapped in special structures.

Reproduction and development

A pair of *Simosyrphus grandicornis* hoverflies mating in flight.

The majority of insects hatch from eggs. The fertilization and development takes place inside the egg, enclosed by a shell (chorion). Some species of insects, like the cockroach *Blaptica dubia*, as well as juvenile aphids and tsetse flies, are ovoviviparous. The eggs of ovoviviparous animals develop entirely inside the female, and then hatch immediately upon being laid. Some other species, such as those in the genus of cockroaches known as *Diploptera*, are viviparous, and thus gestate inside the mother and are born alive. Some insects, like parasitic wasps, show polyembryony, where a single fertilized egg divides into many and in some cases thousands of separate embryos.

The different forms of the male (top) and female (bottom) tussock moth *Orgyia recens* is an example of sexual dimorphism in insects.

Other developmental and reproductive variations include haplodiploidy, polymorphism, paedomorphosis or peramorphosis, sexual dimorphism, parthenogenesis and more rarely hermaphroditism. In haplodiploidy, which is a type of sex-determination system, the offspring's sex is determined by the number of sets of chromosomes an individual receives. This system is typical in bees and wasps. Polymorphism is the where a species may have different *morphs* or *forms*, as in the oblong winged katydid, which has four different varieties: green, pink, and yellow or tan. Some insects may retain phenotypes that are normally only seen in juveniles; this is called paedomorphosis. In peramorphosis, an opposite sort of phenomenon, insects take on previously unseen traits after they have matured into adults. Many insects display sexual dimorphism, in which males and females have notably different appearances, such as the moth *Orgyia recens* as an exemplar of sexual dimorphism in insects.

Some insects use parthenogenesis, a process in which the female can reproduce and give birth without having the eggs fertilized by a male. Many aphids undergo a form of parthenogenesis, called cyclical parthenogenesis, in which they alternate between one or many generations of asexual and sexual reproduction. In summer, aphids are generally female and parthenogenetic; in the autumn, males may be produced for sexual reproduction. Other insects produced by parthenogenesis are bees, wasps, and ants, in which they spawn males. However, overall, most individuals are female, which are produced by fertilization. The males are haploid and the females are diploid. More rarely, some insects display hermaphroditism, in which a given individual has both male and female reproductive organs.

Insect life-histories show adaptations to withstand cold and dry conditions. Some temperate region insects are capable of activity during winter, while some others migrate to a warmer climate or go into a state of torpor. Still other insects have evolved mechanisms of diapause that allow eggs or pupae to survive these conditions.

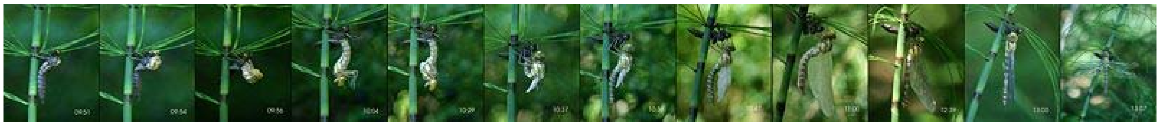
Metamorphosis

Metamorphosis in insects is the biological process of development all insects must undergo. There are two forms of metamorphosis: incomplete metamorphosis and complete metamorphosis.

Incomplete metamorphosis

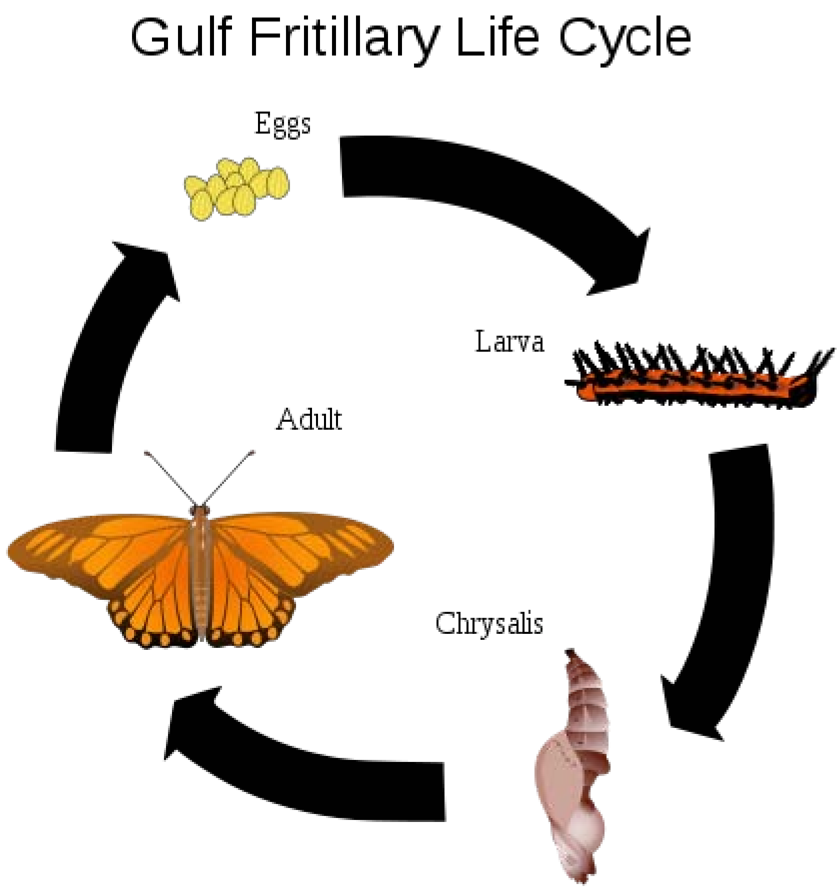
Insects that show hemimetabolism, or incomplete metamorphosis, change gradually by undergoing a series of molts. An insect molts when it outgrows its exoskeleton, which does not stretch and would otherwise restrict the insect's growth. The molting process begins as the insect's epidermis secretes a new epicuticle. After this new epicuticle is secreted, the epidermis releases a mixture of enzymes that digests the endocuticle and thus detaches the old cuticle. When this stage is complete, the insect makes its body swell by taking in a large quantity of water or air, which makes the old cuticle split along predefined weaknesses where the old exocuticle was thinnest. Other arthropods have a much different process and only molt; though must accommodate for the difference in exoskeleton structure and make up with other enzymes.

Immature insects that go through incomplete metamorphosis are called nymphs or in the case of dragonflies and damselflies as naiads. Nymphs are similar in form to the adult except for the presence of wings, which are not developed until adulthood. With each molt, nymphs grow larger and become more similar in appearance to adult insects.



Like other insects that develop through incomplete metamorphosis, this Southern Hawker dragonfly molts its exoskeleton (shown above) several times during its pre-adult life.

Complete metamorphosis



Gulf Fritillary life cycle, an example of holometabolism.

Holometabolism, or complete metamorphosis, is where the insect changes all in four stages, an egg or embryo, a larva, a pupa, and the adult or imago. In these species, egg hatches to produce a larva, which is generally worm-like in form. This worm-like form can be one of several varieties: eruciform (caterpillar-like), scarabaeiform (grub-like), campodeiform (elongated, flattened, and active), elateriform (wireworm-like) or vermiform (maggot-like). The larva grows and eventually becomes a pupa, a stage marked by reduced movement and often sealed within a cocoon. There are three types of pupae: obtect, exarate or coarctate. Obtect pupae are compact, with the legs and other appendages enclosed. Exarate pupae have their legs and other appendages free and extended. Coarctate pupae develop inside the larval skin. Insects undergo considerable change in form during the pupal stage, and emerge as adults. Butterflies are a well known example of an insects that undergo complete metamorphosis, although most insects use this life cycle. Some insects have evolved this system to hypermetamorphosis.

Some of the oldest and most successful insect groups, such Endopterygota, use a system of complete metamorphosis. Strangely though, complete metamorphosis is unique to certain insect orders, like Diptera, Lepidoptera, and Hymenoptera, and no other arthropods undergo it, but incomplete metamorphosis.

Senses and communication

Many insects possess very sensitive and/or specialized organs of perception. Some insects such as bees can perceive ultraviolet wavelengths, or detect polarized light, while the antennae of male moths can detect the pheromones of female moths over distances of many kilometers. There is a pronounced tendency for there to be a trade-off between visual acuity and chemical or tactile acuity, such that most insects with well-developed eyes have reduced or simple antennae, and vice-versa. There are a variety of different mechanisms by which insects perceive sound, while the patterns are not universal, insects can generally hear sound if they can produce it. Different insect species can have varying hearing, though most insects can hear only a narrow range of frequencies related to the frequency of the sounds they can produce. Mosquitoes have been found to hear up to 2 MHz., and some grasshoppers can hear up to 50 MHz. Certain predatory and parasitic insects can detect the characteristic sounds made by their prey or hosts, respectively. For instance, some nocturnal moths can perceive the ultrasonic emissions of bats, which helps them avoid predation. Insects that feed on blood have special sensory structures that can detect infrared emissions, and use them to home in on their hosts.

Some insects display a rudimentary sense of numbers, such as the solitary wasps that prey upon a single species. The mother wasp lays her eggs in individual cells and provides each egg with a number of live caterpillars on which the young feed when hatched. Some species of wasp always provide five, others twelve, and others as high as twenty-four caterpillars per cell. The number of caterpillars is different among species, but always the same for each sex of larva. The male solitary wasp in the genus *Eumenes* is smaller than the female, so the mother of one species supplies him with only five caterpillars; the larger female receives ten caterpillars in her cell.

Light production and vision

Insects have compound eyes and two antennae.

A few insects, such as members of the families Poduridae and Onychiuridae (Collembola), Mycetophilidae (Diptera), and the beetle families Lampyridae, Phengodidae, Elateridae and Staphylinidae are bioluminescent. The most familiar group are the fireflies, beetles of the family Lampyridae. Some species are able to control this light generation to produce flashes. The function varies with some species using them to attract mates, while others use them to lure prey. Cave dwelling larvae of *Arachnocampa* (Mycetophilidae, Fungus gnats) glow to lure small flying insects into sticky strands of silk. Some fireflies of the genus *Photuris* mimic the flashing of female *Photinus* species to attract males of that species, which are then captured and devoured. The colors of emitted light vary from dull blue (*Orfelia fultoni*, Mycetophilidae) to the familiar greens and the rare reds (*Phrixothrix tiemanni*, Phengodidae).

Most insects, except some species of cave dwelling crickets, are able to perceive light and dark. Many species have acute vision capable of detecting minute movements. The eyes include simple eyes or ocelli as well as compound eyes of varying sizes. Many species are able to detect light in the infrared, ultraviolet and the visible light wavelengths. Color vision has been demonstrated in many species and phylogenetic analysis suggests that UV-green-blue trichromacy existed from at least the Devonian period between 416 and 359 million years ago.

Sound production and hearing

Insects were the earliest organisms to produce and sense sounds. Insects make sounds mostly by mechanical action of appendages. In grasshoppers and crickets, this is achieved by stridulation. Cicadas make the loudest sounds among the insects by producing and amplifying sounds with special modifications to their body and musculature. The African cicada *Brevisana brevis* has been measured at 106.7 decibels at a distance of 50 cm (20 in). Some insects, such as the hawk moths and Hedylid butterflies, can hear ultrasound and take evasive action when they sense that they have been detected by bats. Some moths produce ultrasonic clicks that were once thought to have a role in jamming bat echolocation. The ultrasonic clicks were subsequently found to be produced mostly by unpalatable moths to warn bats, just as warning colorations are used against predators that hunt by sight. Some otherwise palatable moths have evolved to mimic these calls.

Very low sounds are also produced in various species of Coleoptera, Hymenoptera, Lepidoptera, Mantodea, and Neuroptera. These low sounds are simply the sounds made by the insect's movement. Through microscopic stridulatory structures located on the insect's muscles and joints, the normal sounds of the insect moving are amplified and can be used to warn or communicate with other insects. Most sound-making insects also have tympanal organs that can perceive airborne sounds. Some species in Hemiptera, such as the corixids (water boatmen), are known to communicate via underwater sounds. Most insects are also able to sense vibrations transmitted through surfaces. For example, an insect is caught in a spider web and struggles to escape. The vibrations it produces are sensed by the spider, who is alerted to its presence. Through these vibrations, the spider can tell where on the web the insect is located, as well as how big it is.

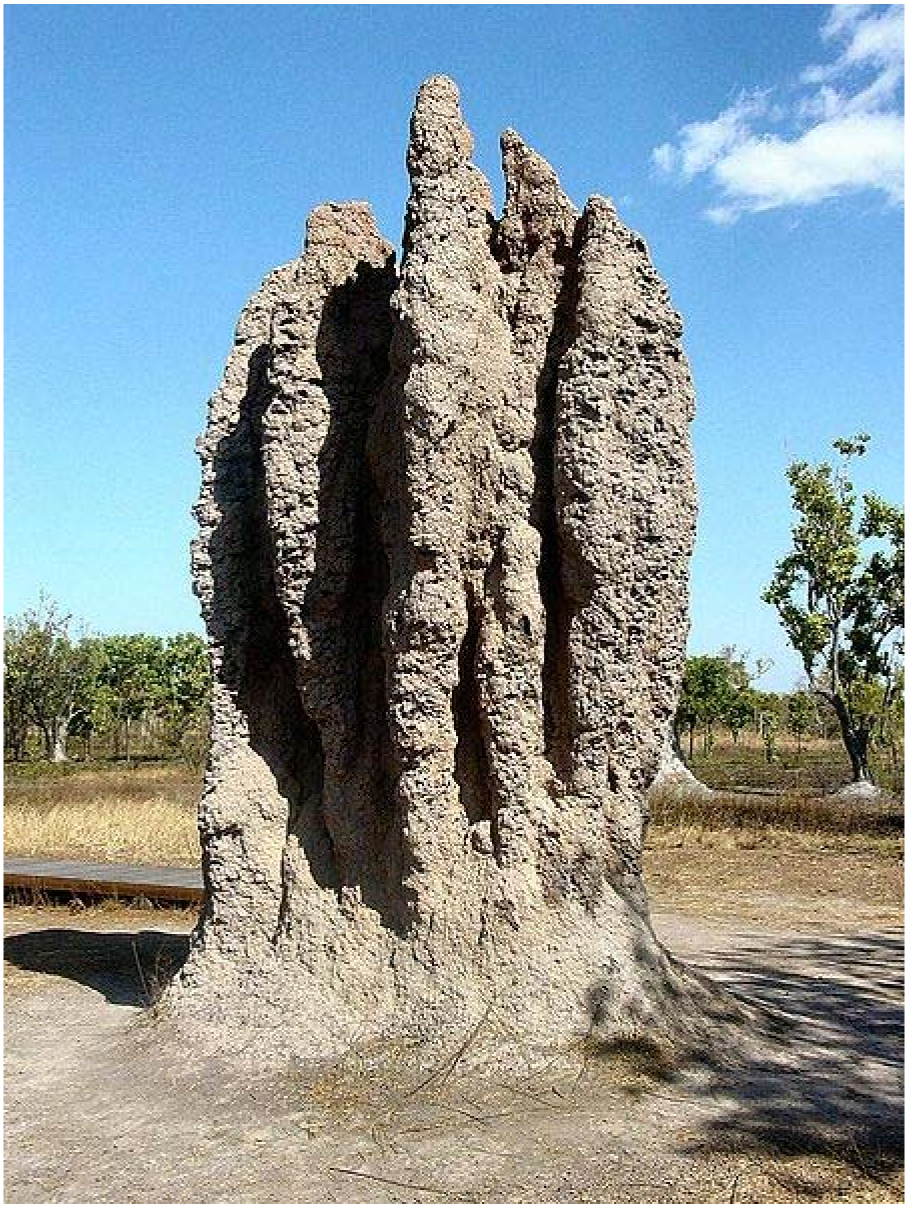
Communication using surface-borne vibrational signals is more widespread among insects because of size constraints in producing air-borne sounds. Insects cannot effectively produce low-frequency sounds, and high-frequency sounds tend to disperse more in a dense environment (such as foliage), so insects living in such environments communicate primarily using substrate-borne vibrations. The mechanisms of production of vibrational signals are just as diverse as those for producing sound in insects.

Some species use vibrations for communicating within members of the same species, such as to attract mates as in the songs of the shield bug *Nezara viridula*. Vibrations can also be used to communicate between entirely different species; lycaenid (gossamer-winged butterfly) caterpillars which are myrmecophilous (living in a mutualistic association with ants) communicate with ants in this way. The Madagascar hissing cockroach has the ability to press air through its spiracles to make a hissing noise as a sign of aggression; the Death's-head Hawkmoth makes a squeaking noise by forcing air out of their pharynx when agitated, which may also reduce aggressive worker honey bee behavior when the two are in close proximity.

Chemical communication

In addition to the use of sound for communication, a wide range of insects have evolved chemical means for communication. These chemicals, termed semiochemicals, are often derived from plant metabolites include those meant to attract, repel and provide other kinds of information. Pheromones, a type of semiochemical, are used for attracting mates of the opposite sex, for aggregating conspecific individuals of both sexes, for deterring other individuals from approaching, to mark a trail, and to trigger aggression in nearby individuals. Allomonea benefit their producer by the effect they have upon the receiver. Kairomones benefit their receiver instead of their producer. Synomones benefit the producer and the receiver. While some chemicals are targeted at individuals of the same species, others are used for communication across species. The use of scents is especially well known to have developed in social insects.

Social behavior



A cathedral mound created by termites (Isoptera).

Social insects, such as termites, ants and many bees and wasps, are the most familiar species of eusocial animal. They live together in large well-organized colonies that may be so tightly integrated and genetically similar that the colonies of some species are sometimes considered superorganisms. It is sometimes argued that the various species of honey bee are the only invertebrates (and indeed one of the few non-human groups) to have evolved a system of abstract symbolic communication where a behavior is used to *represent* and convey specific information about something in the environment. In this communication system, called dance language, the angle at which a bee dances represents a direction relative to the sun, and the length of the dance represents the distance to be flown.

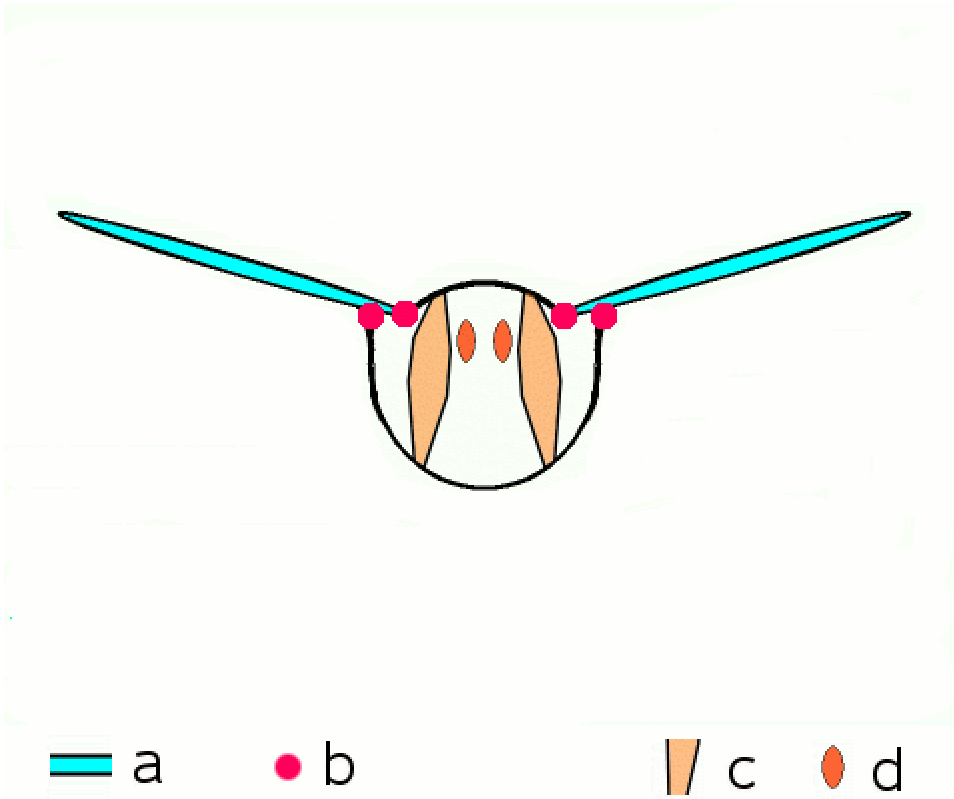
Only insects which live in nests or colonies demonstrate any true capacity for fine-scale spatial orientation or homing. This can allow an insect to return unerringly to a single hole a few millimeters in diameter among thousands of apparently identical holes clustered together, after a trip of up to several kilometers' distance. In a phenomenon known as philopatry, insects that hibernate have shown the ability to recall a specific location up to a year after last viewing the area of interest. A few insects seasonally migrate large distances between different geographic regions (e.g., the overwintering areas of the Monarch butterfly).

Care of young

Most insects lead short lives as adults, and rarely interact with one another except to mate or compete for mates. A small number exhibit some form of parental care, where they will at least guard their eggs, and sometimes continue guarding their offspring until adulthood, and possibly even feeding them. Another simple form of parental care is to construct a nest (a burrow or an actual construction, either of which may be simple or complex), store provisions in it, and lay an egg upon those provisions. The adult does not contact the growing offspring, but it nonetheless does provide food. This sort of care is typical of bees and various types of wasps.

Locomotion

Flight



Basic motion of the insect wing in insect with an indirect flight mechanism scheme of dorsoventral cut through a thorax segment with
a wings
b joints
c dorsoventral muscles
d longitudinal muscles.

Insects are the only group of invertebrates to have developed flight. The evolution of insect wings has been a subject of debate. Some entomologists suggest that the wings are from paranotal lobes, or extensions from the insect's exoskeleton called the nota, called the *paranotal theory*. Other theories are based on a pleural origin. The pleuron is membrane on the sides of the thorax. These theories include suggestions that wings originated from modified gills, spiracular flaps or as from an appendage of the epicoxa. The *epicoxal theory* suggests the insect wings are modified epicoxal exites, a modified appendage at the base of the legs or coxa. In the Carboniferous age, some of the *Meganeura* dragonflies had as much as a 50 cm (20 in) wide wingspan. The appearance of gigantic insects has been found to be consistent with high atmospheric oxygen. The respiratory system of insects constrains their size, however the high oxygen in the atmosphere allowed larger sizes. The largest flying insects today are much smaller and include several moth species such as the Atlas moth and the White Witch (*Thysania* *agrippina*). Insect flight has been a topic of great interest in aerodynamics due partly to the inability of steady-state theories to explain the lift generated by the tiny wings of insects.

Unlike birds, many small insects are swept along by the prevailing winds although many of the larger insects are known to make migrations. Aphids are known to be transported long distances by low-level jet streams. As such, fine line patterns associated with converging winds within weather radar imagery, like the WSR-88D radar network, often represent large groups of insects.

Walking

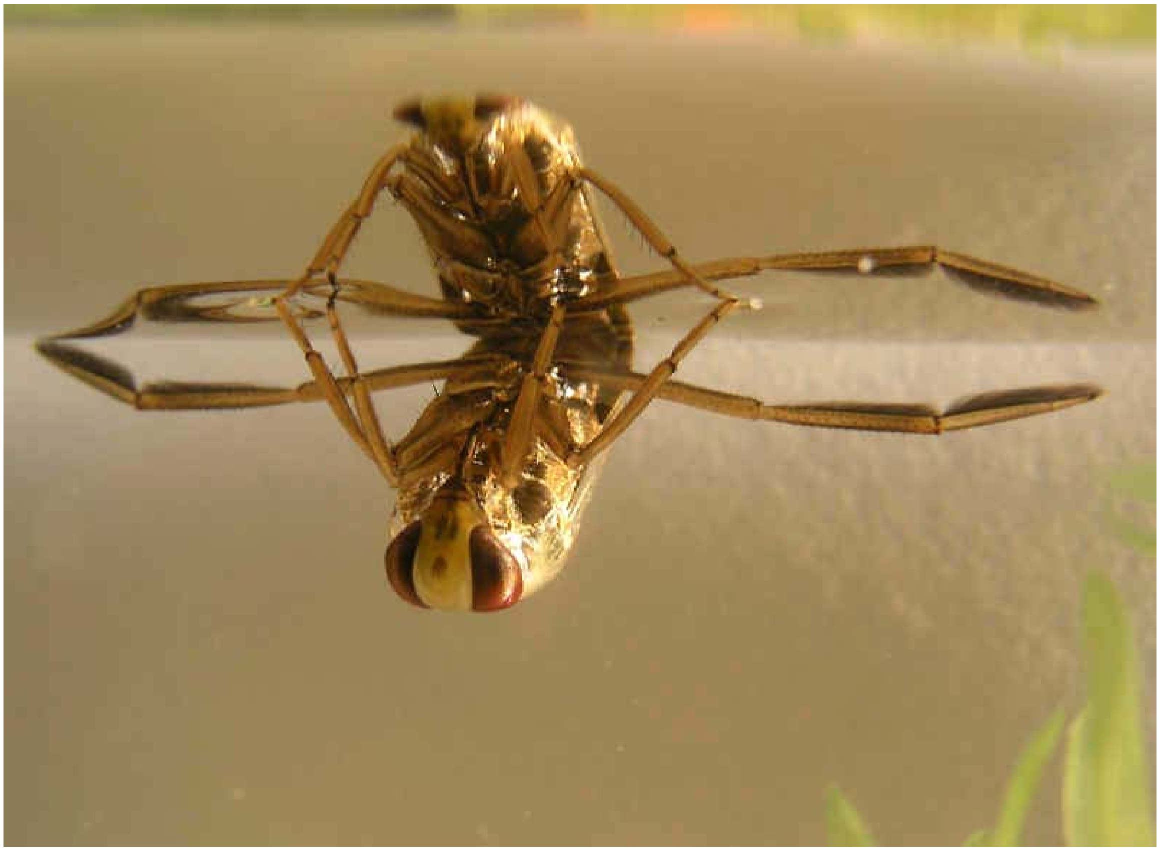
Many adult insects use six legs for walking and have adopted a tripedal gait. The tripedal gait allows for rapid walking while always having a stable stance and has been studied extensively in cockroaches. The legs are used in alternate triangles touching the ground. For the first step, the middle right leg and the front and rear left legs are in contact with the ground and move the insect forward, while the front and rear right leg and the middle left leg are lifted and moved forward to a new position. When they touch the ground to form a new stable triangle the other legs can be lifted and brought forward in turn and so on. The purest form of the tripedal gait is seen in insects moving at high speeds. However, this type of locomotion is not rigid and insects can adapt a variety of gaits. For example, when moving slowly, turning, or avoiding obstacles, four or more feet may be touching the ground. Insects can also adapt their gait to cope with the loss of one or more limbs.

Cockroaches are among the fastest insect runners and, at full speed, adopt a bipedal run to reach a high velocity in proportion to their body size. As cockroaches move very quickly, they need to be video recorded at several hundred frames per second to reveal their gait. More sedate locomotion is seen in the stick insects or walking sticks (Phasmatodea). A few insects have evolved to walk on the surface of the water, especially the bugs of the Gerridae family, commonly known as water striders. A few species of ocean-skaters in the genus *Halobates* even live on the surface of open oceans, a habitat that has few insect species.

Use in robotics

Insect walking is of particular interest as an alternative form of locomotion in robots. The study of insects and bipeds has a significant impact on possible robotic methods of transport. This may allow new robots to be designed that can traverse terrain that robots with wheels may be unable to handle.

Swimming



The backswimmer *Notonecta glauca* underwater, showing its paddle-like hindleg adaptation.

A large number of insects live either parts or the whole of their lives underwater. In many of the more primitive orders of insect, the immature stages are spent in an aquatic environment. Some groups of insects, like certain water beetles, have aquatic adults as well.

Many of these species have adaptations to help in under-water locomotion. Water beetles and water bugs have legs adapted into paddle-like structures. Dragonfly naiads use jet propulsion, forcibly expelling water out of their rectal chamber. Some species like the water striders are capable of walking on the surface of water. They can do this because their claws are not at the tips of the legs as in most insects, but recessed in a special groove further up the leg; this prevents the claws from piercing the water's surface film. Other insects such as the Rove beetle *Stenus* are known to emit pygidial gland secretions that reduce surface tension making it possible for them to move on the surface of water by Marangoni propulsion (also known by the German term *Entspannungsschwimmen*).

Phylogeny and systemics

Evolution has produced astonishing variety in insects. Pictured are some of the possible shapes of antennae.

The evolutionary relationships of insects to other animal groups remain unclear. Although more traditionally grouped with millipedes and centipedes, evidence has emerged favoring closer evolutionary ties with crustaceans. In the Pancrustacea theory, insects, together with Remipedia and Malacostraca, make up a natural clade. Other terrestrial arthropods, such as centipedes, millipedes, scorpions and spiders, are sometimes confused with insects since their body plans can appear similar, sharing (as do all arthropods) a jointed exoskeleton. However, upon closer examination their features differ significantly; most noticeably they do not have the six legs characteristic of adult insects.

The higher-level phylogeny of the arthropods continues to be a matter of debate and research. In 2008, researchers at Tufts University uncovered what they believe is the world's oldest known full-body impression of a primitive flying insect, a 300 million-year-old specimen from the Carboniferous Period. The oldest definitive insect fossil is the Devonian *Rhyniognatha hirsti*, from the 396 million year old Rhynie chert. It may have superficially resembled a modern-day silverfish insect. This species already possessed dicondylic mandibles (two articulations in the mandible), a feature associated with winged insects, suggesting that wings may already have evolved at this time. Thus, the first insects probably appeared earlier, in the Silurian period.

The origins of insect flight remain obscure, since the earliest winged insects currently known appear to have been capable fliers. Some extinct insects had an additional pair of winglets attaching to the first segment of the thorax, for a total of three pairs. As of 2009, there is no evidence that suggests that the insects were a particularly successful group of animals before they evolved to have wings.

Late Carboniferous and Early Permian insect orders include both extant groups and a number of Paleozoic species, now extinct. During this era, some giant dragonfly-like forms reached wingspans of 55 to 70 cm (22 to 28 in) making them far larger than any living insect. This gigantism may have been due to higher atmospheric oxygen levels that allowed increased respiratory efficiency relative to today. The lack of flying vertebrates could have been another factor. Most extinct orders of insects developed during the Permian period that began around 270 million years ago. Many of the early groups became extinct during the Permian-Triassic extinction event, the largest mass extinction in the history of the Earth, around 252 million years ago.

The remarkably successful Hymenopterans appeared as long as 146 million years ago in the Cretaceous period, but achieved their wide diversity more recently in the Cenozoic era, which began 66 million years ago. A number of highly successful insect groups evolved in conjunction with flowering plants, a powerful illustration of coevolution.

Many modern insect genera developed during the Cenozoic. Insects from this period on are often found preserved in amber, often in perfect condition. The body plan, or *morphology*, of such specimens is thus easily compared with modern species. The study of fossilized insects is called paleoentomology.

Evolutionary relationships

Insects are prey for a variety of organisms, including terrestrial vertebrates. The earliest vertebrates on land existed 400 million years ago and were large amphibious piscivores, through gradual evolutionary change, insectivory was the next diet type to evolve.

Insects were among the earliest terrestrial herbivores and acted as major selection agents on plants. Plants evolved chemical defenses against this herbivory and the insects in turn evolved mechanisms to deal with plant toxins. Many insects make use of these toxins to protect themselves from their predators. Such insects often advertise their toxicity using warning colors. This successful evolutionary pattern has also been utilized by mimics. Over time, this has led to complex groups of coevolved species. Conversely, some interactions between plants and insects, like pollination, are beneficial to both organisms. Coevolution has led to the development of very specific mutualisms in such systems.

Taxonomy

Traditional morphology-based or appearance-based systematics has usually given Hexapoda the rank of superclass, and identified four groups within it: insects (Ectognatha), springtails (Collembola), Protura and Diplura, the latter three being grouped together as Entognatha on the basis of internalized mouth parts. Supraordinal relationships have undergone numerous changes with the advent of methods based on evolutionary history and genetic data. A recent theory is that Hexapoda is polyphyletic (where the last common ancestor was not a member of the group), with the entognath classes having separate evolutionary histories from Insecta. Many of the traditional appearance-based taxa have been shown to be paraphyletic, so rather than using ranks like subclass, superorder and infraorder, it has proved better to use monophyletic groupings (in which the last common ancestor is a member of the group). The following represents the best supported monophyletic groupings for the Insecta.

Insects can be divided into two groups historically treated as subclasses: wingless insects, known as Apterygota, and winged insects, known as Pterygota. The Apterygota consist of the primitively wingless order of the silverfish (Thysanura). Archaeognatha make up the Monocondylia based on the shape of their mandibles, while Thysanura and Pterygota are grouped together as Dicondylia. It is possible that the Thysanura themselves are not monophyletic, with the family Lepidotrichidae being a sister group to the Dicondylia (Pterygota and the remaining Thysanura).

Paleoptera and Neoptera are the winged orders of insects differentiated by the presence of hardened body parts called sclerites; also, in Neoptera, muscles that allow their wings to fold flatly over the abdomen. Neoptera can further be divided into incomplete metamorphosis-based (Polyneoptera and Paraneoptera) and complete metamorphosis-based groups. It has proved difficult to clarify the relationships between the orders in Polyneoptera because of constant new findings calling for revision of the taxa. For example, Paraneoptera has turned out to be more closely related to Endopterygota than to the rest of the Exopterygota. The recent molecular finding that the traditional louse orders Mallophaga and Anoplura are derived from within Psocoptera has led to the new taxon Psocodea. Phasmatodea and Embiidina have been suggested to form Eukinolabia. Mantodea, Blattodea and Isoptera are thought to form a monophyletic group termed Dictyoptera.

It is likely that Exopterygota is paraphyletic in regard to Endopterygota. Matters that have had a lot of controversy include Strepsiptera and Diptera grouped together as Halteria based on a reduction of one of the wing pairs – a position not well-supported in the entomological community. The Neuropterida are often lumped or split on the whims of the taxonomist. Fleas are now thought to be closely related to boreid mecopterans. Many questions remain to be answered when it comes to basal relationships amongst endopterygote orders, particularly Hymenoptera.

The study of the classification or taxonomy of any insect is called systematic entomology. If one works with a more specific order or even a family, the term may also be made specific to that order or family, for example systematic dipterology.

Relationship to humans

Aedes aegypti, a parasite, and vector of dengue fever and yellow fever.

Many insects are considered pests by humans. Insects commonly regarded as pests include those that are parasitic (mosquitoes, lice, bed bugs), transmit diseases (mosquitoes, flies), damage structures (termites), or destroy agricultural goods (locusts, weevils). Many entomologists are involved in various forms of pest control, as in research for companies to produce insecticides, but increasingly relying on methods of biological pest control, or biocontrol. Biocontrol uses one organism to reduce the population density of another organism — the pest — and is considered a key element of integrated pest management.

Despite the large amount of effort focused at controlling insects, human attempts to kill pests with insecticides can backfire. If used carelessly the poison can kill all kinds of organisms in the area, including insects' natural predators such as birds, mice, and other insectivores. The effects of DDT's use exemplifies how some insecticides can threaten wildlife beyond intended populations of pest insects.

Because they help flowering plants to cross-pollinate, some insects are critical to agriculture. This European honey bee is gathering nectar while pollen collects on its body.

Although pest insects attract the most attention, many insects are beneficial to the environment and to humans. Some insects, like wasps, bees, butterflies, and ants, pollinate flowering plants. Pollination is a mutualistic relationship between plants and insects. As insects gather nectar from different plants of the same species, they also spread pollen from plants on which they have previously fed. This greatly increases plants' ability to cross-pollinate, which maintains and possibly even improves their evolutionary fitness. This ultimately affects humans since ensuring healthy crops is critical to agriculture. A serious environmental problem is the decline of populations of pollinator insects, and a number of species of insects are now cultured primarily for pollination management in order to have sufficient pollinators in the field, orchard or greenhouse at bloom time. Insects also produce useful substances such as honey, wax, lacquer and silk. Honey bees have been cultured by humans for thousands of years for honey, although contracting for crop pollination is becoming more significant for beekeepers. The silkworm has greatly affected human history, as silk-driven trade established relationships between China and the rest of the world.

The common fruitfly *Drosophila melanogaster* is one of the most widely used organisms in biological research.

Insects play important roles in biological research. For example, because of its small size, short generation time and high fecundity, the common fruit fly *Drosophila melanogaster* is a model organism for studies in the genetics of higher eukaryotes. *D. melanogaster* has been an essential part of studies into principles like genetic linkage, interactions between genes, chromosomal genetics, development, behavior, and evolution. Because genetic systems are well conserved among eukaryotes, understanding basic cellular processes like DNA replication or transcription in fruit flies can help to understand those processes in other eukaryotes, including humans. The genome of *D. melanogaster* was sequenced in 2000, reflecting the organism's important role in biological research.

A robberfly with its prey, a hoverfly. Insectivorous relationships such as these help control insect populations.

Insectivorous insects, or insects which feed on other insects, are beneficial to humans because they eat insects that could cause damage to agriculture and human structures. For example, aphids feed on crops and cause problems for farmers, but ladybugs feed on aphids, and can be used as a means to get significantly reduce pest aphid populations. While birds are perhaps more visible predators of insects, insects themselves account for the vast majority of insect consumption. Without predators to keep them in check, insects can undergo almost unstoppable population explosions.

Many insects, especially beetles, are scavengers that feed on dead animals and fallen trees and thereby recycle biological materials into forms found useful by other organisms. Insects are responsible for much of the process by which topsoil is created. The ancient Egyptian religion considered dung beetles sacred, and represented them as beetle-shaped amulets, or scarabs. Dung beetles have been used in countries including Australia as an agent of biological pest control to reduce the populations of pestilent flies and parasitic worms. The Australian Dung Beetle Project successfully introduced 23 species of dung beetle, including *Onthophagus gazella* and *Euoniticellus intermedius* from South Africa and Europe. This resulting in a 90% reduction in bush flies as well as improved soil fertility and quality.

Insects are also used in medicine, for example fly larvae (maggots) were formerly used to treat wounds to prevent or stop gangrene, as they would only consume dead flesh. This treatment is finding modern usage in some hospitals. Adult insects, such as crickets, and insect larvae of various kinds are also commonly used as fishing bait.

Entomophagy

In some parts of the world, insects are used for human food, while being a taboo in other places. In some cultures, insects, especially deep-fried cicadas, are considered to be delicacies, while in other places they form part of the normal diet as they have a high protein content for their mass. In most first-world countries, however, entomophagy, or the consumption of insects, is taboo. There are proponents of developing this use to provide a major source of protein in human nutrition. Since it is impossible to entirely eliminate pest insects from the human food chain, insects are present in many foods, especially grains. Food safety laws in many countries do not prohibit insect parts in food, but rather limit the quantity. According to cultural materialist anthropologist Marvin Harris, the eating of insects is taboo in cultures that have other protein sources such as fish or livestock.

In culture

Scarab beetles held religious and cultural symbolism in Old Egypt, Greece and some shamanistic Old World cultures. The ancient Chinese regarded cicadas as symbols of rebirth or immortality. In Mesopotamian literature, the epic poem of Gilgamesh has allusions to Odonata which signify the impossibility of immortality. Amongst the Aborigines of Australia of the Arrernte language groups, honey ants and witchety grubs served as personal clan totems. In the case of the 'San' bush-men of the Kalahari, it is the praying mantis which holds much cultural significance including creation and zen-like patience in waiting.

Chapter 7

Centipede

Centipedes Temporal range: 418–0 Ma Late Silurian to Recent	

Scolopendra sp. (Scolopendromorpha: Scolopendridae)

Scientific classification	
Kingdom:	Animalia
Phylum:	Arthropoda
Subphylum:	Myriapoda
Class:	**Chilopoda** Latreille, 1817

Orders and Families

Scutigeromorpha

- Pselliodidae
- Scutigeridae
- Scutigerinidae

Lithobiomorpha

- Henicopidae
- Lithobiidae

Craterostigmomorpha

- Craterostigmidae

Scolopendromorpha

- Cryptopidae
- Scolopendridae
- Scolopocryptopidae

Geophilomorpha

- Mecistocephalidae
- Neogeophilidade
- Geophilidae
- Geophilidae
- Linotaeniidae

Centipedes are arthropods belonging to the class **Chilopoda** of the subphylum Myriapoda. They are elongated metameric animals with one pair of legs per body segment. Despite the name, centipedes can have a varying number of legs from under 20 to over 300. Centipedes have an odd number of pairs of legs, e.g. 15 or 17 pairs of legs (30 or 34 legs) but never 16 pairs (32 legs). A key trait uniting this group is a pair of venom claws or "forcipules" formed from a modified first appendage. Centipedes are a predominantly carnivorous taxon.

Centipedes normally have a drab coloration combining shades of brown and red. Cavernicolous (cave-dwelling) and subterranean species may lack pigmentation and many tropical scolopendromorphs have bright aposematic colours. Size can range from a few millimetres in the smaller lithobiomorphs and geophilomorphs to about 30 cm (12 in) in the largest scolopendromorphs. Centipedes can be found in a wide variety of environments.

Worldwide there are estimated to be 8,000 species of centipede, of which 3,000 have been described. Centipedes have a wide geographical range, reaching beyond the Arctic Circle. Centipedes are found in an array of terrestrial habitats from tropical rainforests to deserts. Within these habitats centipedes require a moist micro-habitat because they lack the waxy cuticle of insects and arachnids, and so lose water rapidly through the skin. Accordingly, they are found in soil and leaf litter, under stones and dead wood, and inside logs. Centipedes are among the largest terrestrial invertebrate predators and often contribute significantly to the invertebrate predatory biomass in terrestrial ecosystems.

Description

Centipedes have a rounded or flattened head, bearing a pair of antennae at the forward margin. They have a pair of elongated mandibles, and two pairs of maxillae. The first pair of maxillae form the lower lip, and bear short palps. The first pair of limbs stretch forward from the body to cover the remainder of the mouth. These limbs, or maxillipeds, end in sharp claws and include venom glands that help the animal to kill or paralyse its prey.

Centipedes possess a variable number of ocelli, which are sometimes clustered together to form true compound eyes. Even so, it appears that centipedes are only capable of discerning light and dark, and not of true vision. Indeed, many species lack eyes altogether. In some species the final pair of legs act as sense organs similar to antennae, but facing backwards. An unusual sense organ found in some groups are the organs of Tömösvary. These are located at the base of the antennae, and consist of a disc-like structure with a central pore surrounded by sensory cells. They are probably used for sensing vibrations, and may even provide a sense of hearing.

Underside of *Scolopendra cingulata*, showing the forcipules

Forcipules are a unique feature found only in centipedes and in no other arthropods. The forcipules are modifications of the first pair of legs, forming a pincer-like appendage always found just behind the head. Forcipules are not true mouthparts, although they are used in the capture of prey items, injecting venom and holding onto captured prey. Venom glands run through a tube almost to the tip of each forcipule.

Behind the head, the body consists of fifteen or more segments. Most of the segments bear a single pair of legs, with the maxillipeds projecting forward from the first body segment, and the final two segments being small and legless. Each pair of legs is slightly longer than the pair immediately in front of it, ensuring that they do not overlap, and therefore reducing the chance that they will collide with each other while moving swiftly.

In extreme cases, the last pair of legs may be twice the length of the first pair. The final segment bears a telson and includes the openings of the reproductive organs.

Centipedes are predators, and mainly use their antennae to seek out their prey. The digestive tract forms a simple tube, with digestive glands attached to the mouthparts. Like insects, centipedes breathe through a tracheal system, typically with a single opening, or spiracle on each body segment. They excrete waste through a single pair of malpighian tubules.

Scolopendra gigantea, also known as the **Amazonian giant centipede**, is the largest existing species of centipede in the world, reaching over 30 cm (12 in) in length. It is known to eat lizards, frogs, birds, mice, and even bats, catching them in midflight, as well as rodents and spiders. The now extinct *Euphoberia* was the largest centipede, growing up to 1 m (39 in) in length.

Life cycle

A centipede protecting her eggmass

Centipede reproduction does not involve copulation. Males deposit a spermatophore for the female to take up. In one clade, this spermatophore is deposited in a web, and the male undertakes a courtship dance to encourage the female to engulf his sperm. In other cases, the males just leave them for the females to find. In temperate areas egg laying occurs in spring and summer but in subtropical and tropical areas there appears to be little seasonality to centipede breeding. It is also notable that there are a few known species of parthenogenetic centipedes.

The Lithobiomorpha, and Scutigeromorpha lay their eggs singly in holes in the soil, the female fills the hole in on the egg and leaves it. The number of eggs laid ranges from about 10 to 50. Time of development of the embryo to hatching is highly variable and may take from one to a few months. Time of development to reproductive period is highly variable within and among species. For example, it can take 3 years for *S. coleoptera* to achieve adulthood, whereas under the right conditions Lithiobiomorph species may reach a reproductive period in 1 year. In addition, centipedes are relatively long-lived when compared to their insect cousins. For example: the European *Lithobius forficatus* can live for 5 or 6 years. The combination of a small number of eggs laid, long gestation period, and long time of development to reproduction has led authors to label Lithobiomorph centipedes as K-selected.

Females of Geophilomorpha and Scolopendromorpha show far more parental care, the eggs 15 to 60 in number are laid in a nest in the soil or in rotten wood, the female stays with the eggs, guarding and licking them to protect them from fungi. The female in some species stays with the young after they have hatched, guarding them until they are ready to leave. If disturbed the females tend to either abandon the eggs of their young or eat them; abandoned eggs tend to fall prey to fungi rapidly. Some species of Scolopendromorpha are matriphagic, meaning that the offspring eat their mother.

Little is known of the life history of Craterostigmomorpha.

Anamorphy vs. epimorphy

Centipedes grow their legs at different points in their development. In the primitive condition, exhibited by the L, Scutigeromorpha and Craterostigmomorpha, development is anamorphic. That is to say, more pairs of legs are grown between moults; for example, *Scutigera coleoptrata*, the American house centipede, hatches with only 4 pairs of legs and in successive moults has 5, 7, 9, 11, 15, 15, 15 and 15 before becoming a sexually mature adult. Life stages with fewer than 15 pairs of legs are called larval stadia (~5 stages). After the full complement of legs is achieved, the now post-larval stadia (~5 stages) develop gonopods, sensory pores, more antennal segments, and more ocelli. All mature Lithobiomorph centipedes have 15 leg-bearing segments.

The Craterostigmomorpha only have one phase of anamorphis, with embryos having 12 pairs, and moultees 15.

The clade Epimorpha, consisting of orders Geophilomorpha and Scolopendromorpha, derived epimorphy. Here, all pairs of legs are developed in the embryonic stages, offspring do not develop more legs between moults. It is this clade that contains the *longest* centipedes; the maximum number of thoracic segments may also vary intra-specifically, often on a geographical basis; in most cases, females bear more legs than males. The number of leg-bearing segments varies widely, from 15 to 191, but the developmental mode of their creation means that they are always added in pairs – hence the total number of pairs is always odd.

Ecology

A centipede being eaten by a European roller

Centipedes are a predominantly predatory taxon. They are known as generalist predators which means that they have adapted to eat a variety of different available prey items. Examination of centipede gut contents suggest that plant material is an unimportant part of their diet although centipedes have been observed to eat vegetable matter when starved during laboratory experiments.

Centipedes are also known to be nocturnal. Studies on centipede activity rhythms confirm this, although there are a few observations of centipedes active during the day and one species *Strigamia chinophila* that is diurnal. What centipedes actually eat is not well known because of their cryptic lifestyle and thorough mastication of food. Laboratory feeding trials support that they will feed as generalists, taking most anything that is soft-bodied and in a reasonable size range. It has been suggested that earthworms provide the bulk of diets for Geophilomorphs, since Geophilomorphs burrow through the soil and earthworm bodies would be easily pierced by their poison claws. Observations suggest that Geophilomorphs cannot subdue earthworms larger than themselves, and so smaller earthworms may be a substantial proportion of their diet. Scolopendromorphs, given their size, are able to feed on vertebrates as well as invertebrates. They have been observed eating reptiles, amphibians, small mammals, bats and birds. Collembola may provide a large proportion of Lithiobiomorph diet. Little is known about Scutigeromorph or Craterostigmomorph diets. All centipedes are potential intraguild predators. Centipedes and spiders may frequently prey on one another.

Centipedes are eaten by a great many vertebrates and invertebrates, such as mongooses, mice, salamanders, beetles and snakes. They form an important item of diet for many species and the staple diet of some such as the African ant *Amblyopone pluto*, which feeds solely on geophilomorph centipedes, and the South African Cape black-headed snake *Aparallactus capensis*.

Centipedes are found in moist microhabitats. Water relations are an important aspect of their ecology, since they lose water rapidly in dry conditions. Water loss is a result of centipedes lacking a waxy covering of their exoskeleton and excreting waste nitrogen as ammonia, which requires extra water. Centipedes deal with water loss through a variety of adaptations. Geophilomorphs lose water less rapidly than Lithobiomorphs even though they have a greater surface area to volume ratio. This may be explained by the fact that Geophilomorphs have a more heavily sclerotized pleural membrane. Spiracle shape, size and ability to constrict also have an influence on rate of water loss. In addition, it has been suggested that number and size of coxal pores may be variables affecting centipede water balance.

Centipedes live in many different habitat types; forest, savannah, prairie, and desert to name a few. Some Geophilomorphs are adapted to littoral habitats, where they feed on barnacles. Species of all orders excluding Craterostigmomorpha have adapted to caves. Centipede densities have been recorded as high as $600/m^2$ and biomass as high as 500 mg/m^2 wet weight. Small geophilomorphs attain highest densities, followed by small Lithobiomorphs. Large Lithobiomorphs attain densities of $20/m^2$. One study of scolopendromorphs records *Scolopendra morsitans* in a Nigerian savannah at a density of $0.16/m^2$ and a biomass of 140 mg/m^2 wet weight.

Hazards to humans

Some species of centipede can be hazardous to humans because of their bite. Although a bite to an adult human is usually very painful and may cause severe swelling, chills, fever, and weakness, it is unlikely to be fatal. Bites can be dangerous to small children and those with allergies to bee stings. The bite of larger centipedes can induce anaphylactic shock in such people. Smaller centipedes usually do not puncture human skin.

Evolution

he fossil record of centipedes extends back to 430 million years ago, during the Late Silurian. They belong to the subphylum Myriapoda which includes Diplopoda, Symphyla, and Pauropoda. The oldest known fossil land animal, *Pneumodesmus newmani*, is a myriapod. Being among the earliest terrestrial animals, centipedes were one of the first to fill a fundamental niche as ground level generalist predators in detrital food webs. Today, centipedes are abundant and exist in many harsh habitats.

Within the myriapods, centipedes are believed to be the first of the extant classes to branch from the last common ancestor. There are five orders of centipedes: Craterostigmomorpha, Geophilomorpha, Lithobiomorpha, Scolopendromorpha, and Scutigeromorpha. These orders are united into the clade Chilopoda by the following synapomorphies:

1. The first post-cephalic appendage is modified to poison claws.
2. The embryonic cuticle on second maxilliped has an egg tooth.
3. The trochanter–prefemur joint is fixed.
4. There is a spiral ridge on the nucleus of the spermatozoon.

Chilopoda is then split into two clades: the Notostigmomorpha including the Scutigeromorpha and the Pluerostigmomorpha including the other four orders. The main difference is that the Notostigmomorpha have their spiracles located mid-dorsally. It was previously believed that Chilopoda was split into Anamorpha (Lithobiomorpha and Scutigeromorpha) and Epimorpha (Geophilomorpha and Scolopendromorpha), based on developmental modes, with the relationship of Craterostigmomorpha being uncertain. Recent phylogenetic analyses using combined molecular and morphological characters supports the previous phylogeny. Epimorpha still exists as a monophyletic group within the Pleurostigmomorpha, but Anamorpha is paraphyletic.

Geophilomorph centipedes have bene used to argue for the developmental constraint of evolution: that the evolvability of a trait, the number of segments in the case of geophilomorph centipedes, was constrained by the mode of development. The geophilomorph centipedes have variable segment numbers within species, yet as with all centipedes they always have an odd number of pairs of legs. In this taxon, the number of segments range from 27 to 191 but is never an even number.

Orders and families

Representatives of centipede orders

Scutigera coleoptrata (Scutigeromorpha: Scutigeridae)

Lithobius forficatus (Lithobiomorpha: Lithobiidae)

Geophilus flavus (Geophilomorpha: Geophilidae)

Scutigeromorpha

The **Scutigeromorpha** are anamorphic, reaching 15 leg-bearing segments in length. They are very fast creatures, and able to withstand falling at great speed: they reach up to 15 body lengths per second when dropped, surviving the fall. They are the only centipede group to retain their original compound eyes, with which a crystalline layer analogous to that seen in chelicerates and insects can be observed. They also bear long and multi-segmented antennae. Adaptation to a burrowing lifestyle has led to the degeneration of compound eyes in other orders. This feature is of great use in phylogenetic analysis. The group is the sole extant representative of the Notostigmomorpha, defined by having a single spiracle opening at the posterior of each dorsal plate. The more derived groups bear a plurality of spiracular openings on their sides, and are termed the Pleurostigmomorpha. Some even have several unpaired spiracles that can be found along the mid-dorsal line and closer to their posterior section of tergites. There are three families: Psellioididae, Scutigeridae and Scutigerinidae.

Lithobiomorpha

The **Lithobiomorpha** represent the other main group of anamorphic centipedes; they also reach a mature length of 15 thoracic segments. This group has lost the compound eyes, and sometimes has no eyes altogether. Instead, its eyes have facets or groups of facets. Its spiracles are paired and can be found laterally. Every leg-bearing segment of this organism has a separate tergite. It also has relatively short antennae and legs. Two families are included, Henicopidae and Lithobiidae.

Craterostigmomorpha

The **Craterostigmomorpha** are the least diverse centipede clade, comprising only two extant species, both in the genus *Ceratostigmus*. Their geographic range is restricted to Tasmania and New Zealand. They have a distinct body plan; their anamorphosis comprises a single stage; they grow from 12 to 15 segments in their first moult. Their low diversity and intermediate position between the primitive Anamorphic centipedes and the derived Epimorpha has led to them being likened to the platypus. They represent the survivors of a once diverse clade. Maternal brooding unites Craterostigomomorpha with the Epimorpha into the clade Phylactometria. This trait is thought to be closely linked with the presence of sternal pores, which secrete sticky or noxious secretions, which mainly serve to repel predators and parasites. The presence of these pores on the Devonian *Devonobius* permits its inclusion in this clade, allowing its divergence to be dated to 375 (or more) million years ago.

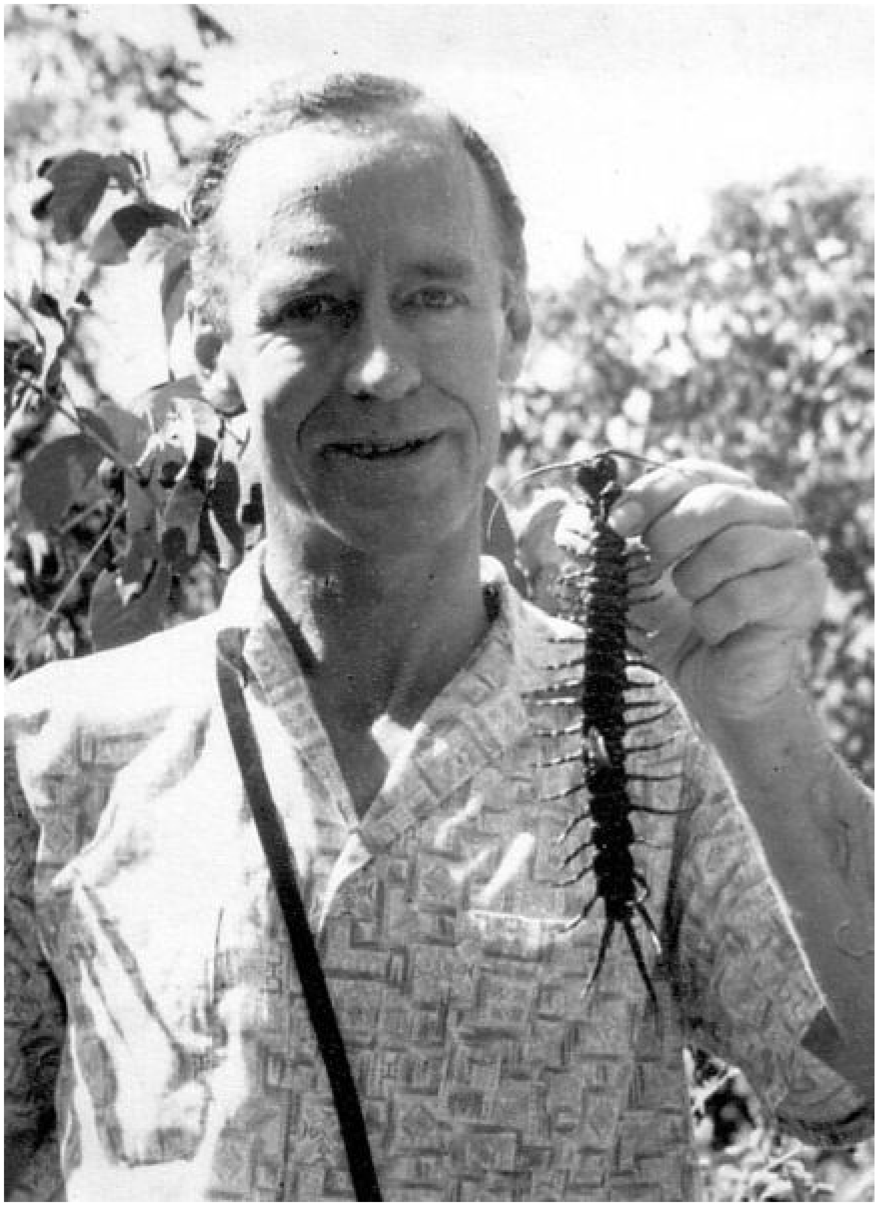
Scolopendromorpha

The **Scolopendromorpha** comprise 21 or more segments with the same number of paired legs. Their antennae have 17 or more segments. Their eyes have at least 4 facets on each side. The order comprises the three families Cryptopidae, Scolopendridae and Scolopocryptopidae.

Geophilomorpha

The Geophilomorpha bear upwards of 27 leg-bearing segments. They are eyeless and blind, and bear spiracles on all leg-bearing segments – in contrast to other groups, who only bear them on their 3rd, 5th, 8th, 10th and 12th segments – a "mid-body break", accompanied by a change in tagmatic shape, occurring roughly at the interchange from odd to even segments. This group, at 1260 spp. the most diverse, also contains the largest and leggiest specimens at 29 or more pairs of legs. They also have 14–segmented antennae. The group includes four families: Mecistocephalidae, Neogeophilidade, Geophilidae and Linotaeniidae.

Selected species



Man holding *Scolopendra gigantea*. Trinidad, 1961

Scientific name	Common name
Alipes grandidieri	Feather tail centipede
Ethmostigmus trigonopodus	Blue ring centipede
Lithobius forficatus	Stone centipede
Pachymerium ferrugineum	Earth centipede
Scolopendra galapagoensis	Galápagos centipede
Scolopendra gigantea	Peruvian giant orange leg centipede
Scolopendra heros	Giant red-headed centipede

Scolopendra morsitans	Red-headed centipede
Scolopendra polymorpha	Giant Sonoran centipede
Scolopendra subspinipes	Vietnamese centipede
Scutigera coleoptrata	House centipede

Chapter 8

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 - List of Anuran families	

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*)

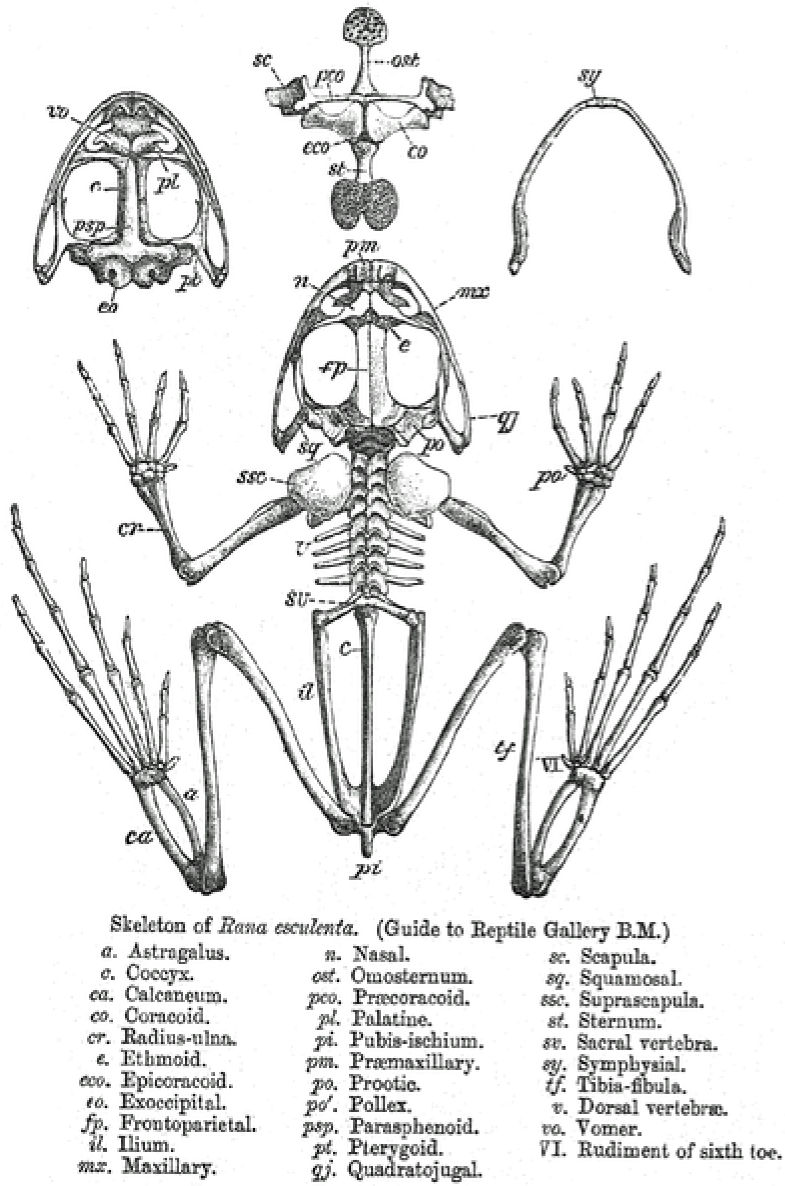
Young American bullfrog found in a stream in New Jersey

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*

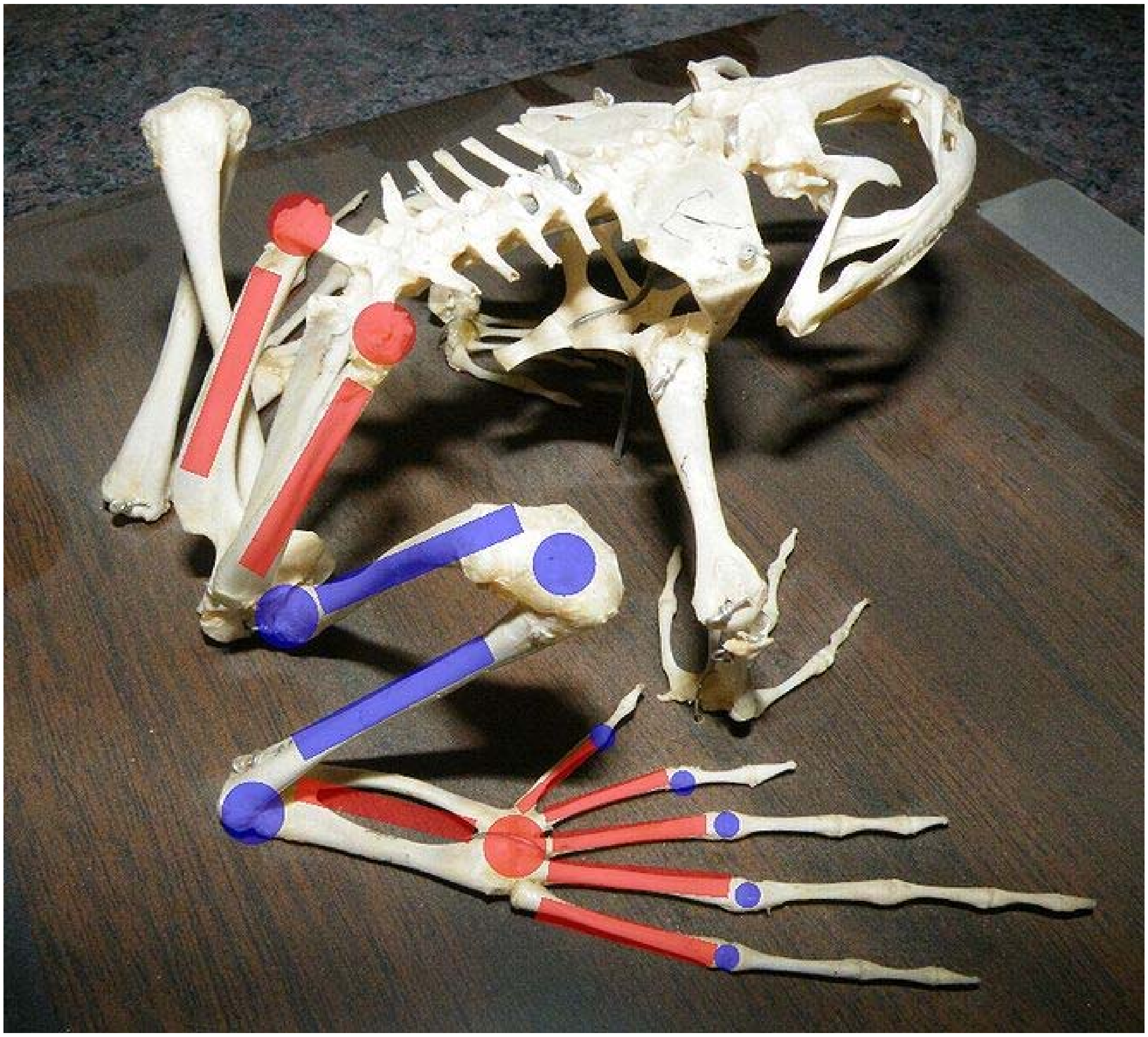
The morphology of frogs is unique among amphibians. Compared with the other two groups of amphibians, (salamanders and caecilians), frogs are unusual because they lack tails as adults and their legs are more suited to jumping than walking. The physiology of frogs is generally like that of other amphibians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

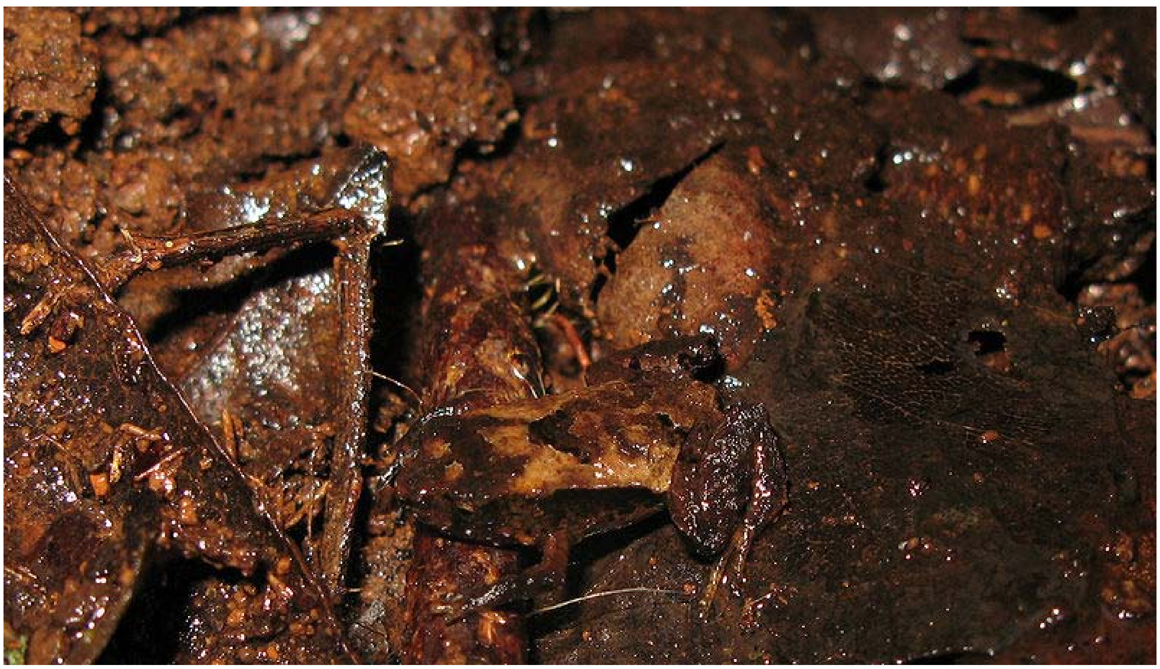
While frog species can use a variety of locomotor modes (running, walking, gliding, swimming, and climbing), more are either proficient at jumping or descended from ancestors who were, with much of the musculo-skeletal morphology modified for this purpose. The tibia, fibula and tarsals have been fused 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 illium 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.

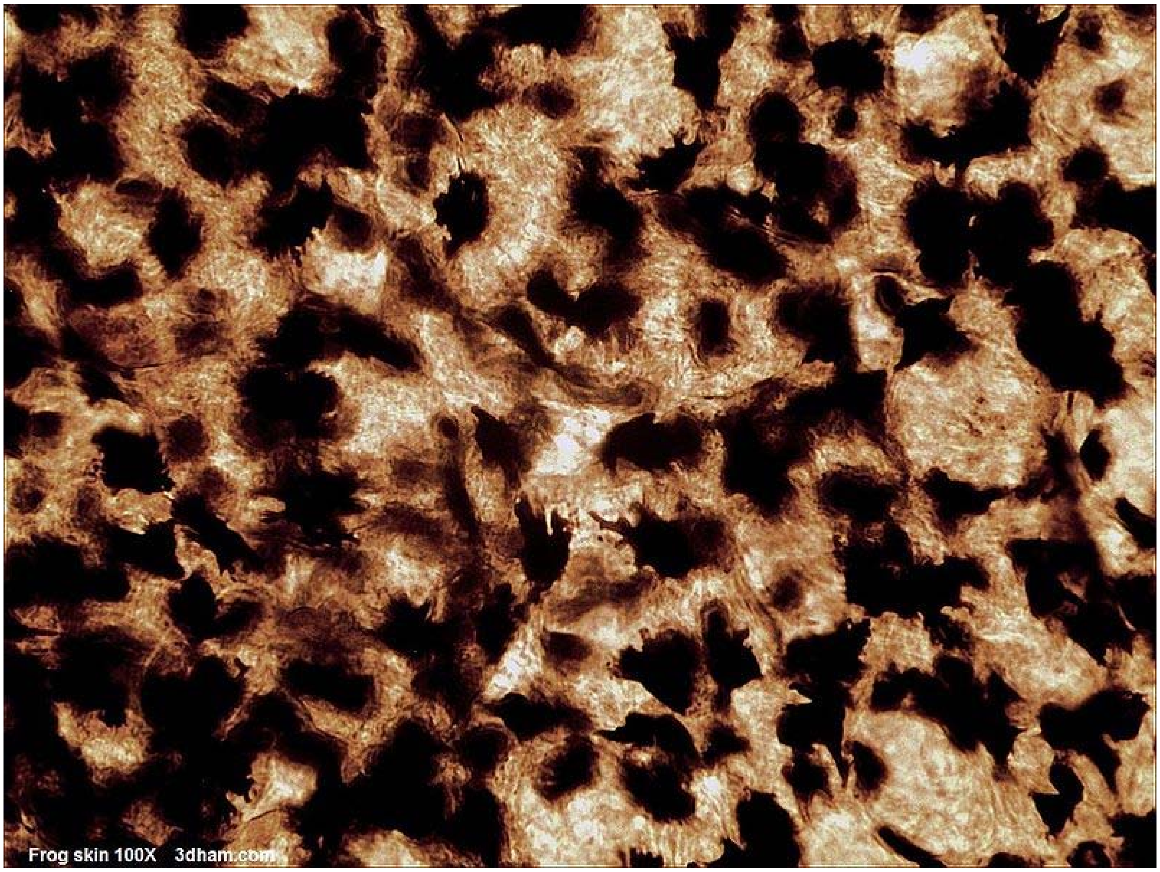
However, in modern frogs, almost all muscles have been modified to contribute to the action of jumping, with only a few small muscles remaining to bring the limb back to the starting position and maintain posture. The muscles have also been greatly enlarged, with the muscles involved in jumping accounting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



Microscopic view of frog skin

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.

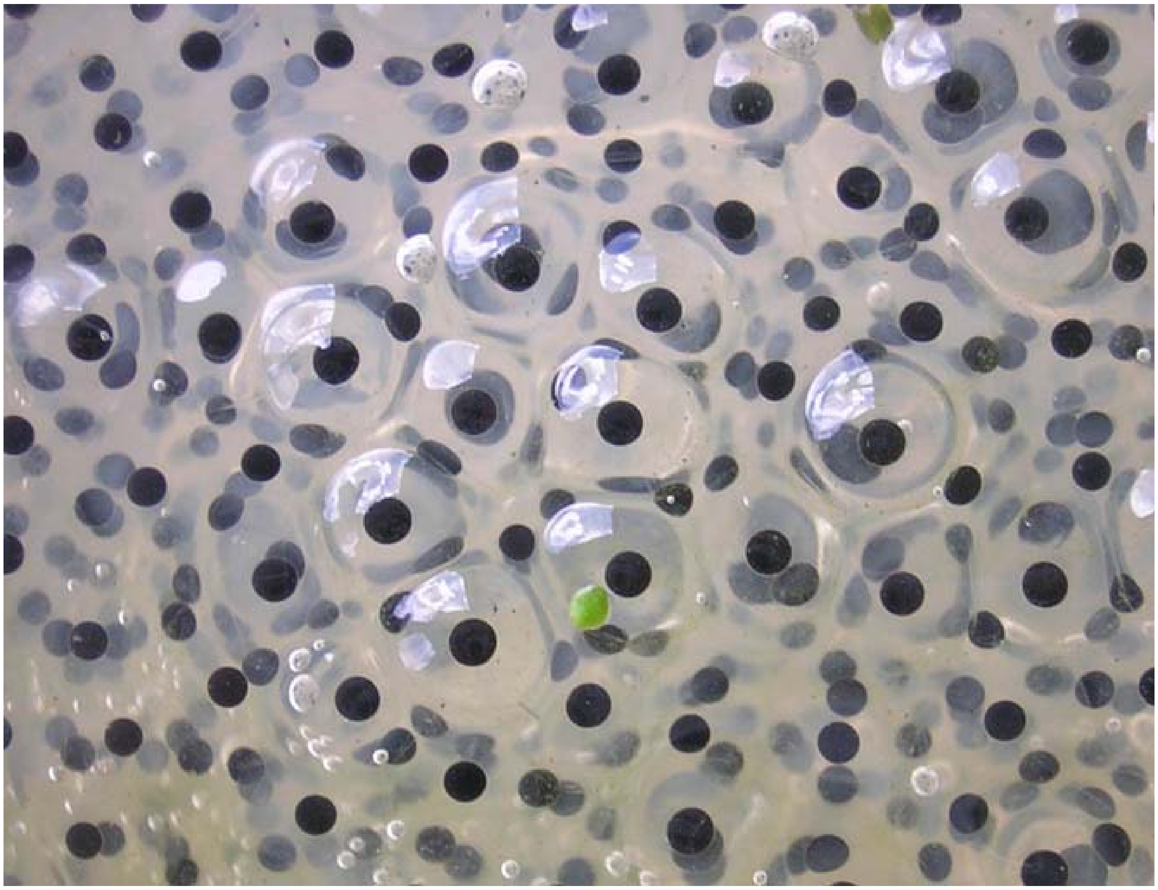
Nervous system

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.

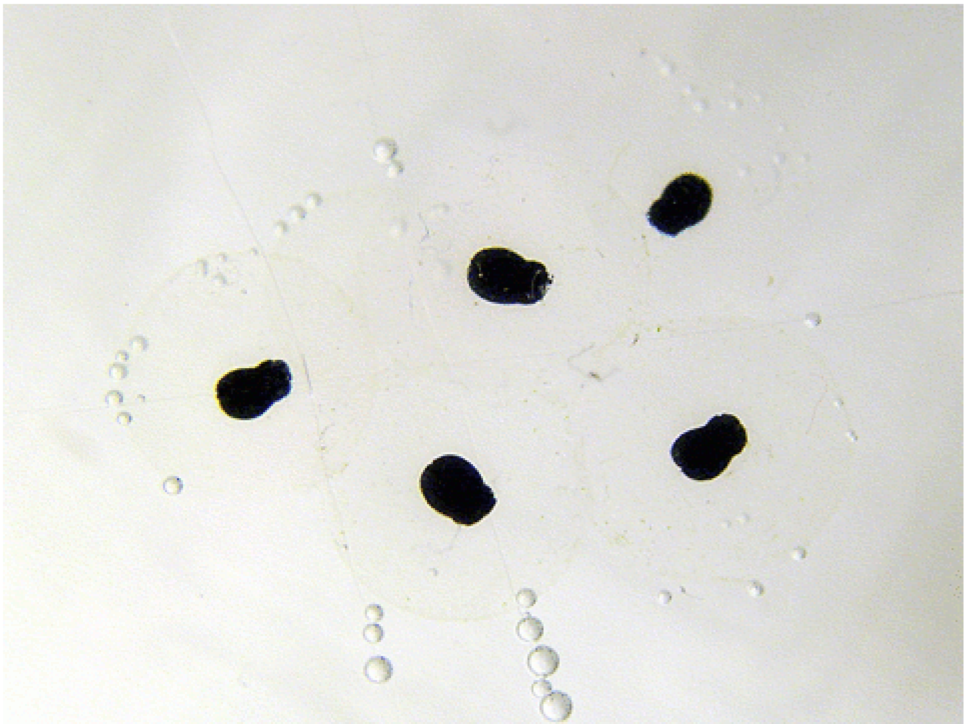
Natural history

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 metamorphisis

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.

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

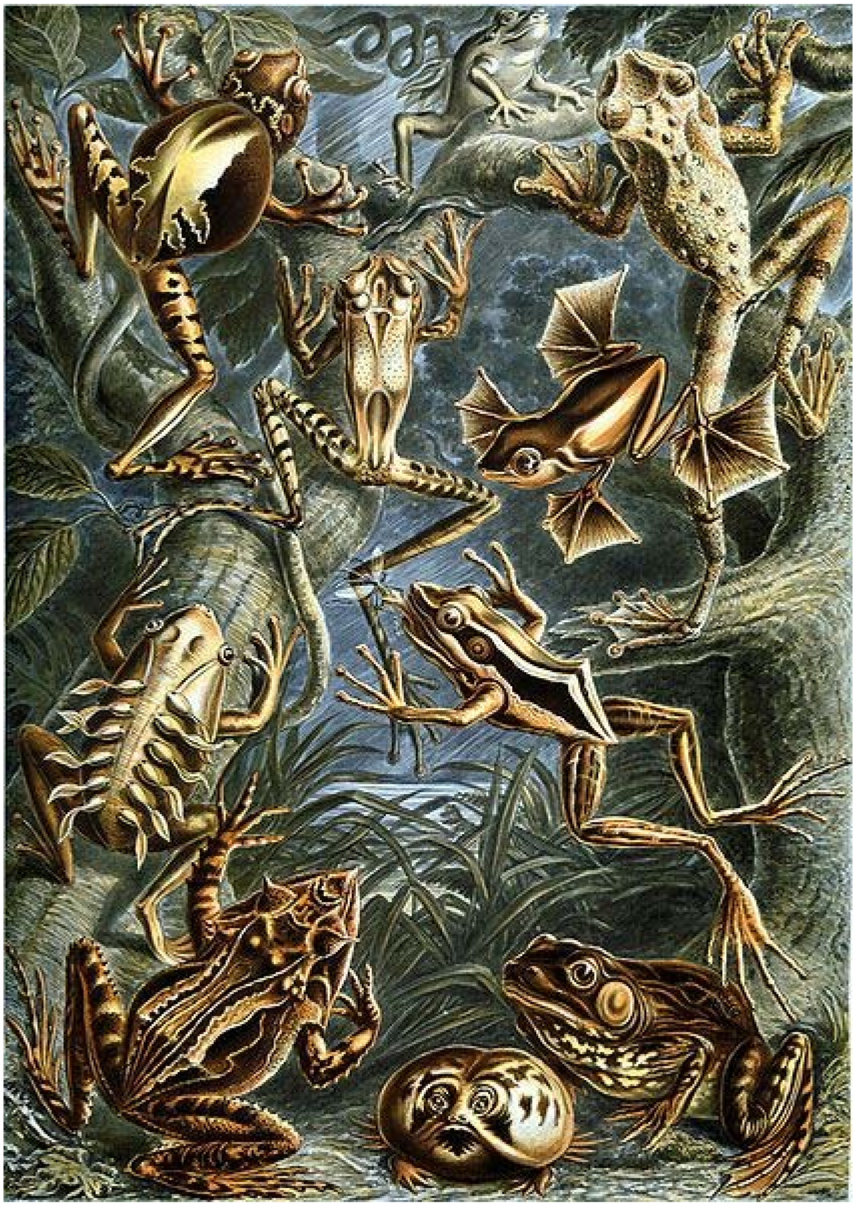
A Male and Female common toad in amplexus. The black strands are eggs released into open water minutes after birth.

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 darwinii*) 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.

Cultural beliefs

Moche Frog 200 A.D. Larco Museum Collection Lima, Peru

Frogs feature prominently in folklore, fairy tales and popular culture. They tend to be portrayed as benign, ugly, clumsy, but with hidden talents. Examples include Michigan J. Frog, *The Frog Prince*, and Kermit the Frog. Michigan J. Frog, featured in the Warner Brothers cartoon *One Froggy Evening*, only performs his singing and dancing routine for his owner. Once another person looks at him, he will return to a frog-like pose. "The Frog Prince" is a fairy tale of a frog who turns into a handsome prince once kissed. Kermit the Frog, on the other hand, is a conscientious and disciplined character of *The Muppet Show* and *Sesame Street*; while openly friendly and greatly talented, he is often portrayed as cringing at the fanciful behavior of more flamboyant characters.

The Moche people of ancient Peru worshipped animals and often depicted frogs in their art. In Panama local legend promised luck to anyone who spotted a golden frog in the wild and some believed that when Panamanian Golden Frogs died, they would turn into a gold talisman, known as a huaca. Today, despite being extinct in the wild, Panamanian Golden Frogs remain an important cultural symbol and can be found on decorative cloth molas made by the Kuna Indians, on T-shirts, as inlaid design on a new overpass in Panama City and even on lottery tickets.

Chapter 9

Tiger

Tiger	

A Bengal Tiger (*P. tigris tigris*) in India's Ranthambhore National Park.

Conservation status	

Endangered (IUCN 3.1)

Scientific classification	
Kingdom:	Animalia
Phylum:	Chordata
Class:	Mammalia
Order:	Carnivora
Family:	Felidae
Genus:	*Panthera*
Species:	***P. tigris***

Binomial name

Panthera tigris
(Linnaeus, 1758)

Subspecies

P. t. tigris
P. t. corbetti
P. t. jacksoni
P. t. sumatrae
P. t. altaica
P. t. amoyensis
†*P. t. virgata*
†*P. t. balica*
†*P. t. sondaica*

Historical distribution of tigers (pale yellow) and 2006 (green).

Synonyms

Felis tigris Linnaeus, 1758

Tigris striatus Severtzov, 1858

Tigris regalis Gray, 1867

The **tiger** (*Panthera tigris*), a member of the Felidae family, is the largest of the four "big cats" in the genus *Panthera*. The tiger is native to much of eastern and southern Asia, and is an apex predator and an obligate carnivore. The larger tiger subspecies are comparable in size to the biggest extinct felids, reaching up to 3.3 metres (11 ft) in total length, weighing up to 300 kilograms (660 pounds), and having canines up to 4 inches long, Aside from their great bulk and power, their most recognisable feature is a pattern of dark vertical stripes that overlays near-white to reddish-orange fur, with lighter underparts. The most numerous tiger subspecies is the Bengal tiger, while the largest is the Siberian tiger.

Tigers have a lifespan of 10–15 years in the wild, but can live longer than 20 years in captivity. They are highly adaptable and range from the Siberian taiga to open grasslands and tropical mangrove swamps.

They are territorial and generally solitary animals, often requiring large contiguous areas of habitat that support their prey demands. This, coupled with the fact that they are indigenous to some of the more densely populated places on earth, has caused significant conflicts with humans. Three of the nine subspecies of modern tiger have gone extinct, and the remaining six are classified as endangered, some critically so. The primary direct causes are habitat destruction, fragmentation, and hunting.

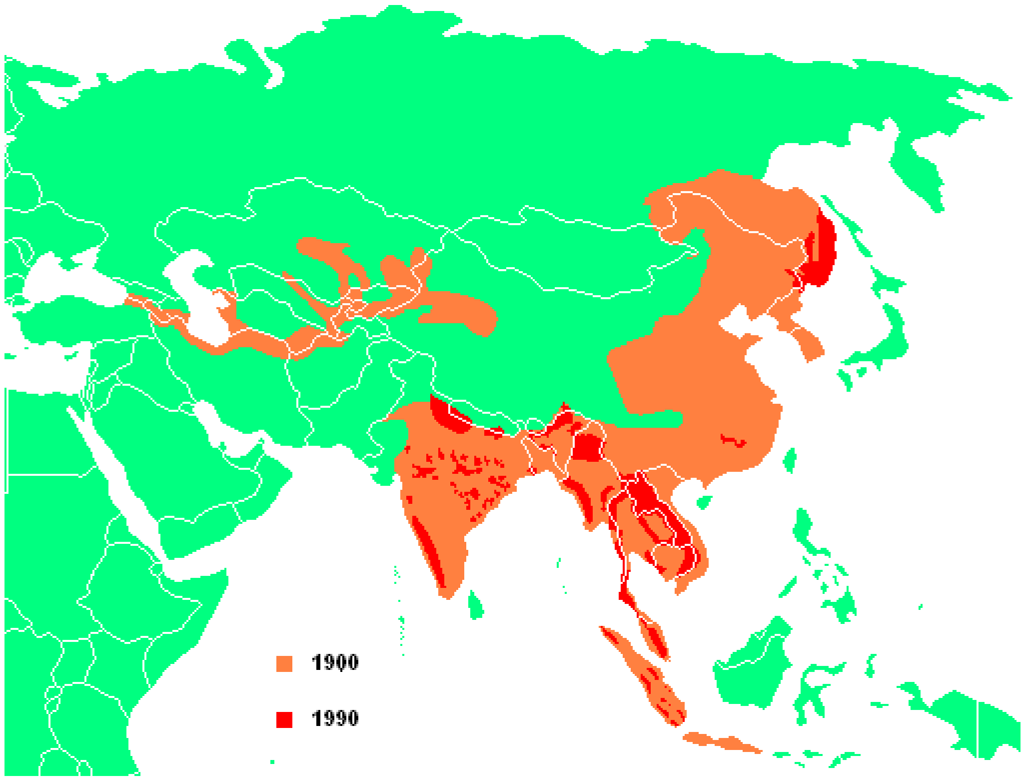
Historically, tigers have existed from Mesopotamia and the Caucasus throughout most of South and East Asia. Today, the range of the species is radically reduced. All surviving species are under formal protection, yet poaching, habitat destruction, and inbreeding depression continue to threaten the tigers.

Tigers are among the most recognisable and popular of the world's charismatic megafauna. They have featured prominently in ancient mythology and folklore, and continue to be depicted in modern films and literature. Tigers appear on many flags and coats of arms, as mascots for sporting teams, and as the national animal of several Asian nations, including India.

Naming and etymology

The word "tiger" is taken from the Greek word "*tigris*", which is possibly derived from a Persian source meaning "arrow", a reference to the animal's speed and also the origin for the name of the Tigris river. In American English, "tigress" was first recorded in 1611. It was one of the many species originally described by Linnaeus in his 18th century work, *Systema Naturae*: he called it *Felis tigris*. The generic component of its scientific designation, *Panthera tigris*, is often presumed to derive from Greek *pan-* ("all") and *theron* ("beast"), but this may be a folk etymology. Although it came into English through the classical languages, *panthera* is probably of Indian origin, meaning "the yellowish animal", or "whitish-yellow".

Tigers rarely form groups (see below), but collective nouns sometimes used when they do are "streak".



Range of the tiger including the western part 1900 and 1990

Range and habitat

In the past, tigers were found throughout Asia, from the Caucasus and the Caspian Sea to Siberia and Indonesia. Today the range of the tiger is only 7% of what it used to be. Furthermore, within the past decade alone, the estimated area known to be occupied by tigers has declined by 41%.

During the 19th century, the tiger completely vanished from western Asia and became restricted to isolated pockets in the remaining parts of their range. Today, their range is fragmented, and certain parts degraded, and extends from India in the west to China and Southeast Asia in the east. The northern limit is close to the Amur River in south eastern Siberia. The only large island inhabited by tigers today is Sumatra. Tigers vanished from Java and Bali during the 20th century. In Borneo they are known only from fossil remains.

Tiger habitats will usually include sufficient cover, proximity to water, and an abundance of prey. Bengal Tigers live in many types of forests, including wet; evergreen; the semi-evergreen of Assam and eastern Bengal; the mangrove forest of the Ganges Delta; the deciduous forest of Nepal, and the thorn forests of the Western Ghats. Compared to the lion, the tiger prefers denser vegetation, for which its camouflage colouring is ideally suited, and where a single predator is not at a disadvantage compared with the multiple felines in a pride.

Among the big cats, only the tiger and jaguar are strong swimmers; tigers are often found bathing in ponds, lakes, and rivers. During the extreme heat of the day, they often cool off in pools. Tigers are excellent swimmers, and are able to carry prey through the water.

Physical characteristics, taxonomy and evolution

The oldest remains of a tiger-like cat, called *Panthera palaeosinensis*, have been found in China and Java. This species lived about 2 million years ago, at the beginning of the Pleistocene, and was smaller than a modern tiger. The earliest fossils of true tigers are known from Java, and are between 1.6 and 1.8 million years old. Distinct fossils from the early and middle Pleistocene were also discovered in deposits from China, and Sumatra. A subspecies called the **Trinil tiger** (*Panthera tigris trinilensis*) lived about 1.2 million years ago and is known from fossils found at Trinil in Java.

Tigers first reached India and northern Asia in the late Pleistocene, reaching eastern Beringia (but not the American Continent), Japan, and Sakhalin. Fossils found in Japan indicate that the local tigers were, like the surviving island subspecies, smaller than the mainland forms. This may be due to the phenomenon in which body size is related to environmental space, or perhaps the availability of prey. Until the Holocene, tigers also lived in Borneo, as well as on the island of Palawan in the Philippines.

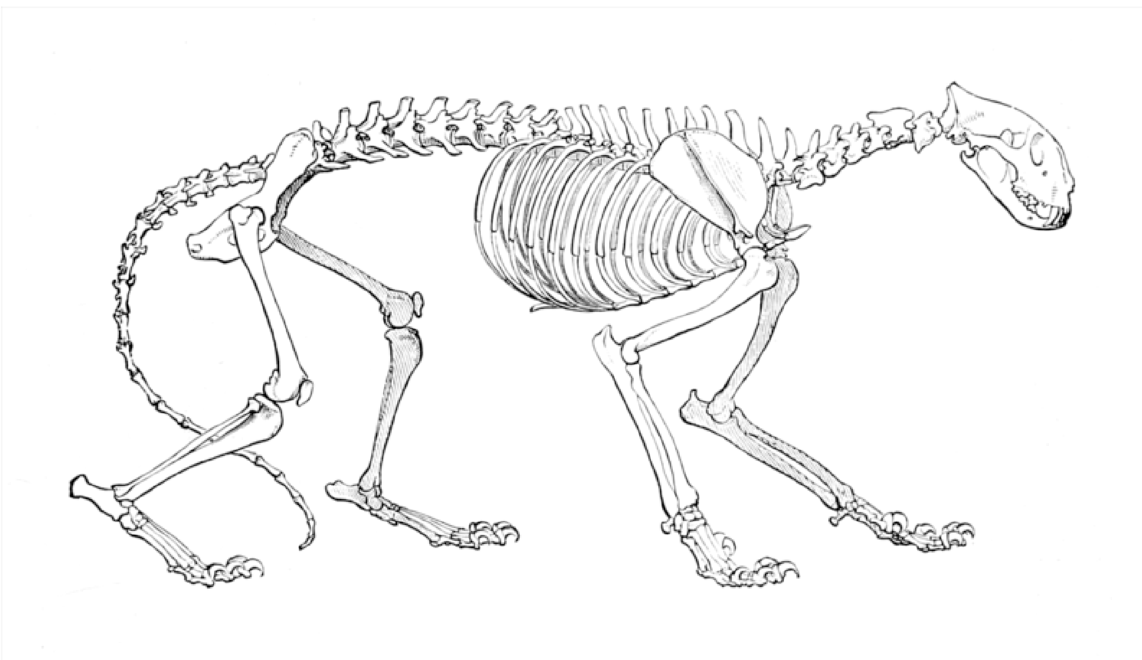
Physical characteristics

Siberian tiger

Tigers typically have rusty-reddish to brown-rusty coats, a whitish medial and ventral area, a white "fringe" that surrounds the face, and stripes that vary from brown or gray to pure black. The form and density of stripes differs between subspecies (as well as the ground coloration of the fur; for instance, Siberian tigers are usually paler than other tiger subspecies), but most tigers have over 100 stripes.

The pattern of stripes is unique to each animal, these unique markings can be used by researchers to identify individuals (both in the wild and captivity), much in the same way that fingerprints are used to identify humans. It seems likely that the function of stripes is camouflage, serving to help tigers conceal themselves amongst the dappled shadows and long grass of their environment as they stalk their prey. The stripe pattern is also found on the skin of the tiger. If a tiger were to be shaved, its distinctive camouflage pattern would be preserved.

Like other big cats, tigers have a white spot on the backs of their ears. These spots, called ocelli, serve a social function, by communicating the animal's mental state to conspecifics in the gloom of dense forest or in tall grass.



Skeleton

Tigers have the additional distinction of being the heaviest cats found in the wild. They also have powerfully built legs and shoulders, with the result that they, like lions, have the ability to pull down prey substantially heavier than themselves. However, the subspecies differ markedly in size, tending to increase proportionally with latitude, as predicted by Bergmann's Rule.

Large male Siberian Tigers (*Panthera tigris altaica*) can reach a total length of 3.5 m "over curves" (3.3 m. "between pegs") and a weight of 306 kilograms,. This is considerably larger than the sizes reached by island-dwelling tigers such as the Sumatran, the smallest living subspecies, with a body weight of only 75–140 kg.

Tigresses are smaller than the males in each subspecies, although the size difference between male and female tigers tends to be more pronounced in the larger subspecies of tiger, with males weighing up to 1.7 times more than the females. In addition, male tigers have wider forepaw pads than females. Biologists use this difference to determine gender based on tiger tracks. The skull of the tiger is very similar to that of the lion, though the frontal region is usually not as depressed or flattened, with a slightly longer postorbital region. The skull of a lion has broader nasal openings. However, due to the amount of skull variation in the two species, usually, only the structure of the lower jaw can be used as a reliable indicator of species.

Tigers have round pupils and yellow irises (except for the blue eyes of white tigers). Due to a retinal adaptation that reflects light back to the retina, the night vision of tigers is six times better than that of humans.

Subspecies

A Bengal tigress with her cub.

There are nine recent subspecies of tiger, three of which are extinct. Their historical range (severely diminished today) ran through Bangladesh, Siberia, Iran, Afghanistan, India, China, and southeast Asia, including some Indonesian islands. The surviving subspecies, in descending order of wild population, are:

- The **Bengal tiger** or the **Royal Bengal tiger** (*Panthera tigris tigris*) is the most common subspecies of tiger and is found primarily in India and Bangladesh. It lives in varied habitats: grasslands, subtropical and tropical rainforests, scrub forests, wet and dry deciduous forests, and mangroves. Males in the wild usually weigh 205 to 227 kg (450 to 500 lb), while the average female will weigh about 141 kg. However, the northern Indian and the Nepalese Bengal tigers are somewhat bulkier than those found in the south of the Indian Subcontinent, with males averaging around 235 kilograms (520 lb). While conservationists already believed the population to be below 2,000, the most recent audit by the Indian Government's National Tiger Conservation Authority has estimated the number at just 1,411 wild tigers (1165–1657 allowing for statistical error), a drop of 60% in the past decade. Since 1972, there has been a massive wildlife conservation project, known as Project Tiger, to protect the Bengal tiger. Despite increased efforts by Indian officials, poaching remains rampant and at least one Tiger Reserve (Sariska Tiger Reserve) has lost its entire tiger population to poaching. The passing of the Forest Rights Act by the Indian government in 2006 has worsened the situation as evidence has shown that human habitats and tigers cannot co-exist and has pushed the Indian tiger on the brink of extinction.

Indochinese tiger

- The **Indochinese Tiger** (*Panthera tigris corbetti*), also called *Corbett's* tiger, is found in Cambodia, China, Laos, Burma, Thailand, and Vietnam. These tigers are smaller and darker than Bengal tigers: Males weigh from 150–190 kg (330–420 lb) while females are smaller at 110–140 kg (240–310 lb). Their preferred habitat is forests in mountainous or hilly regions. Estimates of the Indochinese tiger population vary between 1,200 to 1,800, with only several hundred left in the wild. All existing populations are at extreme risk from poaching, prey depletion as a result of poaching of primary prey species such as deer and wild pigs, habitat fragmentation and inbreeding. In Vietnam, almost three-quarters of the tigers killed provide stock for Chinese pharmacies.

Malayan tiger

- The **Malayan Tiger** (*Panthera tigris jacksoni*), exclusively found in the southern part of the Malay Peninsula, was not considered a subspecies in its own right until 2004. The new classification came about after a study by Luo et al. from the Laboratory of Genomic Diversity Study, part of the National Cancer Institute of the United States. Recent counts showed there are 600–800 tigers in the wild, making it the third largest tiger population, behind the Bengal tiger and the Indochinese tiger. The Malayan tiger is the smallest of the mainland tiger subspecies, and the second smallest living subspecies, with males averaging about 120 kg and females about 100 kg in weight. The Malayan tiger is a national icon in Malaysia, appearing on its coat of arms and in logos of Malaysian institutions, such as Maybank.

Sumatran tiger

- The **Sumatran Tiger** (*Panthera tigris sumatrae*) is found only on the Indonesian island of Sumatra, and is critically endangered. It is the smallest of all living tiger subspecies, with adult males weighing between 100–140 kg (220–310 lb) and females 75–110 kg (170–240 lb). Their small size is an adaptation to the thick, dense forests of the island of Sumatra where they reside, as well as the smaller-sized prey. The wild population is estimated at between 400 and 500, seen chiefly in the island's national parks. Recent genetic testing has revealed the presence of unique genetic markers, indicating that it may develop into a separate species, if it does not go extinct. This has led to suggestions that Sumatran tigers should have greater priority for conservation than any other subspecies. While habitat destruction is the main threat to existing tiger population (logging continues even in the supposedly protected national parks), 66 tigers were recorded as being shot and killed between 1998 and 2000, or nearly 20% of the total population.

Siberian tiger

- The **Siberian tiger** (*Panthera tigris altaica*), also known as the *Amur*, *Manchurian*, *Altaic*, *Korean* or *North China* tiger, which is the most northernmost subspecies, is confined to the Amur-Ussuri region of Primorsky Krai and Khabarovsk Krai in far eastern Siberia, where it is now protected. The largest subspecies of tiger, it has a head and body length of 160–180 cm for females and 190–230+ cm for males, plus a tail of about 60–110 cm long (about 270–330 cm in total length) and an average weight of around 227 kilograms (500 lb) for males, the Amur tiger is also noted for its thick coat, distinguished by a paler golden hue and fewer stripes. The heaviest wild Siberian tiger on record weighed in at 384 kg, but according to Mazak these giants are not confirmed via reliable references. Even so, a six-month old Siberian tiger can be as big as a fully grown leopard. The last two censuses (1996 and 2005) found 450–500 Amur tigers within their single, and more or less continuous, range making it one of the largest undivided tiger populations in the world. Genetic research in 2009 demonstrated that the Siberian tiger, and the western "Caspian tiger" (once thought to have been a separate subspecies that became extinct in the wild in the late 1950s) are actually the same subspecies, since the separation of the two populations may have occurred as recently as the past century due to human intervention.

South China tiger

- The **South China Tiger** (*Panthera tigris amoyensis*), also known as the *Amoy* or *Xiamen* tiger, is the most critically endangered subspecies of tiger and is listed as one of the 10 most endangered animals in the world. One of the smaller tiger subspecies, the length of the South China tiger ranges from 2.2–2.6 m (87–100 in) for both males and females. Males weigh between 127 and 177 kg (280 and 390 lb) while females weigh between 100 and 118 kg (220 and 260 lb). From 1983 to 2007, no South China tigers were sighted. In 2007 a farmer spotted a tiger and handed in photographs to the authorities as proof. The photographs in question, however, were later exposed as fake, copied from a Chinese calendar and digitally altered, and the "sighting" turned into a massive scandal.
  In 1977, the Chinese government passed a law banning the killing of wild tigers, but this may have been too late to save the subspecies, since it is possibly already extinct in the wild. There are currently 59 known captive South China tigers, all within China, but these are known to be descended from only six animals. Thus, the genetic diversity required to maintain the subspecies may no longer exist. Currently, there are breeding efforts to reintroduce these tigers to the wild.

Extinct subspecies

A hunted down Balinese tiger

- The **Bali Tiger** (*Panthera tigris balica*) was limited to the island of Bali. They were the smallest of all tiger subspecies, with a weight of 90–100 kg in males and 65–80 kg in females. These tigers were hunted to extinction—the last Balinese tiger is thought to have been killed at Sumbar Kima, West Bali on 27 September 1937; this was an adult female. No Balinese tiger was ever held in captivity. The tiger still plays an important role in Balinese Hinduism.

A photograph of a Javan tiger.

- The **Javan tiger** (*Panthera tigris sondaica*) was limited to the Indonesian island of Java. It now seems likely that this subspecies became extinct in the 1980s, as a result of hunting and habitat destruction, but the extinction of this subspecies was extremely probable from the 1950s onwards (when it is thought that fewer than 25 tigers remained in the wild). The last confirmed specimen was sighted in 1979, but there were a few reported sightings during the 1990s. With a weight of 100–141 kg for males and 75–115 kg for females, the Javan tiger was one of the smaller subspecies, approximately the same size as the Sumatran tiger.

A captive Caspian Tiger, Berlin Zoo 1899

- The **Caspian Tiger** (formerly *Panthera tigris virgata)*, also known as the **Persian tiger** or **Turanian tiger** was the westernmost population of Siberian tiger, found in Iran, Iraq, Afghanistan, Turkey, Mongolia, Kazakhstan, the Caucasus, Tajikistan, Turkmenistan, and Uzbekistan until it apparently became extinct in the late 1950s, though there have been several alleged more recent sightings of the tiger. Though originally thought to have been a distinct subspecies, genetic research in 2009 suggest that the animal was largely identical to the Siberian tiger.

Hybrids

Hybridisation among the big cats, including the tiger, was first conceptualised in the 19th century, when zoos were particularly interested in the pursuit of finding oddities to display for financial gain. Lions have been known to breed with tigers (most often the Amur and Bengal subspecies) to create hybrids called ligers and tigons. Such hybrids were once commonly bred in zoos, but this is now discouraged due to the emphasis on conserving species and subspecies. Hybrids are still bred in private menageries and in zoos in China.

The liger is a cross between a male lion and a tigress. Because the lion sire passes on a growth-promoting gene, but the corresponding growth-inhibiting gene from the female tiger is absent, ligers grow far larger than either parent. They share physical and behavioural qualities of both parent species (spots and stripes on a sandy background). Male ligers are sterile, but female ligers are often fertile. Males have about a 50% chance of having a mane, but, even if they do, their manes will be only around half the size of that of a pure lion. Ligers are typically between 10 to 12 feet in length, and can be between 800 and 1,000 pounds or more.

The less common tigon is a cross between the lioness and the male tiger.

Colour variations

White tigers

A Bengal white tiger in Bannerghatta National Park in Bangalore

A pair of white tigers at the Singapore Zoo.

There is a well-known mutation that produces the white tiger, technically known as *chinchilla albinistic*, an animal which is rare in the wild, but widely bred in zoos due to its popularity. Breeding of white tigers will often lead to inbreeding (as the trait is recessive). Many initiatives have taken place in white and orange tiger mating in an attempt to remedy the issue, often mixing subspecies in the process. Such inbreeding has led to white tigers having a greater likelihood of being born with physical defects, such as cleft palates and scoliosis (curvature of the spine). Furthermore, white tigers are prone to having crossed eyes (a condition known as strabismus). Even apparently healthy white tigers generally do not live as long as their orange counterparts. Recordings of white tigers were first made in the early 19th century. They can only occur when both parents carry the rare gene found in white tigers; this gene has been calculated to occur in only one in every 10,000 births. The white tiger is not a separate sub-species, but only a colour variation; since the only white tigers that have been observed in the wild have been Bengal tigers (and all white tigers in captivity are at least part Bengal), it is commonly thought that the recessive gene that causes the white colouring is probably carried only by Bengal tigers, although the reasons for this are not known. Nor are they in any way more endangered than tigers are generally, this being a common misconception. Another misconception is that white tigers are albinos, despite the fact that pigment is evident in the white tiger's stripes. They are distinct not only because of their white hue; they also have blue eyes.

Golden tabby tigers

A rare golden tabby/strawberry tiger at the Buffalo Zoo.

In addition, another recessive gene may create a very unusual "golden tabby" colour variation, sometimes known as "strawberry." Golden tabby tigers have light gold fur, pale legs and faint orange stripes. Their fur tends to be much thicker than normal. There are extremely few golden tabby tigers in captivity, around 30 in all. Like white tigers, strawberry tigers are invariably at least part Bengal. Some golden tabby tigers, called heterozygous tigers, carry the white tiger gene, and when two such tigers are mated, can produce some stripeless white offspring. Both white and golden tabby tigers tend to be larger than average Bengal tigers.

Other colour variations

There are also unconfirmed reports of a "blue" or slate-coloured tiger, the Maltese Tiger, and largely or totally black tigers, and these are assumed, if real, to be intermittent mutations rather than distinct species.

Biology and behaviour

Territorial behaviour

Tigers are essentially solitary and territorial animals. The size of a tiger's home range mainly depends on prey abundance, and, in the case of male tigers, on access to females. A tigress may have a territory of 20 square kilometres, while the territories of males are much larger, covering 60–100 km^2. The range of a male tends to overlap those of several females.

Tigers for the most part are solitary animals

The relationships between individuals can be quite complex, and it appears that there is no set "rule" that tigers follow with regards to territorial rights and infringing territories.

For instance, although for the most part tigers avoid each other, both male and female tigers have been documented sharing kills. George Schaller observed a male tiger share a kill with two females and four cubs. Females are often reluctant to let males near their cubs, but Schaller saw that these females made no effort to protect or keep their cubs from the male, suggesting that the male might have been the father of the cubs. In contrast to male lions, male tigers will allow the females and cubs to feed on the kill first. Furthermore, tigers seem to behave relatively amicably when sharing kills, in contrast to lions, which tend to squabble and fight. Unrelated tigers have also been observed feeding on prey together. The following quotation is from Stephen Mills' book *Tiger*, as he describes an event witnessed by Valmik Thapar and Fateh Singh Rathore in Ranthambhore:

A dominant tigress they called Padmini killed a 250 kg (550-lb) male nilgai – a very large antelope. They found her at the kill just after dawn with her three 14-month-old cubs and they watched uninterrupted for the next ten hours. During this period the family was joined by two adult females and one adult male – all offspring from Padmini's previous litters and by two unrelated tigers, one female the other unidentified. By three o'clock there were no fewer than nine tigers round the kill.

When young female tigers first establish a territory, they tend to do so fairly close to their mother's area. The overlap between the female and her mother's territory tends to wane with increasing time. Males, however, wander further than their female counterparts, and set out at a younger age to mark out their own area. A young male will acquire territory either by seeking out a range devoid of other male tigers, or by living as a transient in another male's territory until he is old and strong enough to challenge the resident male. The highest mortality rate (30–35% per year) amongst adult tigers occurs for young male tigers who have just left their natal area, seeking out territories of their own.

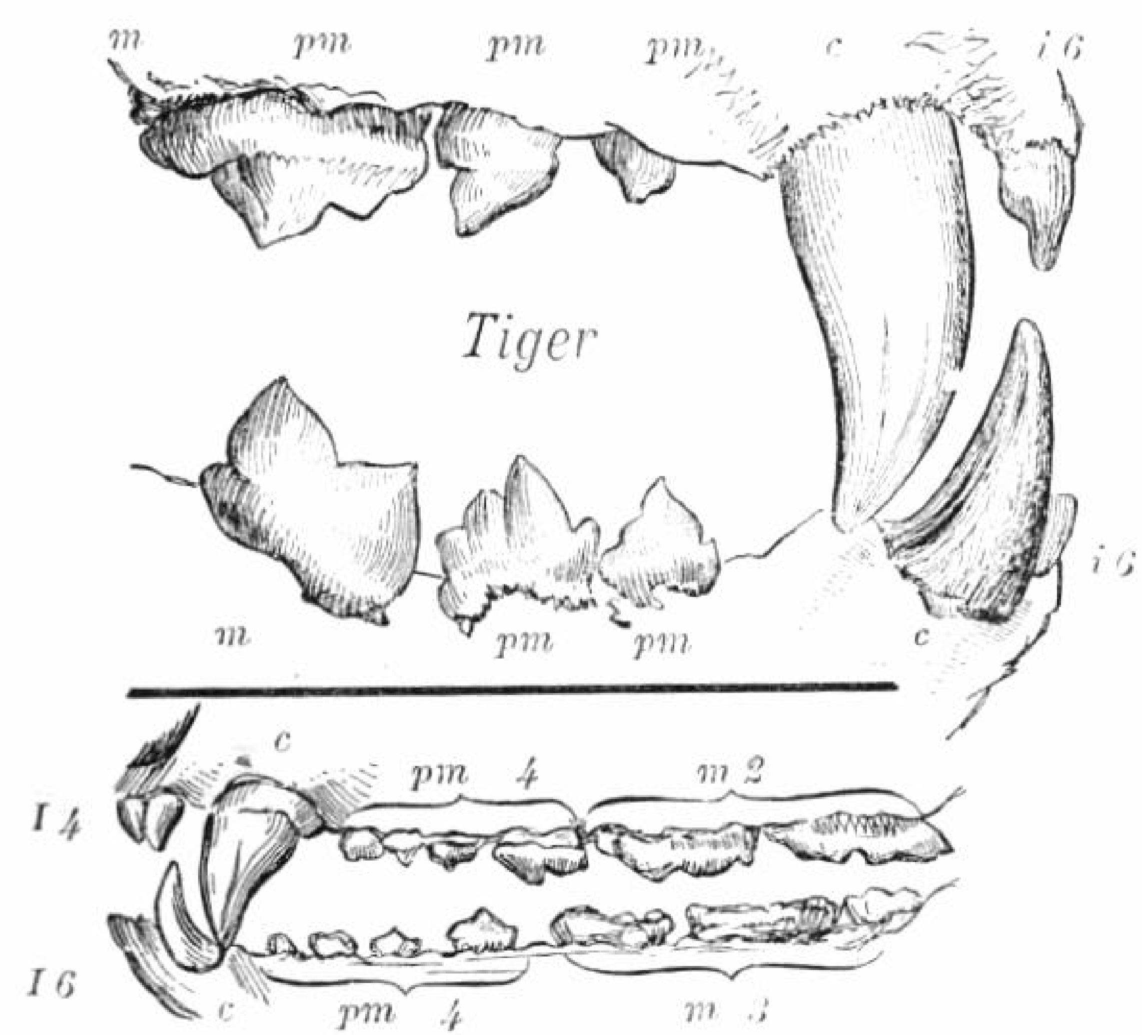
Two male Bengal tiger siblings play with each other in the Pilibhit Tiger Reserve, India.

Male tigers are generally more intolerant of other males within their territory than females are of other females. For the most part, however, territorial disputes are usually solved by displays of intimidation, rather than outright aggression. Several such incidents have been observed, in which the subordinate tiger yielded defeat by rolling onto its back, showing its belly in a submissive posture. Once dominance has been established, a male may actually tolerate a subordinate within his range, as long as they do not live in too close quarters. The most violent disputes tend to occur between two males when a female is in oestrus, and may result in the death of one of the males, although this is a rare occurrence.

To identify his territory, the male marks trees by spraying of urine and anal gland secretions, as well as marking trails with scat. Males show a grimacing face, called the Flehmen response, when identifying a female's reproductive condition by sniffing their urine markings. Like the other *Panthera* cats, tigers can roar. Tigers will roar for both aggressive and non-aggressive reasons. Other tiger vocal communications include moans, hisses, growls and chuffs.

Tigers have been studied in the wild using a variety of techniques. The populations of tigers were estimated in the past using plaster casts of their pugmarks. This method was found faulty and attempts were made to use camera trapping instead. Newer techniques based on DNA from their scat are also being evaluated. Radio collaring has also been a popular approach to tracking them for study in the wild.

Hunting and diet



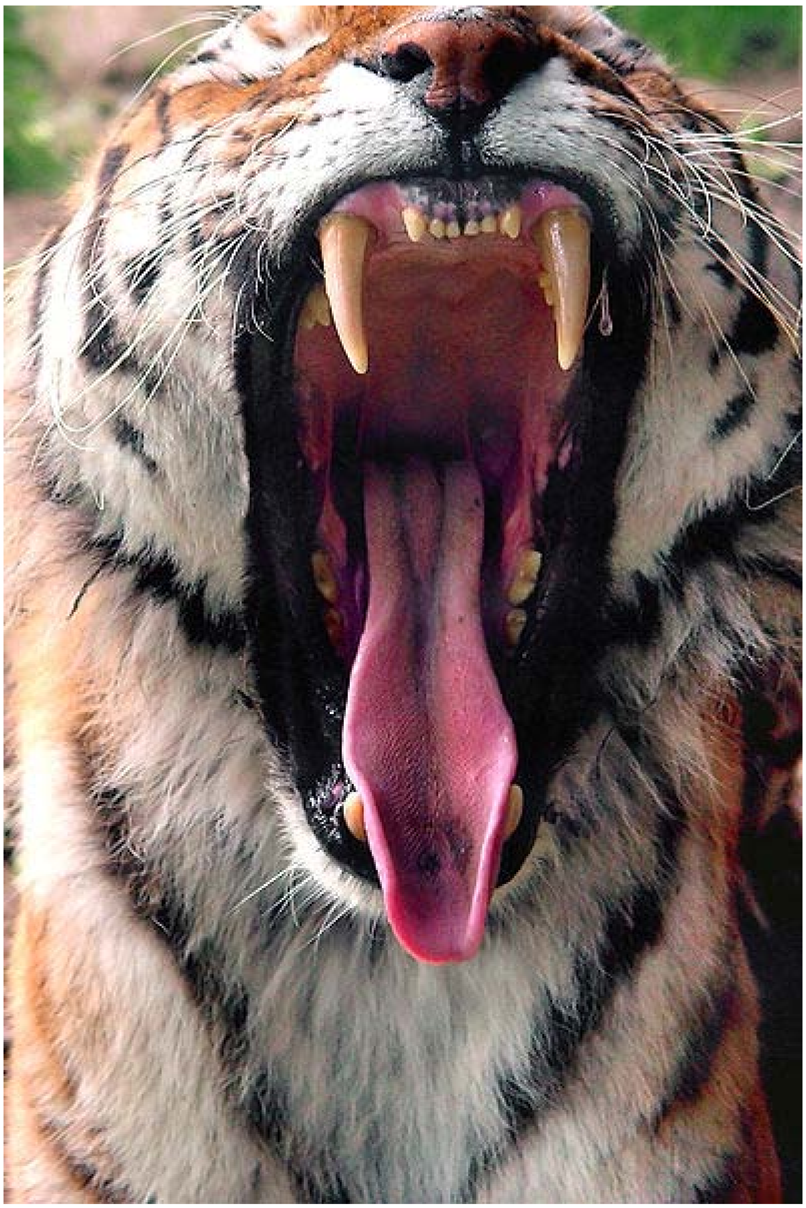
Tiger dentition(above), compared with that of an Asian black bear (below). The large canines are used to make the killing bite, but they tear meat when feeding using the carnassial teeth.

In the wild, tigers mostly feed on larger and medium sized animals. Sambar, gaur, chital, barasingha, wild boar, nilgai and both water buffalo and domestic buffalo are the tiger's favoured prey in India. Sometimes, they also prey on leopards, pythons, sloth bears and crocodiles. In Siberia the main prey species are manchurian wapiti, wild boar, sika deer, moose, roe deer, and musk deer. In Sumatra, sambar, muntjac, wild boar, and malayan tapir are preyed on. In the former Caspian tiger's range, prey included saiga antelope, camels, caucasian wisent, yak, and wild horses. Like many predators, they are opportunistic and will eat much smaller prey, such as monkeys, peafowls, hares, and fish.

Adult elephants are too large to serve as common prey, but conflicts between tigers and elephants do sometimes take place. A case where a tiger killed an adult Indian Rhinoceros has been observed. Young elephant and rhino calves are occasionally taken.

Tigers also sometimes prey on domestic animals such as dogs, cows, horses, and donkeys. These individuals are termed cattle-lifters or cattle-killers in contrast to typical game-killers.

Old tigers, or those wounded and rendered incapable of catching their natural prey, have turned into man-eaters; this pattern has recurred frequently across India. An exceptional case is that of the Sundarbans, where healthy tigers prey upon fishermen and villagers in search of forest produce, humans thereby forming a minor part of the tiger's diet. Tigers will occasionally eat vegetation for dietary fiber, the fruit of the Slow Match Tree being favoured.



Tigers' extremely strong jaws and sharp teeth make them superb predators.

Tigers are thought to be nocturnal predators, hunting at night. However, in areas where humans are absent, they have been observed via remote controlled, hidden cameras hunting during the daylight hours. They generally hunt alone and ambush their prey as most other cats do, overpowering them from any angle, using their body size and strength to knock large prey off balance. Even with their great masses, tigers can reach speeds of about 49–65 kilometres per hour (35–40 miles per hour), although they can only do so in short bursts, since they have relatively little stamina; consequently, tigers must be relatively close to their prey before they break their cover. Tigers have great leaping ability; horizontal leaps of up to 10 metres have been reported, although leaps of around half this amount are more typical. However, only one in twenty hunts ends in a successful kill.

When hunting large prey, tigers prefer to bite the throat and use their forelimbs to hold onto the prey, bringing it to the ground. The tiger remains latched onto the neck until its prey dies of strangulation. By this method, gaurs and water buffalos weighing over a ton have been killed by tigers weighing about a sixth as much. With small prey, the tiger bites the nape, often breaking the spinal cord, piercing the windpipe, or severing the jugular vein or common carotid artery. Though rarely observed, some tigers have been recorded to kill prey by swiping with their paws, which are powerful enough to smash the skulls of domestic cattle, and break the backs of sloth bears.

During the 1980s, a tiger named "Genghis" in Ranthambhore National Park was observed frequently hunting prey through deep lake water, a pattern of behaviour that had not been previously witnessed in over 200 years of observations. Moreover, he appeared to be extraordinarily successful for a tiger, with as many as 20% of hunts ending in a kill.

Reproduction

A tigress with her cubs in the Kanha Tiger Reserve, India.

Mating can occur all year round, but is generally more common between November and April. A female is only receptive for a few days and mating is frequent during that time period. A pair will copulate frequently and noisily, like other cats. The gestation period is 16 weeks. The litter size usually consists of around 3–4 cubs of about 1 kilogram (2.2 lb) each, which are born blind and helpless. The females rear them alone, sheltering them in dens such as thickets and rocky crevices. The father of the cubs generally takes no part in rearing them. Unrelated wandering male tigers may even kill cubs to make the female receptive, since the tigress may give birth to another litter within 5 months if the cubs of the previous litter are lost. The mortality rate of tiger cubs is fairly high – approximately half do not survive to be more than two years old.

There is generally a dominant cub in each litter, which tends to be male but may be of either sex. This cub generally dominates its siblings during play and tends to be more active, leaving its mother earlier than usual. At 8 weeks, the cubs are ready to follow their mother out of the den, although they do not travel with her as she roams her territory until they are older. The cubs become independent around 18 months of age, but it is not until they are around 2–2½ years old that they leave their mother. Females reach sexual maturity at 3–4 years, whereas males reach sexual maturity at 4–5 years.

Over the course of her life, a female tiger will give birth to an approximately equal number of male and female cubs. Tigers breed well in captivity, and the captive population in the United States may rival the wild population of the world.

Interspecific predatory relationships

Tiger hunted by wild dogs (dholes) as illustrated in *Samuel Howett & Edward Orme, Hand Coloured, Aquatint Engravings*, Published London 1807.

Tigers may kill such formidable predators as leopards, pythons and even crocodiles on occasion, although predators typically avoid one another. When seized by a crocodile, a tiger will strike at the reptile's eyes with its paws. Eighteenth century Physician Oliver Goldsmith described the frequent conflicts between mugger crocodiles and tigers that occurred during that time. When the tigers impelled by thirst, frequently descended to the rivers to drink and, on these occasions tigers were seized and killed by the muggers, though more often the tiger escaped and the reptile was disabled. Leopards dodge competition from tigers by hunting in different times of the day and hunting different prey. With relatively abundant prey, tigers and leopards were seen to successfully coexist without competitive exclusion or inter-species dominance hierarchies that may be more common to the savanna. Tigers have been known to suppress wolf populations in areas where the two species coexist. Dhole packs have been observed to attack and kill tigers in disputes over food, though not usually without heavy losses. Lone golden jackals expelled from their pack have been known to form commensal relationships with tigers. These solitary jackals, known as *kol-bahl*, will attach themselves to a particular tiger, trailing it at a safe distance in order to feed on the big cat's kills. A *kol-bahl* will even alert a tiger to a kill with a loud *pheal*. Tigers have been known to tolerate these jackals: one report describes how a jackal confidently walked in and out between three tigers walking together a few feet away from each other. Siberian tigers and brown bears can be competitors and usually avoid confrontation; however, tigers will kill bear cubs and even some adults on occasion. Bears (Asiatic black bears and brown bears) make up 5–8% of the tiger's diet in the Russian Far East. There are also a few records of brown bears killing tigers, either in self defense or in disputes over kills. Some bears emerging from hibernation will try to steal tigers' kills, although the tiger will sometimes defend its kill. Sloth bears are quite aggressive and will sometimes drive young tigers away from their kills, although it is more common for Bengal tigers to prey on sloth bears.

Conservation efforts

Poaching for fur and destruction of habitat have greatly reduced tiger populations in the wild. At the start of the 20th century, it is estimated there were over 100,000 tigers in the world but the population has dwindled to between 1,500 and 3,500 in the wild. Some estimates suggest that there are less than 2,500 mature breeding individuals, with no subpopulation containing more than 250 mature breeding individuals.

India

A Bengal tiger in a national park in southern India. Indian officials successfully reintroduced two Bengal tigers in the Sariska Tiger Reserve in July 2008.

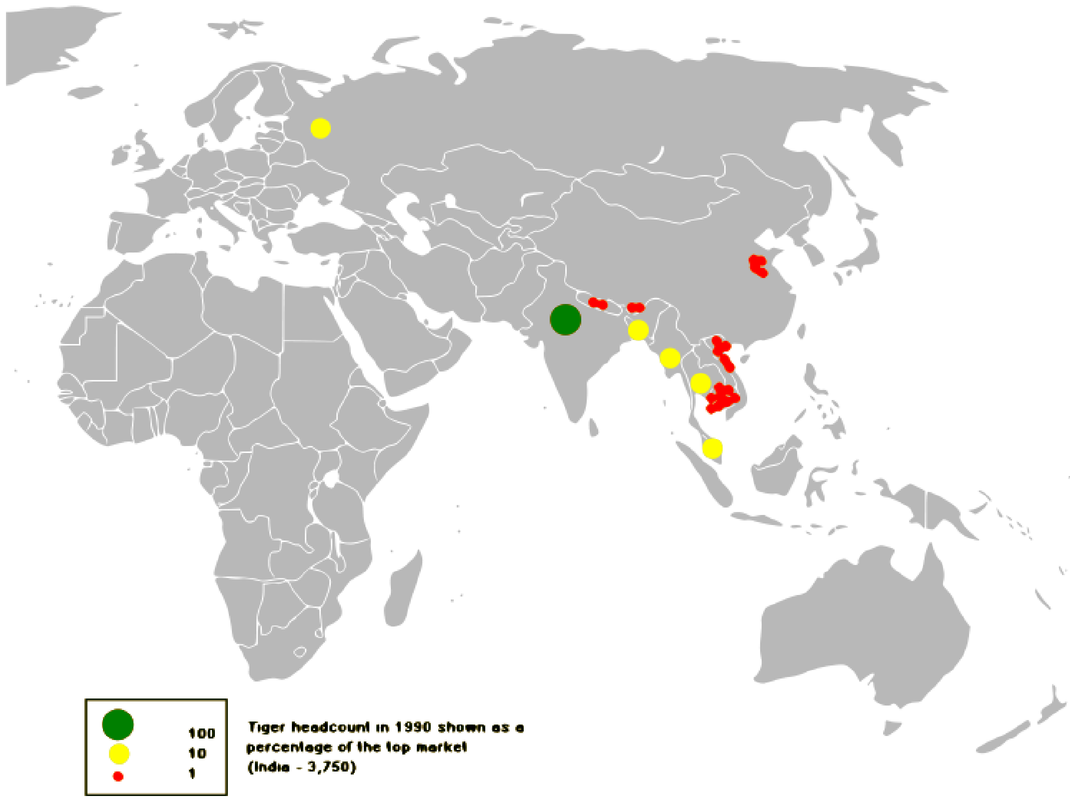
India is home to the world's largest population of tigers in the wild. According to the World Wildlife Fund, of the 3,500 tigers around the world, 1,400 are found in India. Only 11% of original Indian tiger habitat remains, and it is becoming significantly fragmented and often degraded.

A major concerted conservation effort, known as *Project Tiger*, has been underway since 1973, initially spearheaded by Indira Gandhi. The fundamental accomplishment has been the establishment of over 25 well-monitored tiger reserves in reclaimed land where human development is categorically forbidden. The program has been credited with tripling the number of wild Bengal tigers from roughly 1,200 in 1973 to over 3,500 in the 1990s. However, a tiger census carried out in 2007, whose report was published on February 12, 2008, stated that the wild tiger population in India declined by 60% to approximately 1,411. It is noted in the report that the decrease of tiger population can be attributed directly to poaching.

Following the release of the report, the Indian government pledged $153 million to further fund the Project Tiger initiative, set-up a Tiger Protection Force to combat poachers, and fund the relocation of up to 200,000 villagers to minimise human-tiger interaction. Additionally, eight new tiger reserves in India are being set up. Indian officials successfully started a project to reintroduce the tigers into the Sariska Tiger Reserve. The Ranthambore National Park is often cited as a major success by Indian officials against poaching.

Tigers Forever is a collaboration between the Wildlife Conservation Society and Panthera Corporation to serve as both a science-based action plan and a business model to ensure that tigers live in the wild forever. Initial field sites of *Tigers Forever* include the world’s largest tiger reserve, the 21,756 km^2 Hukaung Valley in Myanmar, the Western Ghats in India, Thailand’s Huai Khai Khaeng-Thung Yai protected areas, and other sites in Laos PDR, Cambodia, the Russian Far East and China covering approximately 260,000 km2 of critical tiger habitat.

Russia



Tiger headcount in 1990

The Siberian tiger was on the brink of extinction with only about 40 animals in the wild in the 1940s. Under the Soviet Union, anti-poaching controls were strict and a network of protected zones (zapovedniks) were instituted, leading to a rise in the population to several hundred. Poaching again became a problem in the 1990s, when the economy of Russia collapsed, local hunters had access to a formerly sealed off lucrative Chinese market, and logging in the region increased. While an improvement in the local economy has led to greater resources being invested in conservation efforts, an increase of economic activity has led to an increased rate of development and deforestation. The major obstacle in preserving the species is the enormous territory individual tigers require (up to 450 km^2 needed by a single female and more for a single male). Current conservation efforts are led by local governments and NGO's in consort with international organisations, such as the World Wide Fund and the Wildlife Conservation Society. The competitive exclusion of wolves by tigers has been used by Russian conservationists to convince hunters in the Far East to tolerate the big cats, as they limit ungulate populations less than wolves, and are effective in controlling the latter's numbers. Currently, there are about 400–550 animals in the wild.

Tibet

The trade in tiger skins is illegal in the People's Republic of China, of which Tibet is a part. However, the law banning the trade in endangered animal parts is not enforced in Tibet. An undercover investigation in 2000 by the Wildlife Protection Society of India produced much news about the tiger skin trade and pictures of Tibetans wearing tiger skins. The tigers poached for their skins, subsequent investigations found, originated in India, in a "highly sophisticated" smuggling operation that crossed through Nepal, that "had less to do with old customs than new money" and even attracted European tourists for the tiger skin products of Lhasa. When in 2005, officials in Tibet intercepted "32 tiger, 579 leopard and 665 otter skins", the 14th Dalai Lama called on exiled Tibetans, who are involved in the trade, to cease their activity. The 14th Dalai Lama had spoken out about wearing furs before, but he repeated his condemnation during the 2006 Kalachakra festival in India to expatriate Tibetans. Afterwards, the Dalai Lama issued a press release claiming to have received video of Tibetans burning their animal skin coats, and reports of arrests of eight Tibetans involved for conspiring with the Dalai Lama's government.

Rewilding

Although the term "rewilding" was used in conservation in other contexts since at least 1990, it was first applied to the restoration of a single species of carnivores by conservationist and ex-carnivore manager of Pilanesberg National Park, Gus Van Dyk in 2003. In an effort to find the most appropriate translation of the Chinese term “野化” Van Dyk chose to adopt the term "rewilding" to describe the Save China's Tigers rewilding project of the South China Tiger.

A South China tiger of the Save China's Tigers project with his blesbuck kill

One attempt at rewilding was by Indian conservationist Billy Arjan Singh, who reared a zoo-born tigress named Tara, and released her in the wilds of Dudhwa National Park in 1978. This was soon followed by a large number of people being eaten by a tigress who was later shot. Government officials claim that this tigress was Tara, an assertion hotly contested by Singh and conservationists. Later on, this rewilding gained further disrepute when it was found that the local gene pool had been sullied by Tara's introduction as she was partly Siberian tiger, a fact not known at the time of release, ostensibly due to poor record-keeping at Twycross Zoo, where she had been raised.

Another organisation, Save China's Tigers, working with the Wildlife Research Centre of the State Forestry Administration of China and the Chinese Tigers South Africa Trust, secured an agreement on the reintroduction of Chinese tigers into the wild. The agreement, which was signed in Beijing on 26 November 2002, calls for the establishment of a Chinese tiger conservation model through the creation of a pilot reserve in China where indigenous wildlife, including the South China Tiger, will be reintroduced. Save China's Tigers aims to rewild the critically endangered South China Tiger by bringing a few captive-bred individuals to South Africa for rehabilitation training for them to regain their hunting instincts. At the same time, a pilot reserve in China is being set-up and the Tigers will be relocated and release back in China when the reserve in China is ready. The offspring of the trained tigers will be released into the pilot reserves in China, while the original animals will stay in South Africa to continue breeding.

Chapter 10

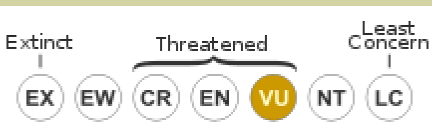
Lion

Lion Temporal range: Early Pleistocene to recent

Male

Female (lioness)

Conservation status



Vulnerable (IUCN 3.1)

Scientific classification

Kingdom:	Animalia
Phylum:	Chordata
Class:	Mammalia
Order:	Carnivora
Family:	Felidae
Genus:	*Panthera*
Species:	***P. leo***

Binomial name

Panthera leo

(Linnaeus, 1758)

Distribution of Lions in Africa

Distribution of lions in India. The Gir Forest, in the State of Gujarat, is the last natural range of approximately 300 wild Asiatic Lions. There are plans to reintroduce some lions to Kuno Wildlife Sanctuary in the neighboring State of Madhya Pradesh.

Synonyms

Felis leo

Linnaeus, 1758

The **lion** (*Panthera leo*) is one of the four big cats in the genus *Panthera*, and a member of the family Felidae. With some males exceeding 250 kg (550 lb) in weight, it is the second-largest living cat after the tiger. Wild lions currently exist in Sub-Saharan Africa and in Asia with an endangered remnant population in Gir Forest National Park in India, having disappeared from North Africa and Southwest Asia in historic times. Until the late Pleistocene, about 10,000 years ago, the lion was the most widespread large land mammal after humans. They were found in most of Africa, across Eurasia from western Europe to India, and in the Americas from the Yukon to Peru. The lion is a vulnerable species, having seen a possibly irreversible population decline of thirty to fifty percent over the past two decades in its African range. Lion populations are untenable outside designated reserves and national parks. Although the cause of the decline is not fully understood, habitat loss and conflicts with humans are currently the greatest causes of concern.

Lions live for ten to fourteen years in the wild, while in captivity they can live longer than twenty years. In the wild, males seldom live longer than ten years, as injuries sustained from continual fighting with rival males greatly reduce their longevity. They typically inhabit savanna and grassland, although they may take to bush and forest. Lions are unusually social compared to other cats. A pride of lions consists of related females and offspring and a small number of adult males. Groups of female lions typically hunt together, preying mostly on large ungulates. Lions are apex and keystone predators, although they scavenge as opportunity allows. While lions do not typically hunt humans, some have been known to do so.

Highly distinctive, the male lion is easily recognized by its mane, and its face is one of the most widely recognized animal symbols in human culture. Depictions have existed from the Upper Paleolithic period, with carvings and paintings from the Lascaux and Chauvet Caves, through virtually all ancient and medieval cultures where they once occurred. It has been extensively depicted in sculptures, in paintings, on national flags, and in contemporary films and literature. Lions have been kept in menageries since Roman Empire and have been a key species sought for exhibition in zoos the world over since the late eighteenth century. Zoos are cooperating worldwide in breeding programs for the endangered Asiatic subspecies.

Etymology

The lion's name, similar in many Romance languages, is derived from the Latin *leo*; and the Ancient Greek λέων (leon). The Hebrew word לָבִיא (*lavi*) may also be related. It was one of the many species originally described by Linnaeus, who gave it the name *Felis leo*, in his eighteenth century work, *Systema Naturae*. The generic component of its scientific designation, *Panthera leo*, often is presumed to derive from Greek *pan-* ("all") and *ther* ("beast"), but this may be a folk etymology. Although it came into English through the classical languages, it shows a striking resemblance to Sanskrit *pundarikam* "tiger", which in turn may come from *pandarah* "whitish-yellow".

Taxonomy and evolution

The lion is a species of the genus *Panthera* and its closest relatives are the other species of this genus: the tiger, the jaguar, and the leopard. *Panthera leo* itself evolved in Africa between 1 million and 800,000 years ago, before spreading throughout the Holarctic region. It appeared in Europe for the first time 700,000 years ago with the subspecies *Panthera leo fossilis* at Isernia in Italy. From this lion derived the later Cave Lion (*Panthera leo spelaea*), which appeared about 300,000 years ago. During the upper Pleistocene the lion spread to North and South America, and developed into *Panthera leo atrox*, the American Lion. Lions died out in northern Eurasia and America at the end of the last glaciation, about 10,000 years ago; this may have been secondary to the extinction of Pleistocene megafauna.

Subspecies

Traditionally, twelve recent subspecies of lion were recognized, distinguished by mane appearance, size, and distribution. Because these characteristics are very insignificant and show a high individual variability, most of these forms were probably not true subspecies, especially as they were often based upon zoo material of unknown origin that may have had "striking, but abnormal" morphological characteristics. Today only eight subspecies are usually accepted, although one of these (the Cape Lion, formerly described as *Panthera leo melanochaita*) probably is invalid. Even the remaining seven subspecies might be too many; mitochondrial variation in recent African lions is modest, which suggests that all sub-Saharan lions could be considered a single subspecies, possibly divided in two main clades: one to the west of the Great Rift Valley and the other to the east. Lions from Tsavo in Eastern Kenya are much closer genetically to lions in Transvaal (South Africa), than to those in the Aberdare Range in Western Kenya. Conversely, Per Christiansen found that using skull morphology allowed him to identify the subspecies *krugeri*, *nubica*, *persica*, and *senegalensis*, while there was overlap between *bleyenberghi* with *senegalensis* and *krugeri*. The Asiatic lion *persica* was the most distinctive, and the Cape lion had characteristics allying it more with persica than the other subsaharan lions. He had analysed 58 lion skulls in three European museums.

Recent

Eight recent (Holocene) subspecies are recognized today:

- *P. l. persica*, known as the Asiatic Lion or South Asian, Persian, or Indian Lion, once was widespread from Turkey, across Southwest Asia, to Pakistan, India, and even to Bangladesh. However, large prides and daylight activity made them easier to poach than tigers or leopards; now around 300 exist in and near the Gir Forest of India. Genetic evidence suggests its ancestors split from the ancestors of subsaharan African lions between 74 and 203 thousand years ago.
- *P. l. leo*, known as the Barbary Lion, originally ranged from Morocco to Egypt. It is extinct in the wild due to excessive hunting, as the last wild Barbary lion was killed in Morocco in 1922. This was one of the largest of the lion subspecies, with

reported lengths of 3–3.3 metres (10–10.8 ft) and weights of more than 200 kilograms (440 lb) for males. It appears to be more closely related to the Asiatic rather than subsaharan lions. There are a number of animals in captivity likely to be Barbary lions, particularly 90 animals descended from the Moroccan Royal collection at Rabat Zoo.

- *P. l. senegalensis*, known as the West African Lion, is found in western Africa, from Senegal to Nigeria.
- *P. l. azandica*, known as the Northeast Congo Lion, is found in the northeastern parts of the Congo.
- *P. l. nubica*, known as the East African, Massai Lion or Tsavo Lion, is found in east Africa, from Ethiopia and Kenya to Tanzania and Mozambique.
- *P. l. bleyenberghi*, known as the Southwest African or Katanga Lion, is found in southwestern Africa, Namibia, Botswana, Angola, Katanga (Zaire), Zambia, and Zimbabwe.
- *P. l. krugeri*, known as the Southeast African Lion or Transvaal Lion, is found in the Transvaal region of southeastern Africa, including Kruger National Park.
- *P. l. melanochaita*, known as the Cape Lion, became extinct in the wild around 1860. Results of mitochondrial DNA research do not support the status as a distinct subspecies. It seems probable that the Cape lion was only the southernmost population of the extant *P. l. krugeri*.

Pleistocene

Several additional subspecies of lion existed in prehistoric times:

- *P. l. atrox*, known as the American Lion or American cave lion, was abundant in the Americas from Canada to Peru in the Pleistocene Epoch until about 10,000 years ago. This form as well as the cave lion sometimes are considered to represent separate species, but recent phylogenetic studies suggest that they are in fact, subspecies of the lion (*Panthera leo*). One of the largest lion subspecies to have existed, its body length is estimated to have been 1.6–2.5 m (5–8 ft).
- *P. l. fossilis*, known as the Early Middle Pleistocene European cave lion, flourished about 500,000 years ago; fossils have been recovered from Germany and Italy. It was larger than today's African lions, reaching the American cave lion in size

Cave Lions, Chamber of Felines, Lascaux caves

- *P. l. spelaea*, known as the European cave lion, Eurasian cave lion, or Upper Pleistocene European cave lion, occurred in Eurasia 300,000 to 10,000 years ago. This species is known from Paleolithic cave paintings (such as the one displayed to the right), ivory carvings, and clay busts, indicating it had protruding ears, tufted tails, perhaps faint tiger-like stripes, and that at least some males had a ruff or primitive mane around their necks.

Dubious

- *P. l. sinhaleyus*, known as the Sri Lanka Lion, appears to have become extinct around 39,000 years ago. It is only known from two teeth found in deposits at Kuruwita. Based on these teeth, P. Deraniyagala erected this subspecies in 1939.
- *P. l. europaea*, known as the European Lion, was probably identical with *Panthera leo persica* or *Panthera leo spelea*; its status as a subspecies is unconfirmed. It became extinct around 100 AD due to persecution and over-exploitation. It inhabited the Balkans, the Italian Peninsula, southern France, and the Iberian Peninsula. It was a very popular object of hunting among Romans and Greeks.

- *P. l. youngi* or *Panthera youngi*, flourished 350,000 years ago. Its relationship to the extant lion subspecies is obscure, and it probably represents a distinct species.
- *P. l. maculatus*, known as the Marozi or Spotted lion, sometimes is believed to be a distinct subspecies, but may be an adult lion that has retained its juvenile spotted pattern. If it was a subspecies in its own right, rather than a small number of aberrantly colored individuals, it has been extinct since 1931. A less likely identity is a natural leopard-lion hybrid commonly known as a leopon.

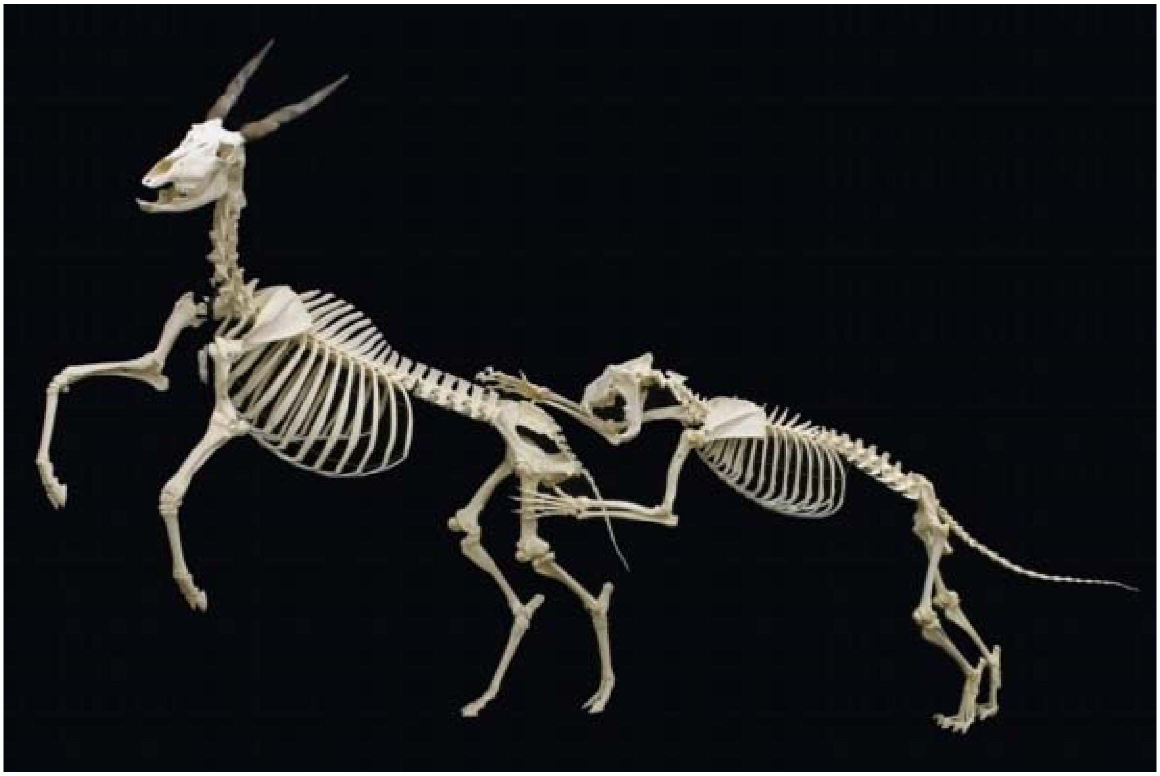
Hybrids

lion cubs in the wild, South Africa

Lions have been known to breed with tigers (most often the Siberian and Bengal subspecies) to create hybrids called ligers and tiglons. They also have been crossed with leopards to produce leopons, and jaguars to produce jaglions. The marozi is reputedly a spotted lion or a naturally occurring leopon, while the Congolese Spotted Lion is a complex lion-jaguar-leopard hybrid called a lijagulep. Such hybrids were once commonly bred in zoos, but this is now discouraged due to the emphasis on conserving species and subspecies. Hybrids are still bred in private menageries and in zoos in China.

The liger is a cross between a male lion and a tigress. Because the growth-inhibiting gene from the female tiger is absent, a growth-promoting gene is passed on by the male lion, the resulting ligers grow far larger than either parent. They share physical and behavioural qualities of both parent species (spots and stripes on a sandy background). Male ligers are sterile, but female ligers are often fertile. Males have about a 50 percent chance of having a mane, but if they grow one, their manes will be modest: around 50 percent of a pure lion mane. Ligers are typically between 3.0 and 3.7 m (10 to 12 feet) in length, and can be between 360 and 450 kg (800 to 1,000 pounds) or more. The less common tigon is a cross between the lioness and the male tiger.

Characteristics



A skeletal mount of an African Lion attacking a Common Eland on display at The Museum of Osteology, Oklahoma City, Oklahoma

The lion is the tallest (at the shoulder) of the felines, and also is the second-heaviest feline after the tiger. Its skull is very similar to that of the tiger, although the frontal region is usually more depressed and flattened, with a slightly shorter postorbital region. The lion's skull has broader nasal openings than the tiger. However, due to the amount of skull variation in the two species, usually, only the structure of the lower jaw can be used as a reliable indicator of species. Lion coloration varies from light buff to yellowish, reddish, or dark ochraceous brown. The underparts are generally lighter and the tail tuft is black. Lion cubs are born with brown rosettes (spots) on their body, rather like those of a leopard. Although these fade as lions reach adulthood, faint spots often may still be seen on the legs and underparts, particularly on lionesses.

Lions are the only members of the cat family to display obvious sexual dimorphism—that is, males and females look distinctly different. They also have specialized roles that each gender plays in the pride. For instance, the lioness, the hunter, lacks the male's thick cumbersome mane. It seems to impede the male's ability to be camouflaged when stalking the prey and create overheating in chases. The color of the male's mane varies from blond to black, generally becoming darker as the lion grows older.

During confrontations with others, the mane makes the lion look larger.

Weights for adult lions range between 150–250 kg (330–550 lb) for males and 120–182 kg (264–400 lb) for females. Nowell and Jackson report average weights of 181 kg for males and 126 kg for females; one male shot near Mount Kenya was weighed at 272 kg (600 lb). Lions tend to vary in size depending on their environment and area, resulting in a wide spread in recorded weights. For instance, lions in southern Africa tend to be about 5 percent heavier than those in East Africa, in general.

Head and body length is 170–250 cm (5 ft 7 in – 8 ft 2 in) in males and 140–175 cm (4 ft 7 in – 5 ft 9 in) in females; shoulder height is about 123 cm (4 ft) in males and 107 cm (3 ft 6 in) in females. The tail length is 90–105 cm (2 ft 11 in - 3 ft 5 in) in males and 70–100 cm in females (2 ft 4 in – 3 ft 3 in). The longest known lion was a black-maned male shot near Mucsso, southern Angola in October 1973; the heaviest lion known in the wild was a man-eater shot in 1936 just outside Hectorspruit in eastern Transvaal, South Africa and weighed 313 kg (690 lb). Lions in captivity tend to be larger than lions in the wild—the heaviest lion on record is a male at Colchester Zoo in England named Simba in 1970, which weighed 375 kg (826 lb).

The most distinctive characteristic shared by both females and males is that the tail ends in a hairy tuft. In some lions, the tuft conceals a hard "spine" or "spur", approximately 5 mm long, formed of the final sections of tail bone fused together. The lion is the only felid to have a tufted tail—the function of the tuft and spine are unknown. Absent at birth, the tuft develops around 5½ months of age and is readily identifiable at 7 months.

Mane

The mane of the adult male lion, unique among cats, is one of the most distinctive characteristics of the species. It makes the lion appear larger, providing an excellent intimidation display; this aids the lion during confrontations with other lions and with the species' chief competitor in Africa, the spotted hyena. The presence, absence, color, and size of the mane is associated with genetic precondition, sexual maturity, climate, and testosterone production; the rule of thumb is the darker and fuller the mane, the healthier the lion. Sexual selection of mates by lionesses favors males with the densest, darkest mane. Research in Tanzania also suggests mane length signals fighting success in male–male relationships. Darker-maned individuals may have longer reproductive lives and higher offspring survival, although they suffer in the hottest months of the year. In prides including a coalition of two or three males, it is possible that lionesses solicit mating more actively with the males who are more heavily maned.

A maneless male lion, who also has little body hair—from Tsavo East National Park, Kenya

Scientists once believed that the distinct status of some subspecies could be justified by morphology, including the size of the mane. Morphology was used to identify subspecies such as the Barbary Lion and Cape Lion. Research has suggested, however, that environmental factors influence the color and size of a lion's mane, such as the ambient temperature. The cooler ambient temperature in European and North American zoos, for example, may result in a heavier mane. Thus the mane is not an appropriate marker for identifying subspecies. The males of the Asiatic subspecies, however, are characterized by sparser manes than average African lions.

Maneless male lions have been reported in Senegal and Tsavo East National Park in Kenya, and the original male white lion from Timbavati also was maneless. The testosterone hormone has been linked to mane growth, therefore castrated lions often have minimal to no mane, as the removal of the gonads inhibits testosterone production. The lack of a mane sometimes is found in inbred lion populations; inbreeding also results in poor fertility.

Cave paintings of extinct European Cave Lions exclusively show animals with no mane, or just the hint of a mane, suggesting that they were maneless.

White lions

White lions owe their coloring to a recessive gene; they are rare forms of the subspecies *Panthera leo krugeri*

The white lion is not a distinct subspecies, but a special morph with a genetic condition, leucism, that causes paler colouration akin to that of the white tiger; the condition is similar to melanism, which causes black panthers. They are not albinos, having normal pigmentation in the eyes and skin. White Transvaal lion *(Panthera leo krugeri)* individuals occasionally have been encountered in and around Kruger National Park and

the adjacent Timbavati Private Game Reserve in eastern South Africa, but are more commonly found in captivity, where breeders deliberately select them. The unusual cream color of their coats is due to a recessive gene. Reportedly, they have been bred in camps in South Africa for use as trophies to be killed during canned hunts.
Kevin Richardson is an animal behaviorist who works with the native big cats of Africa. He currently works in a special facility called the Kingdom of the White Lion in Broederstroom which is 50 miles form Johannesburg. The site was built with the help of Rodney Fuhr and was made for the movie set of White Lion: Home is a Journey. He has 39 white lions on-site and works diligently to protect and preserve the white lion species. While the park is currently a private property, there are plans to open it to the public soon.

Behavior

Lions spend much of their time resting and are inactive for about 20 hours per day. Although lions can be active at any time, their activity generally peaks after dusk with a period of socializing, grooming, and defecating. Intermittent bursts of activity follow through the night hours until dawn, when hunting most often takes place. They spend an average of two hours a day walking and 50 minutes eating.

Group organization

Lions are predatory carnivores who manifest two types of social organization. Some are *residents,* living in groups, called *prides*. The pride usually consists of five or six related females, their cubs of both sexes, and one or two males (known as a *coalition* if more than one) who mate with the adult females (although extremely large prides, consisting of up to 30 individuals, have been observed). The number of adult males in a coalition is usually two, but may increase to four and decrease again over time. Male cubs are excluded from their maternal pride when they reach maturity.

Two lionesses and a mature male of a pride, northern Serengeti

The second organizational behaviour is labeled *nomads*, who range widely and move about sporadically, either singularly or in pairs. Pairs are more frequent among related males who have been excluded from their birth pride. Note that a lion may switch lifestyles; nomads may become residents and vice versa. Males have to go through this lifestyle and some never are able to join another pride. A female who becomes a nomad has much greater difficulty joining a new pride, as the females in a pride are related, and they reject most attempts by an unrelated female to join their family group.

The area a pride occupies is called a *pride area*, whereas that by a nomad is a *range*. The males associated with a pride tend to stay on the fringes, patrolling their territory. Why sociality—the most pronounced in any cat species—has developed in lionesses is the subject of much debate. Increased hunting success appears an obvious reason, but this is less than sure upon examination: coordinated hunting does allow for more successful predation, but also ensures that non-hunting members reduce per capita caloric intake, however, some take a role raising cubs, who may be left alone for extended periods of time. Members of the pride regularly tend to play the same role in hunts. The health of the hunters is the primary need for the survival of the pride and they are the first to consume the prey at the site it is taken. Other benefits include possible kin selection (better to share food with a related lion than with a stranger), protection of the young, maintenance of territory, and individual insurance against injury and hunger.

lion in the wild

Lionesses do the majority of the hunting for their pride, being smaller, swifter and more agile than the males, and unencumbered by the heavy and conspicuous mane, which causes overheating during exertion. They act as a co-ordinated group in order to stalk and bring down the prey successfully. However, if nearby the hunt, males have a tendency to dominate the kill once the lionesses have succeeded. They are more likely to share with the cubs than with the lionesses, but rarely share food they have killed by themselves. Smaller prey is eaten at the location of the hunt, thereby being shared among the hunters; when the kill is larger it often is dragged to the pride area. There is more sharing of larger kills, although pride members often behave aggressively toward each other as each tries to consume as much food as possible.

Both males and females defend the pride against intruders. Some individual lions consistently lead the defense against intruders, while others lag behind. Lions tend to assume specific roles in the pride. Those lagging behind may provide other valuable services to the group. An alternative hypothesis is that there is some reward associated with being a leader who fends off intruders and the rank of lionesses in the pride is reflected in these responses. The male or males associated with the pride must defend their relationship to the pride from outside males who attempt to take over their relationship with the pride. Females form the stable social unit in a pride and do not tolerate outside females; membership only changes with the births and deaths of lionesses, although some females do leave and become nomadic. Subadult males on the other hand, must leave the pride when they reach maturity at around 2–3 years of age.

Hunting and diet

While a lioness such as this one has very sharp teeth, prey is usually killed by strangulation

Lions are powerful animals that usually hunt in coordinated groups and stalk their chosen prey. However, they are not particularly known for their stamina—for instance, a lioness' heart makes up only 0.57 percent of her body weight (a male's is about 0.45 percent of his body weight), whereas a hyena's heart is close to 1 percent of its body weight. Thus, they only run fast in short bursts, and need to be close to their prey before starting the attack. They take advantage of factors that reduce visibility; many kills take place near some form of cover or at night. They sneak up to the victim until they reach a distance of around 30 metres (98 ft) or less. Typically, several lionesses work together and encircle the herd from different points. Once they have closed with a herd, they usually target the closest prey. The attack is short and powerful; they attempt to catch the victim with a fast rush and final leap. The prey usually is killed by strangulation, which can cause cerebral ischemia or asphyxia (which results in hypoxemic, or "general", hypoxia). The prey also may be killed by the lion enclosing the animal's mouth and nostrils in its jaws (which would also result in asphyxia). Smaller prey, though, may simply be killed by a swipe of a lion's paw.

Lioness in a burst of speed while hunting in the Serengeti

The prey consists mainly of large mammals, with a preference for wildebeest, impalas, zebras, buffalo, and warthogs in Africa and nilgai, wild boar, and several deer species in India. Many other species are hunted, based on availability. Mainly this will include ungulates weighing between 50 and 300 kg (110–660 lb) such as kudu, hartebeest, gemsbok, and eland. Occasionally, they take relatively small species such as Thomson's Gazelle or springbok. Lions hunting in groups are capable of taking down most animals, even healthy adults, but in most parts of their range they rarely attack very large prey such as fully grown male giraffes due to the danger of injury.

Extensive statistics collected over various studies show that lions normally feed on mammals in the range 190–550 kg (420–1210 lb). In Africa, wildebeest rank at the top of preferred prey (making nearly half of the lion prey in the Serengeti) followed by zebra. Most adult hippopotamuses, rhinoceroses, elephants, and smaller gazelles, impala, and other agile antelopes are generally excluded. However giraffes and buffalos are often taken in certain regions. For instance, in Kruger National Park, giraffes are regularly hunted. In Manyara Park, Cape buffaloes constitute as much as 62% of the lion's diet, due to the high number density of buffaloes. Occasionally hippopotamus is also taken, but adult rhinoceroses are generally avoided. Even though smaller than 190 kg (420 lb), warthogs are often taken depending on availability. In some areas, lions specialise in hunting atypical prey species; this is the case at the Savuti river, where they prey on elephants. Park guides in the area reported that the lions, driven by extreme hunger, started taking down baby elephants, and then moved on to adolescents and, occasionally, fully grown adults during the night when elephants' vision is poor. Lions also attack domestic livestock; in India cattle contribute significantly to their diet. Lions are capable of killing other predators such as leopards, cheetahs, hyenas, and wild dogs, though (unlike most felids) they seldom devour the competitors after killing them. They also scavenge animals either dead from natural causes (disease) or killed by other predators, and keep a constant lookout for circling vultures, being keenly aware that they indicate an animal dead or in distress. A lion may gorge itself and eat up to 30 kg (66 lb) in one sitting; if it is unable to consume all the kill it will rest for a few hours before consuming more. On a hot day, the pride may retreat to shade leaving a male or two to stand guard. An adult lioness requires an average of about 5 kg (11 lb) of meat per day, a male about 7 kg (15.4 lb).

Four lions take down a cape buffalo in the central Serengeti, Tanzania

Because lionesses hunt in open spaces where they are easily seen by their prey, cooperative hunting increases the likelihood of a successful hunt; this is especially true with larger species. Teamwork also enables them to defend their kills more easily against other large predators such as hyenas, which may be attracted by vultures from kilometers away in open savannas. Lionesses do most of the hunting; males attached to prides do not usually participate in hunting, except in the case of larger quarry such as giraffe and buffalo. In typical hunts, each lioness has a favored position in the group, either stalking prey on the "wing" then attacking, or moving a smaller distance in the centre of the group and capturing prey in flight from other lionesses.

Young lions first display stalking behavior around three months of age, although they do not participate in hunting until they are almost a year old. They begin to hunt effectively when nearing the age of two.

Predator competition

Lions and spotted hyenas occupy the same ecological niche (and hence compete) where they coexist. A review of data across several studies indicates a dietary overlap of 58.6%. Lions typically ignore spotted hyenas, unless they are on a kill or are being harassed by them, while the latter tend to visibly react to the presence of lions, whether there is food or not. Lions seize the kills of spotted hyenas: in the Ngorongoro crater, it is common for lions to subsist largely on kills stolen from hyenas, causing the hyenas to increase their kill rate. Lions are quick to follow the calls of hyenas feeding, a fact which was proven by Dr. Hans Kruuk, who found that lions repeatedly approached him whenever he played the tape-recorded calls of hyenas feeding. When confronted on a kill by lions, spotted hyenas will either leave or wait patiently at a distance of 30–100 m (100–350 ft) until the lions have finished. In some cases, spotted hyenas are bold enough to feed alongside lions, and may occasionally force the lions off a kill. The two species may act aggressively toward one another even when there is no food involved. Lions may charge at hyenas and maul them for no apparent reason: one male lion was filmed killing two matriarch hyenas on separate occasions without eating them, and lion predation can account for up to 71% of hyena deaths in Etosha. Spotted hyenas have adapted to this pressure by frequently mobbing lions which enter their territories. Experiments on captive spotted hyenas revealed that specimens with no prior experience with lions act indifferently to the sight of them, but will react fearfully to the scent.

Lions tend to dominate smaller felines such as cheetahs and leopards where they co-occur, stealing their kills and killing their cubs and even adults when given the chance. The cheetah has a 50 percent chance of losing its kill to lions or other predators. Lions are major killers of cheetah cubs, up to 90 percent of which are lost in their first weeks of life due to attacks by other predators. Cheetahs avoid competition by hunting at different times of the day and hide their cubs in thick brush. Leopards also use such tactics, but have the advantage of being able to subsist much better on small prey than either lions or cheetahs. Also, unlike cheetahs, leopards can climb trees and use them to keep their cubs and kills away from lions. However, lionesses will occasionally be successful in climbing to retrieve leopard kills. Similarly, lions dominate African wild dogs, not only taking their kills but also preying on both young and adult dogs (although the latter are rarely caught).

The Nile crocodile is the only sympatric predator (besides humans) that can singly threaten the lion. Depending on the size of the crocodile and the lion, either can lose kills or carrion to the other. Lions have been known to kill crocodiles venturing onto land, while the reverse is true for lions entering waterways, as evidenced by the occasional lion claws found in crocodile stomachs.

Reproduction and life cycle

Most lionesses will have reproduced by the time they are four years of age. Lions do not mate at any specific time of year, and the females are polyestrous. As with other cats, the male lion's penis has spines which point backwards. Upon withdrawal of the penis, the spines rake the walls of the female's vagina, which may cause ovulation. A lioness may mate with more than one male when she is in heat; during a mating bout, which could last several days, the couple copulates twenty to forty times a day and are likely to forgo eating. Lions reproduce very well in captivity.

Lions mating in Ngorongoro Conservation Area, Tanzania

The average gestation period is around 110 days, the female giving birth to a litter of one to four cubs in a secluded den (which may be a thicket, a reed-bed, a cave or some other sheltered area) usually away from the rest of the pride. She will often hunt by herself while the cubs are still helpless, staying relatively close to the thicket or den where the cubs are kept. The cubs themselves are born blind—their eyes do not open until roughly a week after birth. They weigh 1.2–2.1 kg (2.6–4.6 lb) at birth and are almost helpless, beginning to crawl a day or two after birth and walking around three weeks of age. The lioness moves her cubs to a new den site several times a month, carrying them one by one by the nape of the neck, to prevent scent from building up at a single den site and thus avoiding the attention of predators that may harm the cubs.

Usually, the mother does not integrate herself and her cubs back into the pride until the cubs are six to eight weeks old. However, sometimes this introduction to pride life occurs earlier, particularly if other lionesses have given birth at about the same time. For instance, lionesses in a pride often synchronize their reproductive cycles so that they cooperate in the raising and suckling of the young (once the cubs are past the initial stage of isolation with their mother), who suckle indiscriminately from any or all of the nursing females in the pride. In addition to greater protection, the synchronization of births also has an advantage in that the cubs end up being roughly the same size, and thus have an equal chance of survival. If one lioness gives birth to a litter of cubs a couple of months after another lioness, for instance, then the younger cubs, being much smaller than their older brethren, are usually dominated by larger cubs at mealtimes—consequently, death by starvation is more common amongst the younger cubs.

A pregnant lioness (right)

In addition to starvation, cubs also face many other dangers, such as predation by jackals, hyenas, leopards, martial eagles and snakes. Even buffaloes, should they catch the scent of lion cubs, often stampede towards the thicket or den where they are being kept, doing their best to trample the cubs to death while warding off the lioness. Furthermore, when one or more new males oust the previous male(s) associated with a pride, the conqueror(s) often kill any existing young cubs, perhaps because females do not become fertile and receptive until their cubs mature or die. All in all, as many as 80 percent of the cubs will die before the age of two.

When first introduced to the rest of the pride, the cubs initially lack confidence when confronted with adult lions other than their mother. However, they soon begin to immerse themselves in the pride life, playing amongst themselves or attempting to initiate play with the adults. Lionesses with cubs of their own are more likely to be tolerant of another lioness's cubs than lionesses without cubs. The tolerance of the male lions towards the cubs varies—sometimes, a male will patiently let the cubs play with his tail or his mane, whereas another may snarl and bat the cubs away.

The tolerance of male lions towards the cubs varies. They are, however, generally more likely to share food with the cubs than with the lionesses.

Weaning occurs after six to seven months. Male lions reach maturity at about 3 years of age and, at 4–5 years of age, are capable of challenging and displacing the adult male(s) associated with another pride. They begin to age and weaken between 10 and 15 years of age at the latest, if they have not already been critically injured while defending the pride (once ousted from a pride by rival males, male lions rarely manage a second take-over). This leaves a short window for their own offspring to be born and mature. If they are able to procreate as soon as they take over a pride, potentially, they may have more offspring reaching maturity before they also are displaced. A lioness often will attempt to defend her cubs fiercely from a usurping male, but such actions are rarely successful. He usually kills all of the existing cubs who are less than two years old. A lioness is weaker and much lighter than a male; success is more likely when a group of three or four mothers within a pride join forces against one male.

Contrary to popular belief, it is not only males that are ousted from their pride to become nomads, although most females certainly do remain with their birth pride. However, when the pride becomes too large, the next generation of female cubs may be forced to leave to eke out their own territory. Furthermore, when a new male lion takes over the pride, subadult lions, both male and female, may be evicted. Life is harsh for a female nomad. Nomadic lionesses rarely manage to raise their cubs to maturity, without the protection of other pride members. One scientific study reports that both males and females may interact homosexually.

Health

Although adult lions have no natural predators, evidence suggests that the majority die violently from humans or other lions. Lions often inflict serious injuries on each other, either members of different tribes encountering each other in territorial disputes, or members of the same tribe fighting at a kill. Crippled lions and lion cubs may fall victim to hyenas, leopards, or be trampled by buffalo or elephants, and careless lions may be maimed when hunting prey.

One of the tree climbing Lions of the Serengeti, Tanzania

Various species of tick commonly infest the ears, neck and groin regions of most lions. Adult forms of several species of the tapeworm genus *Taenia* have been isolated from intestines, the lions having ingested larval forms from antelope meat. Lions in the Ngorongoro Crater were afflicted by an outbreak of stable fly (*Stomoxys calcitrans*) in 1962; this resulted in lions becoming covered in bloody bare patches and emaciated. Lions sought unsuccessfully to evade the biting flies by climbing trees or crawling into hyena burrows; many perished or emigrated as the population dropped from 70 to 15 individuals. A more recent outbreak in 2001 killed six lions. Lions, especially in captivity, are vulnerable to the canine distemper virus (CDV), feline immunodeficiency virus (FIV), and feline infectious peritonitis (FIP). CDV is spread through domestic dogs and other carnivores; a 1994 outbreak in Serengeti National Park resulted in many lions developing neurological symptoms such as seizures. During the outbreak, several lions died from pneumonia and encephalitis. FIV, which is similar to HIV while not known to adversely affect lions, is worrisome enough in its effect in domestic cats that the Species Survival Plan recommends systematic testing in captive lions. It occurs with high to endemic frequency in several wild lion populations, but is mostly absent from Asiatic and Namibian lions.

Communication

Head rubbing and licking are common social behaviors within a pride

When resting, lion socialization occurs through a number of behaviors, and the animal's expressive movements are highly developed. The most common peaceful tactile gestures are head rubbing and social licking, which have been compared with grooming in primates. Head rubbing—nuzzling one's forehead, face and neck against another lion—appears to be a form of greeting, as it is seen often after an animal has been apart from others, or after a fight or confrontation. Males tend to rub other males, while cubs and females rub females. Social licking often occurs in tandem with head rubbing; it is generally mutual and the recipient appears to express pleasure. The head and neck are the most common parts of the body licked, which may have arisen out of utility, as a lion cannot lick these areas individually.

Lions have an array of facial expressions and body postures that serve as visual gestures. Their repertoire of vocalizations is also large; variations in intensity and pitch, rather than discrete signals, appear central to communication. Lion sounds include snarling, purring, hissing, coughing, miaowing, woofing and roaring. Lions tend to roar in a very characteristic manner, starting with a few deep, long roars that trail off into a series of shorter ones. They most often roar at night; the sound, which can be heard from a distance of 8 kilometres (5.0 mi), is used to advertise the animal's presence. Lions have the loudest roar of any big cat.

Distribution and habitat

Two male Asiatic Lions in Sanjay Gandhi National Park, Mumbai, India. The wild population of the endangered Asiatic Lions is restricted to the Gir Forest National Park in western India.

In Africa, lions can be found in savanna grasslands with scattered *Acacia* trees which serve as shade; their habitat in India is a mixture of dry savanna forest and very dry deciduous scrub forest. The habitat of lions originally spanned the southern parts of Eurasia, ranging from Greece to India, and most of Africa except the central rainforest-zone and the Sahara desert. Herodotus reported that lions had been common in Greece around 480 BC; they attacked the baggage camels of the Persian king Xerxes on his march through the country. Aristotle considered them rare by 300 BC. By 100 AD they were extirpated. A population of the Asiatic Lion survived until the tenth century in the Caucasus, their last European outpost.

The species was eradicated from Palestine by the Middle Ages and from most of the rest of Asia after the arrival of readily available firearms in the eighteenth century. Between the late nineteenth and early twentieth century they became extinct in North Africa and Southwest Asia. By the late nineteenth century the lion had disappeared from Turkey and most of northern India, while the last sighting of a live Asiatic lion in Iran was in 1941 (between Shiraz and Jahrom, Fars Province), although the corpse of a lioness was found on the banks of the Karun river, Khūzestān Province in 1944. There are no subsequent reliable reports from Iran. The subspecies now survives only in and around the Gir Forest of northwestern India. About 300 lions live in a 1,412 km² (558 square miles) sanctuary in the state of Gujarat, which covers most of the forest. Their numbers are slowly increasing.

Population and conservation status

The Asiatic Lion, whose habitat once ranged from the Mediterranean to north-west Indian subcontinent, is today found only in the Gir Forest of Gujarat, India. Only about 320 Asiatic Lions survive in the wild.

Most lions now live in eastern and southern Africa, and their numbers there are rapidly decreasing, with an estimated 30–50 percent decline over the last two decades. Estimates of the African lion population range between 16,500 and 47,000 living in the wild in 2002–2004, down from early 1990s estimates that ranged as high as 100,000 and perhaps 400,000 in 1950. Primary causes of the decline include climate change, disease and human interference. Habitat loss and conflicts with humans are considered the most significant threats to the species. The remaining populations are often geographically isolated from one another, which can lead to inbreeding, and consequently, reduced genetic diversity. Therefore the lion is considered a vulnerable species by the International Union for Conservation of Nature, while the Asiatic subspecies is endangered. The lion population in the region of West Africa is isolated from lion populations of Central Africa, with little or no exchange of breeding individuals. The number of mature individuals in West Africa is estimated by two separate recent surveys at 850–1,160 (2002/2004). There is disagreement over the size of the largest individual population in West Africa: the estimates range from 100 to 400 lions in Burkina Faso's Arly-Singou ecosystem.

Conservation of both African and Asian lions has required the setup and maintenance of national parks and game reserves; among the best known are Etosha National Park in Namibia, Serengeti National Park in Tanzania, and Kruger National Park in eastern South Africa. Outside these areas, the issues arising from lions' interaction with livestock and people usually results in the elimination of the former. In India, the last refuge of the Asiatic lion is the 1,412 km² (558 square miles) Gir Forest National Park in western India which had about 359 lions (as of April 2006). As in Africa, numerous human habitations are close by with the resultant problems between lions, livestock, locals and wildlife officials. The Asiatic Lion Reintroduction Project plans to establish a second independent population of Asiatic Lions at the Kuno Wildlife Sanctuary in the Indian state of Madhya Pradesh. It is important to start a second population to serve as a gene pool for the last surviving Asiatic lions and to help develop and maintain genetic diversity enabling the species to survive.

The former popularity of the Barbary lion as a zoo animal has meant that scattered lions in captivity are likely to be descended from Barbary Lion stock. This includes twelve lions at Port Lympne Wild Animal Park in Kent, England that are descended from animals owned by the King of Morocco. Another eleven animals believed to be Barbary lions were found in Addis Ababa zoo, descendants of animals owned by Emperor Haile Selassie. WildLink International, in collaboration with Oxford University, launched their ambitious International Barbary Lion Project with the aim of identifying and breeding Barbary lions in captivity for eventual reintroduction into a national park in the Atlas Mountains of Morocco.

Following the discovery of the decline of lion population in Africa, several coordinated efforts involving lion conservation have been organised in an attempt to stem this decline. Lions are one species included in the Species Survival Plan, a coordinated attempt by the Association of Zoos and Aquariums to increase its chances of survival. The plan was originally started in 1982 for the Asiatic lion, but was suspended when it was found that most Asiatic lions in North American zoos were not genetically pure, having been hybridized with African lions. The African lion plan started in 1993, focusing especially on the South African subspecies, although there are difficulties in assessing the genetic diversity of captive lions, since most individuals are of unknown origin, making maintenance of genetic diversity a problem.

Man-eaters

While lions do not usually hunt people, some (usually males) seem to seek out human prey; well-publicized cases include the Tsavo maneaters, where 28 railway workers building the Kenya-Uganda Railway were taken by lions over nine months during the construction of a bridge over the Tsavo River in Kenya in 1898, and the 1991 Mfuwe man-eater, which killed six people in the Laungwa River Valley in Zambia. In both, the hunters who killed the lions wrote books detailing the animals' predatory behavior. The Mfuwe and Tsavo incidents bear similarities: the lions in both incidents were larger than normal, lacked manes, and seemed to suffer from tooth decay. The infirmity theory, including tooth decay, is not favored by all researchers; an analysis of teeth and jaws of man-eating lions in museum collections suggests that, while tooth decay may explain some incidents, prey depletion in human-dominated areas is a more likely cause of lion predation on humans. In their analysis of Tsavo and man-eating generally, Kerbis Peterhans and Gnoske acknowledge that sick or injured animals may be more prone to man-eating, but that the behavior is "not unusual, nor necessarily 'aberrant'" where the opportunity exists; if inducements such as access to livestock or human corpses are present, lions will regularly prey upon human beings. The authors note that the relationship is well-attested amongst other pantherines and primates in the paleontological record. The lion's proclivity for man-eating has been systematically examined. American and Tanzanian scientists report that man-eating behavior in rural areas of Tanzania increased greatly from 1990 to 2005. At least 563 villagers were attacked and many eaten over this period—a number far exceeding the more famed "Tsavo" incidents of a century earlier. The incidents occurred near Selous National Park in Rufiji District and in Lindi Province near the Mozambican border. While the expansion of villagers into bush country is one concern, the authors argue that conservation policy must mitigate the danger because, in this case, conservation contributes directly to human deaths. Cases in Lindi have been documented where lions seize humans from the center of substantial villages.

The Tsavo Man-Eaters on display in the Field Museum of Natural History in Chicago, Illinois.

Author Robert R. Frump wrote in *The Man-eaters of Eden* that Mozambican refugees regularly crossing Kruger National Park at night in South Africa are attacked and eaten by the lions; park officials have conceded that man-eating is a problem there. Frump believes thousands may have been killed in the decades after apartheid sealed the park and forced the refugees to cross the park at night. For nearly a century before the border was sealed, Mozambicans had regularly walked across the park in daytime with little harm.

Packer estimates more than 200 Tanzanians are killed each year by lions, crocodiles, elephants, hippos, and snakes, and that the numbers could be double that amount, with lions thought to kill at least 70 of those. Packer has documented that between 1990 and 2004, lions attacked 815 people in Tanzania, killing 563. Packer and Ikanda are among the few conservationists who believe western conservation efforts must take account of these matters not just because of ethical concerns about human life, but also for the long term success of conservation efforts and lion preservation.

A man-eating lion was killed by game scouts in Southern Tanzania in April 2004. It is believed to have killed and eaten at least 35 people in a series of incidents covering several villages in the Rufiji Delta coastal region. Dr Rolf D. Baldus, the GTZ wildlife programme coordinator, commented that it was likely that the lion preyed on humans because it had a large abscess underneath a molar which was cracked in several places.

He further commented that "This lion probably experienced a lot of pain, particularly when it was chewing." GTZ is the German development cooperation agency and has been working with the Tanzanian government on wildlife conservation for nearly two decades. As in other cases this lion was large, lacked a mane, and had a tooth problem.

The "All-Africa" record of man-eating generally is considered to be not Tsavo, but the lesser-known incidents in the late 1930s through the late 1940s in what was then Tanganyika (now Tanzania). George Rushby, game warden and professional hunter, eventually dispatched the pride, which over three generations is thought to have killed and eaten 1,500 to 2,000 in what is now Njombe district.

In captivity

Lions are part of a group of exotic animals that are the core of zoo exhibits since the late eighteenth century; members of this group are invariably large vertebrates and include elephants, rhinoceroses, hippopotamuses, large primates, and other big cats; zoos sought to gather as many of these species as possible. Although many modern zoos are more selective about their exhibits, there are over 1,000 African and 100 Asiatic lions in zoos and wildlife parks around the world. They are considered an ambassador species and are kept for tourism, education and conservation purposes. Lions can reach an age of over 20 years in captivity; Apollo, a resident lion of Honolulu Zoo in Honolulu, Hawaii, died at age 22 in August 2007. His two sisters, born in 1986, are still living (as of August, 2007). Breeding programs need to note origins to avoid breeding different subspecies and thus reducing conservation value.

Male African lion of the Transvaal subspecies (*P. l. krugeri*)

Lions were kept and bred by Assyrian kings as early as 850 BC, and Alexander the Great was said to have been presented with tame lions by the Malhi of northern India. Later in Roman times, lions were kept by emperors to take part in the gladiator arenas. Roman notables, including Sulla, Pompey, and Julius Caesar, often ordered the mass slaughter of hundreds of lions at a time. In the East, lions were tamed by Indian princes, and Marco Polo reported that Kublai Khan kept lions inside. The first European "zoos" spread amongst noble and royal families in the thirteenth century, and until the seventeenth century were called seraglios; at that time, they came to be called menageries, an extension of the cabinet of curiosities. They spread from France and Italy during the Renaissance to the rest of Europe. In England, although the seraglio tradition was less developed, Lions were kept at the Tower of London in a seraglio established by King John in the thirteenth century, probably stocked with animals from an earlier menagerie started in 1125 by Henry I at his palace in Woodstock, near Oxford; where lions had been reported stocked by William of Malmesbury.

Seraglios served as expressions of the nobility's power and wealth. Animals such as big cats and elephants, in particular, symbolized power, and would be pitted in fights against each other or domesticated animals. By extension, menageries and seraglios served as demonstrations of the dominance of humanity over nature. Consequently, the defeat of such natural "lords" by a cow in 1682 astonished the spectators, and the flight of an elephant before a rhinoceros drew jeers. Such fights would slowly fade out in the seventeenth century with the spread of the menagerie and their appropriation by the commoners. The tradition of keeping big cats as pets would last into the nineteenth century, at which time it was seen as highly eccentric.

Albrecht Dürer, Lions sketch. Circa 1520

The presence of lions at the Tower of London was intermittent, being restocked when a monarch or his consort, such as Margaret of Anjou the wife of Henry VI, either sought or were given animals. Records indicate they were kept in poor conditions there in the seventeenth century, in contrast to more open conditions in Florence at the time. The menagerie was open to the public by the eighteenth century; admission was a sum of three half-pence or the supply of a cat or dog for feeding to the lions. A rival menagerie at the Exeter Exchange also exhibited lions until the early nineteenth century. The Tower menagerie was closed down by William IV, and animals transferred to the London Zoo which opened its gates to the public on 27 April 1828.

Animal species disappear when they cannot peacefully orbit the center of gravity that is man.

Pierre-Amédée Pichot, 1891

The wild animals trade flourished alongside improved colonial trade of the nineteenth century. Lions were considered fairly common and inexpensive. Although they would barter higher than tigers, they were less costly than larger, or more difficult to transport animals such as the giraffe and hippopotamus, and much less than pandas. Like other animals, lions were seen as little more than a natural, boundless commodity that was mercilessly exploited with terrible losses in capture and transportation. The widely reproduced imagery of the heroic hunter chasing lions would dominate a large part of the century. Explorers and hunters exploited a popular Manichean division of animals into "good" and "evil" to add thrilling value to their adventures, casting themselves as heroic figures. This resulted in big cats, always suspected of being man-eaters, representing "both the fear of nature and the satisfaction of having overcome it."

Lion at Melbourne Zoo enjoying an elevated grassy area with some tree shelter

Lions were kept in cramped and squalid conditions at London Zoo until a larger lion house with roomier cages was built in the 1870s. Further changes took place in the early twentieth century, when Carl Hagenbeck designed enclosures more closely resembling a natural habitat, with concrete 'rocks', more open space and a moat instead of bars. He designed lion enclosures for both Melbourne Zoo and Sydney's Taronga Zoo, among others, in the early twentieth century. Though his designs were popular, the old bars and cage enclosures prevailed until the 1960s in many zoos. In the later decades of the twentieth century, larger, more natural enclosures and the use of wire mesh or laminated glass instead of lowered dens allowed visitors to come closer than ever to the animals, with some attractions even placing the den on ground higher than visitors, such as the Cat Forest/Lion Overlook of Oklahoma City Zoological Park. Lions are now housed in much larger naturalistic areas; modern recommended guidelines more closely approximate conditions in the wild with closer attention to the lions' needs, highlighting the need for dens in separate areas, elevated positions in both sun and shade where lions can sit and adequate ground cover and drainage as well as sufficient space to roam.

There have also been instances where a lion was kept by a private individual, such as the lioness Elsa, who was raised by George Adamson and his wife Joy Adamson and came to develop a strong bond with them, particularly the latter. The lioness later achieved fame, her life being documented in a series of books and films.